EFFECTS OF SOWING TIME AND RELATIVE PRAIRIE QUALITY ON FIRST YEAR ESTABLISHMENT OF 23 NATIVE PRAIRIE SPECIES

by

Sarah Krock

A Thesis
Submitted in partial fulfillment
of the requirements for the degree
Master of Environmental Studies
The Evergreen State College
June 2016

This Thesis for the Master of Environmental Studies Degree

by

Sarah Krock

has been approved for

The Evergreen State College

by

Kevin Francis, Ph. D.
Member of the Faculty

Date

ABSTRACT

Effects of sowing time and relative prairie quality on first year establishment of 23 native prairie species.

Sarah Krock

The restoration of south Puget Sound prairie ecosystems requires a considerable input of time and resources. This project aims to identify if sowing seeds at different times of year and/or in different quality sites could increase the first year establishment rates of 23 selected native species. A full-factorial randomized block design was used to test the success of direct seed sowing efforts in September, October, December, and March against an unsown control across three prairies that were designated High, Medium, and Low quality relative to each other. A Shannon-Wiener diversity index of 16 sown species suggests richness and abundance increase when sowing occurs in September or October, regardless of prairie quality. Thirteen species were analyzed independently using generalized regression, while nine were excluded from this analysis, due to extremely low germination. Four species were significantly influenced by sowing time: *Collinsia* spp. (includes *C. grandiflora* and *C. parviflora*), *Lupinus albicaulis*, *Lupinus bicolor, and Plectritis congesta*. Four species were significantly influenced by relative prairie quality: *Achillea millefolium, Danthonia californica Eriophyllum lanatum,* and *Ranunculus occidentalis*. No species responded significantly to both sowing time and relative prairie quality at $\alpha=0.05$. Five species did not show a significant response to any treatment*: Cerastium arvense, Festuca roemeri*, *Koeleria macrantha, Microseris laciniata*, and *Sericocarpus rigidus*. Five species were excluded from generalized linear model analysis due to low abundances: *Balsamorhiza deltoidea, Clarkia amoena, Lomatium utriculatum, Potentilla gracilis*, and *Sisyrinchium idahoense*. Four species were excluded from analysis because they were not found in any treatment or quality combination: *Armeria maritima, Erigeron speciosus, Solidago simplex,* and *Viola adunca*. Overall, first year establishment rates were very low, but these results suggest that fall sowing times and higher quality prairie sites result in higher establishment rates for some native prairie species.

Table of Contents

List of Figures

List of Tables

Acknowledgements

This research would not have been possible without the help of many people. I would especially like to thank my better half, Tel Vaughn, and friends and family that have been supportive throughout this adventure. I am grateful for my colleagues from the Center for Natural Lands Management (CNLM) and Joint Base Lewis-McChord (JBLM) Fish and Wildlife Program staff, many of whom have been instrumental in one or several stages of this research from initial development to implementation to analysis. Thanks to Sarah Hamman, CNLM, for the idea, design, set up, analysis, and interpretation of results; Cara Applestein, CNLM, for help with data analysis; and Sierra Smith, CNLM, for the seed mix calculations and materials. Thanks, as well, to JBLM staff: Paula Cracknell, Kharli Rose, Fiona Edwards, and Amber Martens for helping to identify and count over 13,000 seedlings; Jim Lynch for initial development and set up; Emily Phillips, John Richardson, and Nick Miller for help raking plots, and other co-workers, interns, and volunteers for all of their support with this on-going project. Finally, thank you to my Evergreen MES faculty, especially to my reader, Kevin Francis, for all of his help on various drafts and for encouraging me to explore the ecological theory concepts.

INTRODUCTION

Restoration projects, such as those occurring in the south Puget Sound (SPS) prairies, often take years to carry out and a significant investment of time and resources in the process (Sinclair, Alverson, Dunn, Dunwiddie, & Gray, 2006). Unfortunately, this investment sometimes goes to waste when the restoration doesn't go as planned: sometimes invasive species persist, and sometimes native species fail to grow. Increasing the first year establishment of native plants could go a long way toward jumpstarting a successful restoration process. The restoration process increasingly includes seed sowing to reintroduce or augment native plant populations (Stanley et al., 2011). Unfortunately, seed sowing has often resulted in incredibly low establishment rates, for often unknown reasons. First year establishment rates of 0-33% have been observed for a suite of 24 native prairie species using two different sowing methods and across two different sites (Hamman, Bakker, & Smith, 2015). Establishment rates are even lower for subsequent years post seeding. The second year establishment rates drop to 0-6% for the same suite of 24 native prairie species (Hamman et al., 2015). Low establishment rates are particularly challenging for land managers wishing to establish resilient prairies with limited time and resources. While some resources exist for growers of native plant materials in greenhouses or seed production fields (Native Plant Network, 2016) these protocols are often limited in their applicability to restoration in the field.

Significance

Restoration has endless unknown variables, many of which are out of our immediate control. Will the weather cooperate? Will next June be too hot? Perhaps tweaking one of the variables that we can control (the timing of seed sowing) and understanding the influence of general site conditions (relative site quality) can put the odds of restoration success in our favor. Improved restoration success, however big or small, has the potential to save time and resources in the long term. Long-term persistence of the SPS prairie habitat is necessary for the many plants and animals that depend on them, including four ESA listed species: golden paintbrush (*Castilleja levisecta*), Taylor's checkerspot butterfly (*Euphydryas editha taylori*), streaked horned lark

(*Eremophila alpestris strigata*), and Mazama pocket gopher (*Thomomys mazama*). Additionally, approximately 350 plant species and subspecies are restricted to the prairie-oak ecosystems of the WPG Ecoregion (Sinclair et al., 2006). The phenomenal biodiversity of the SPS prairies make this ecosystem a high priority for conservation and restoration efforts.

Glacial outwash prairies were formed about 8,000-12,000 years ago as a warmer, drier climate caused the Vashon Ice Sheet to retreat northward (Pielou 1991). Prairies all across the Pacific Northwest were historically maintained in an early seral state by Native Americans through intentional burning and other management techniques (Walsh, Pearl, Whitlock, Bartlein, & Worona, 2010; Weiser & Lepofsky, 2009). These types of actions increased production of edible and fibrous plant materials as well as attracted large game. Burning largely ceased in this area when European American settlers began occupying the territory in the mid 1850's (Hamman, Dunwiddie, Nuckols, & McKinley, 2011). This cultural history of the SPS prairies is key to understanding the ecosystem's structure, function, and processes. Today, the SPS prairies face future threats in four main areas: population growth, encroachment of trees and shrubs, invasive non-natives, and climate change (Dunwiddie & Bakker, 2011). Managing the tree/shrub encroachment and invasion of non-native species while simultaneously increasing the diversity and abundance of native species is key to maintaining and restoring the structure and function of diverse prairie ecosystems.

Practical and Theoretical Application

Restoration ecology is uniquely situated between practical and theoretical worlds. On the one hand, research in this field is carried out for very practical reasons, and the results have value in real-world restoration processes. For example the questions: "when should I sow seeds to get the highest plant establishment?" and "which species do better in more or less degraded sites?" are very practically oriented to get the most restoration value from limited resources. On the other hand, research in restoration ecology can also illuminate theoretical questions. For example, the question: “what mechanisms are driving how communities of plants re-assemble after disturbance?” is a question that has been plaguing ecologists such as Frederic Clements (1916), Henry Gleason (1927), and other thinkers for over one hundred years. To what extent are communities assembled randomly through stochastic processes versus deterministically with predictable patterns of succession? These debates of relative influence persist to this day as the neutral versus niche theory of community assemblage.

The practical idea that altering the timing of seed sowing may positively benefit the species that arrive at a site before their competition is parallel to the term “priority effects” in theoretical ecological research. Priority effects represent one mechanism of a larger theory that communities are assembled through stochastic, or neutral, means. Likewise, the practical assumption that species will respond more positively to higher quality sites is analogous to the idea of ecological filtering in theoretical ecological research. Ecological filtering, a process identifying the biotic and abiotic conditions required for establishment, is the basic premise of a larger theory that communities are assembled through deterministic means, often thought of as filling available niches.

Today, neutral and niche theories are not as mutually exclusive as they were back in Clements’ and Gleason’s time. The relative importance of these mechanisms in SPS prairie restoration has not yet been explicitly investigated, to my knowledge. It is not uncommon for research in restoration ecology to only consider practical implications. However, research in restoration ecology may be able to answer both practical and theoretical questions simultaneously. This experiment aims to take advantage of this overlap in order to both solve practical problem and provide insight into a larger theoretical question.

Research questions

This thesis aims to answer two different, yet overlapping questions. The first question is a very practical one, and the second is based in ecological theory. The practical question is: *Does temporal variation of seed sowing affect the first year establishment of 23 native prairie species* *across a gradient of prairie qualities?* The theoretical question is: *To what degree is plant community assembly driven by neutral or niche processes?*

The species tested here are found in ecologically and culturally important landscapes in the south Puget Sound prairies and elsewhere across the Willamette Valley-Puget Trough-Georgia Basin (WPG) Ecoregion, and sometimes in other areas such as the east side of Washington. This suite of species was chosen to represent a broad spectrum of functional groups, including perennial grasses, perennial forbs, and annual forbs. Some of these species are common in SPS prairies, while others are rare and were likely extirpated from many prairie sites. Sowing seeds at the right times and places has the potential to result in more efficient restoration of SPS prairies.

Establishment rates are not often quantified, but research from other studies using the same or similar species in south Puget Sound prairies has shown very low establishment rates. The establishment of all sown species never reached over 10%, and was often less than 5% of total bulk seed (Hamman, Smith, & Bakker, 2015). While seed viability varies greatly among species, generally seeds are healthy and should be capable of becoming established plants. This research aims to examine the mechanisms behind the discrepancy between the expected and observed plant establishment in SPS prairies, and offer suggestions for improving establishment by altering seed sowing time and/or tailoring species selection to appropriate site conditions.

Currently, seed sowing typically occurs during fall and winter. However, most of the seeds ripens and falls in spring or summer. Altering sowing times to more closely match natural dispersal times could improve establishment. Seed sowing typically occurs on medium quality prairie, but all species do not occur equally or evenly across all prairies, thus there is a mismatch between site condition and species selection. This mismatch between site condition and species selection is potentially wasting plant materials. Identifying which species, if any, respond positively to certain site conditions could also improve establishment rates.

Restoration strategies in the SPS prairies can be made more efficient by maximizing the amount of established plants that are produced from a given amount of native seed. Temporal and spatial variability can constrain restoration options, and make it difficult to foresee how these ecosystems will respond to management actions (Dunwiddie & Bakker, 2011). Sowing time is one aspect of the restoration process that is relatively easy to control, unlike the weather or many other abiotic and biotic limitations to recruitment.

Hypotheses

In response to the practical question (*Does temporal variation of seed sowing affect the first year establishment of 23 native prairie species across a gradient of prairie qualities?),* I hypothesized that sowing time and relative prairie quality would affect the establishment of these species. The null hypothesis for the practical question was that the mean count of plants in the seeded plots will not be different than the mean count of plants in the control plots. Of course, there are many reasons that plants fail to establish from seeds (see establishment section in part two of the literature review) but the scope of this research only covered two (sowing time and relative prairie quality) of many possible mechanisms. These two mechanisms address germination and establishment limitations. It was expected that seed sowing will generally overcome the dispersal/seed limitation which others have previously documented in SPS prairies (Stanley et al., 2008, 2011). Thus sowing seeds will likely result in some quantity of established native plants. The real question is whether some species positively respond to differences in sowing time or sowing location. I predicted that some combination of sowing times and prairie qualities will result in higher establishment rates, and could lead to more efficient use of restoration materials.

In response to the theoretical question (*To what degree is plant community assembly driven by neutral or niche processes?)* I hypothesized that both neutral and niche processes are acting upon these plants, driving community assembly. In order to study community assembly theory I used seed sowing time as a proxy for priority effects, which is a mechanism of neutral theory; and relative prairie quality as a proxy for ecological filtering, which is a mechanism of niche theory. Generally, I hypothesize that both neutral and niche processes are at work on these seeds, therefore I expect that some species will respond positively to both earlier sowing times and higher quality prairie. The null hypothesis is that none of the species respond to either the sowing time treatments or the relative site qualities.

If priority effects were the most influential mechanism driving community assemblage, one would expect species to respond more positively to sowing time, rather than to any of the relative site qualities. Specifically, I hypothesize that the earlier the arrival time, the better a species' chances of survival would be. Based on this neutral theory of community assemblage, September should have the highest count of plants, followed by October, December, March, and finally the control. The null hypothesis would be that there is no difference in the mean counts of plants in any sowing time treatment, thus the count of plants found in any of the treatments would not be different from one another.

If ecological filtering is the most influential mechanism driving community assemblage, one would expect species to respond more positively to the relative prairie quality, rather than to any of the sowing times. The high, medium, and low relative prairie qualities are proxies for biotic and abiotic site conditions. Specifically, I hypothesize that the higher quality the site, the higher the native species establishment will be. Based on this niche theory of community assemblage, the high quality site should have the highest count of plants, followed by the medium quality site, and finally the low quality site. The null hypothesis would be that there is no difference in the mean counts of plants in any relative prairie quality, thus the count of plants found in any of site conditions would not be different from another.

Roadmap of Thesis

This thesis investigates whether temporal variation of seed sowing time and relative site quality affects the establishment of 23 native prairie species in the South Puget Sound. The literature review is broken into three parts: 1) current restoration practices; 2) practical implications of sowing time, site conditions, and challenges to establishment; 3) theoretical arguments of neutral and niche community assembly. The second half of this thesis describes the original research undertaken to test the hypotheses. Methods, results, discussion and conclusion sections describe this seed addition experiment. Finally, this thesis concludes with a few practical recommendations for land managers.

LITERATURE REVIEW

This literature review is split into three sections. The first section focuses on current restoration practices and the resulting seedling establishment rates. This section also addresses natural seed dispersal times and the importance of this research.

The second section focuses on practical implications. This section examines practical, restoration-focused studies involving sowing time and relative site quality. Sowing time and relative prairie quality are the two independent variables of this study. Lastly, a thorough examination of the dependent variable, establishment, wraps up this section.

The third section focuses on theoretical implications. This section begins with a description of the current status of the niche versus neutral debate of community assembly. Next, the mechanism of each theory is examined. Niche theory is best supported by ecological filters created by biotic and abiotic conditions. In order to study this mechanism, relative prairie quality is used as a proxy. Neutral theory is best supported by the history of arrival, or priority effects. In order to study this mechanism, sowing time is used as a proxy. The relative contribution of each of these theories is considered, as well as some concluding thoughts about the overlap of practical and theoretical work, and applicability to prairie restoration in the SPS.

Part 1: Current SPS restoration practices

Seed addition is one of several techniques currently being used to restore SPS prairies that are fragmented and degraded. Remnant prairies have experienced significant losses of native plant taxa, and increasing overall species diversity is among the challenges facing prairie restoration throughout the ecoregion (Dunwiddie and Bakker, 2011). Introduction of target species is necessary for many prairie restorations because the seeds no longer persist in the soil seed bank (Stanley et al. 2011). Biodiversity is increasingly recognized as a major determinant of ecosystem functionality (Hooper et al., 2005; Tilman, Isbell, & Cowles, 2014; Zavaleta, Pasari, Hulvey, & Tilman, 2010). Restoring SPS to species rich ecosystems will require reintroduction and augmentation of native plant populations.

Seed addition is not the only technique used in restoration. Planting plugs, small plants grown in cone-shaped containers in the greenhouse, can also be a useful technique for prairie restoration. Plugs have shown to be useful in certain situations (Agee, 1996; Ewing, 2002, Sinclair et al., 2006) but there are advantages to using direct seed addition methods rather than planting plugs. The cost of seed and plug production varies by species and by year, but seeds are generally much cheaper. For example, *Castilleja levisecta* plugs produced by CNLM's nurseries cost about $3.00 each, while *C. levisecta* seeds cost approximately $0.30 per 1,000 (Dunwiddie & Martin, 2016). Additionally, seed sowing is much more cost effective than plug planting, however establishment rates in the field are generally <1% for this species (Dunwiddie & Martin, 2016). The decision to use plugs or seeds in restoration is driven by many factors including cost and availability of materials.

In a review of species introductions for grassland restoration Hedberg and Kotowski (2010) found that direct seeding or hay spreading, rather than plug planting or other methods, is preferable to achieve desired results; though they do note that the method is dependent on the species, size of target area, and funding availability. Both methods are currently employed in SPS prairie restoration, and both are useful techniques. I chose to focus on direct seeding rather than plug production because fine-tuning seed addition techniques has the potential to restore a larger area in a shorter amount of time.

Extensive amounts of native seed are being produced and applied in SPS prairies in order to restore biodiversity and overcome dispersal limitations. Currently, native seed is produced on a large scale at one of several farming facilities designed specifically for that purpose. In 2014 the

Center for Natural Lands Management (CNLM) in partnership with the Sustainability in Prisons Project (SPP) produced 2,109 pounds of seed and 344,000 plugs of 104 prairie species (Smith & Elliot, 2015). Now that dispersal limitation is less of an issue, the focus transitions to the establishment limitations of the native prairie species themselves.

Even as native seed for restoration becomes more available, the timing of seed sowing remains dependent on several factors. After seed is grown, it is collected, cleaned to remove debris, and distributed to partners to be sown into the prairies they manage. Seed sowing is often done with drop seeding implement pulled behind a tractor or utility task vehicle (UTV) to cover many acres of prairie efficiently. For smaller areas, or smaller amounts of seed, hand sowing is usually sufficient. The time of year that seeds are typically sown is in the fall (October or November), due to logistical constraints of harvesting, cleaning, and dispersal, in addition to site preparation and personnel availability. A survey of 38 prairie restorationists across 11 U.S. states showed that most prefer to sow in dormant season (fall or winter) to take advantage of a natural cold stratification, as well as freeze-thaw cycles to bury the seeds, and spring moisture (Rowe, 2010). The timing of seed sowing for restoration purposes depends heavily upon logistical considerations, while underlying assumptions are that mimicking the natural seed dispersal times is beneficial.

Current establishment rates

In order to maintain a stable population, every adult plant must be replaced by an average of one successfully established offspring. Therefore, one would expect short-lived plants to have higher seedling recruitment than longer lived plants (Eriksson & Ehrlén, 2008). This also suggests that perennial plants do not necessarily have to produce new recruits every year in order to maintain some baseline population level. Results from a seed addition field experiment (seed was sown in mid-November) in the SPS, including eight of the species tested here, show first year establishment rates ranging 0-33% across two prairie restoration sites (Hamman et al. 2015). In a seed addition field experiment (seed was sown in late September) in a western Oregon prairie, native prairie seeds established at a rate of <1-66% depending on the species, litter removal treatment, and study location (Maret & Wilson, 2005). This western Oregon study included three of the same species used in this research: *Festuca idahoensis* subsp. *roemeri* establishment rates ranged from 3-32%, *Eriophyllum lanatum* establishment rates ranged from <1-23%, and *Potentilla gracilis* establishment rates ranged from 5-15% (Maret & Wilson, 2005). These low and variable establishment rates indicate that seeds must overcome incredible challenges to become an established plant in the field. When calculating seed mix proportions, if the field establishment of native species is not known from previous seed addition experiments, greenhouse trials, or found in the literature, a standard survival rate of 5% of pure live seed is used (Sierra Smith, CNLM, personal communications, September 2015). Findings from coastal California prairies of 1-2% first year establishment (Holl et al., 2014) suggest that low establishment rates are common in other grassland ecosystems as well. Learning more about native species' natural and artificial establishment rates could provide insights about how to make restoration practices more efficient.

Natural seed dispersal times in SPS

Native species found in SPS prairies typically disperse their seeds in the spring and summer (May-August), though some species may hold a portion of their seeds in seed pods until fall (September-October). After dispersal, seeds experience a natural cold-moist stratification, which is a period of time in cold temperatures that often breaks certain types of dormancy in seeds (Drake, Ewing, & Dunn, 1998; Russell, 2011; Krock et al., 2016). Additionally, cold stratification may involve periods of time when the ground freezes and thaws again, sometimes resulting in frost heave, which could create appropriate microsites for seed germination. In the SPS annual species typically germinate in the fall, while perennial species typically germinate in the spring. Some perennial plants do not reproduce for several years after germinating. Annual species must establish as adult plants in the first year to produce the following year's generation, while it may take more than one growing season for a perennial plant to become a reproductive adult.

Importance

Restoration and conservation of south Puget Sound (SPS) prairies is necessary to ensure the survival of four Endangered Species Act (ESA) listed threatened and endangered species (U.S. Fish and Wildlife, 2015). Additionally, SPS prairies, like other natural areas, provide various ecosystem services such as water filtration, climate regulation, and cultural, spiritual, and recreational services (World Health Organization, 2005). Temperate grasslands and savannahs are one of two biomes at greatest risk due to habitat loss and lack of protection (Hoekstra, Boucher, Ricketts, & Roberts, 2005). Effective and efficient restoration, and in some places re-creation of prairie ecosystems, requires an adaptive management approach (Delvin, 2013; Sinclair et al., 2006). Prairies across the Willamette Valley-Puget Trough-Georgia Basin (WPG) ecoregion have been shown to be limited by availability of native seed, and even relatively high quality remnant prairies are strongly seed-limited (Stanley, Dunwiddie, & Kaye, 2011). Seed limitation, also known as dispersal limitation, is a key variable preventing the successful restoration of many prairies. In fact, many species are dispersal limited due to habitat degradation and fragmentation (Hedberg & Kotowski, 2010). Establishing native flora is also a challenge in the tallgrass prairies of the Midwest (Carter & Blair, 2012), coastal prairies of California (Holl et al., 2014), and elsewhere, thus it is necessary to assess the efficiency of seed sowing in these ecosystems as well.

Part 2: Practical Implications

Sowing time

Currently, in the SPS prairies, timing of seed sowing is typically driven by logistical considerations, such as seed availability and personnel time, rather than an attempt to mimic species biology. Many of these native prairie species naturally disperse their seeds in the spring and summer, leading to a potential mismatch of natural dispersal and sowing times. The status quo (fall-winter sowing) has resulted in extremely low establishment rates, however, adjusting the timing of seed sowing to match the biology of the species could result in higher establishment rates, and more efficient prairie restoration.

Sowing time and establishment have not been well documented in all ecosystems, but there is emerging evidence that sowing time does have an effect on many prairie species. Anecdotal evidence from native seed farms shows that earlier fall sowing of certain species, particularly annual forbs, results in higher establishment and overall vigor of the plants (Kathryn Donovan, CNLM, personal communications, May 2016). It is difficult to completely separate sowing time (i.e. seed arrival time) from seasonality, especially in the field, so no attempt was made to do so in this study.

Studies showing a significant effect of sowing time on establishment rates

Several studies support the idea that sowing time has some amount of influence on establishment rates of plants. Frischie and Rowe (2012) found that of seven tested tallgrass prairie species that naturally dispersed their seeds in early season, five of them had higher establishment rates if the sowing was done in the summer (growing season) rather than the subsequent winter (dormant season). They attributed these findings to abiotic conditions and arrival time- plants were simply germinating and growing earlier because they were seeded earlier. This agrees with my expectation of SPS prairie restoration, and hypotheses for this experiment.

Another study found that a June seeding time resulted in a higher total plant density and lower total biomass than the December seeding treatment for three native tallgrass prairie species, though seeding time did not affect all three species in the same way (Sullivan and Howe, 2009). In this study the effects of seeding time and seeding density could be seen seven years after seeding, with larger, more productive *Echinacea purpurea* plants, and more abundant, larger *Desmanthus illinoensis* plants in the June seeding treatment than in the December seeding treatment (Sullivan & Howe, 2009). The authors suggest that seeding time is important not only for the plant size in subsequent years, but also vole herbivory patterns.

Sowing time may not have a significant effect on establishment when there is generally low establishment of sown species, or a complete dominance of the site by one sown species (Lawson, Ford, & Mitchley, 2004). However at one site that was not dominated by the native grass *Holcus lanatus*, Lawson et al. (2004) found earlier (spring) sowing resulted in higher species richness and abundance of sown species than the following (fall) sowing time. The authors of this study inferred that competition was the main mechanisms driving these results.

In one study aimed at establishing North American prairie species in an urban park in northern England, Hitchmough, de la Fleur, and Findlay (2004) found the emergence across all species tested was significantly higher for winter rather than summer sown seed, though individual species exhibited variable responses. These results are counter to this study's hypothesis. One potential reason for these results are the confounding factors of seed stratification between the summer and winter sowing treatments, and increased moisture stress for the summer sown seeds.

Studies showing multiple factors influencing establishment

Another study has found that sowing time is one factor in combination with other factors that influences plant establishment rates. Establishment of native species is not only affected by the timing of seed sowing, but also the seeding method used. Larson et al. (2011) found that seed drill application was preferable during the growing season, while broadcast application was preferable in the dormant season; and the timing had differential impacts on establishment of functional groups (forbs vs. warm season grasses). They attributed the success of the dormant season broadcast seeding over the subsequent growing season broadcast seeding to arrival time, among other biotic and abiotic factors. These findings are counter to the hypothesis in this study, but this study only uses one sowing method- broadcast application.

Studies showing sowing time as a non-significant factor on establishment

Other studies have shown a marginal or non-significant effect of sowing time on establishment rates. For example, earlier sowing time (March, beginning of fall in southern hemisphere) had a marginally higher maximum percentage emergence than later sowing time (May, end of fall in southern hemisphere), on 21 species sown in a South African grassland field experiment (Sayuti and Hitchmough, 2013). Most of the 21 species tested had higher emergence rates when sown in March rather than May, but statistically significant results were not reported for these findings in the study.

In another study, Doll, Haubensak, Bouressa, and Jackson (2011) found that seeding time, November or subsequent May, was not a significant factor in native grass recruitment in a Wisconsin prairie, however disturbance and nitrogen availability were significant factors. These two studies highlight the need for further investigation of the effects of sowing time on field establishment rates in a wide range of ecosystems.

Conclusion

Several studies outlined here have shown significant effects of sowing time on establishment, but the lack of standardization of time periods, species/functional groups, and life histories makes it difficult to compare studies to each other. To my knowledge, the effects of sowing time on establishment of native plants has not been tested on SPS prairie species. Based on other studies in prairie ecosystems, it is likely that temporal variation of seed sowing in SPS prairies will show a significant effect on establishment rates of at least some of the species tested.

Relative prairie quality

The practical and theoretical implications of site quality is well recognized in restoration ecology. However, within SPS the application of a highly diverse seed mix has not been experimentally tested across a gradient of relative prairie qualities, all occurring on the same soil type and with a relatively similar site history, in order to determine the influence of site conditions on species selection. Knowing which species, if any, respond to different site conditions could make prairie restoration more effective and efficient. Unfortunately, high and low quality sites in the SPS have often been lower priority for restoration due to limited resources. Meanwhile, the medium quality prairie receives the bulk of restoration efforts in order to make it more similar to high quality reference sites. Some native species may establish and persist more readily in high quality prairie rather than low quality, or vice versa, though these species have only been anecdotally identified. Identifying which species perform well under certain site conditions may help tailor species selection and increase efficiency of the restoration process.

Establishment

In order for plants to become successfully established[1] they must overcome many challenges. Every life stage of a plant is met with challenges that are in some way influenced by environmental conditions (Nathan & Muller-Landau, 2000). Environmental conditions provide the basis for relative site quality in this study. In this study, relative site quality has been categorized into three groups (high, medium, and low), reflecting the native species richness at each site (see methods section). However, actual environmental conditions of these three sites are along more of a spectrum, and much less clear-cut. The complex environmental conditions at each site may help or hinder the establishment of native species. Species establishment may be positively or negatively correlated with site quality. Some species are more apt at colonizing or persisting in degraded habitats than other species. There are a suite of reasons that plants are unable to establish in a given site with a unique set of environmental conditions and limitations, which I will examine below.

The literature broaches the topic of establishment limitations in a variety of ways. One study states that “[r]ecruitment limitation may result from any or all of source limitation (recruits

---

[1] Establishment can be defined as “the process that results in a population that persists for many generations” (Liebhold, 2000). The term *establishment* is typically used for longer term >1 year survival studies, though it can be used as a surrogate term to describe abundance, density, emergence, and other measurable terms that indicate living plants. In contrast, “*recruitment* refers to the process by which new individuals found a population or are added to an existing population” (Eriksson & Ehrlén, 2008). Recruitment is thus a pre-requisite for establishment; the seedling phase before the plant becomes an established reproductive adult. Eriksson and Ehrlén (2008) also note that “population studies often define seedlings somewhat arbitrarily, implying also that population processes such as seedling recruitment may be assessed arbitrarily.” The terminology is a bit confusing, especially concerning annual species, regardless, recruitment/establishment here refers to the presence of living plants.

fail to arrive at a site due to reduced fecundity of adults or reduced dispersal of propagules), germination limitation (site conditions prevent or reduce seed germination or increase seed mortality), and establishment limitation (seedlings fail to mature)" (Henry, Stevens, Bunker, Schnitzer, & Carson, 2004). Many other studies list a few key challenges that the author(s) assume are responsible for the loss of establishment. For example, Frischie and Rowe (2012) list low quality seed, predation, inappropriate storage, and unknown germination requirements as potential reasons for a reduction in germination and establishment. Other sources, such as (Martin & Wilsey, 2006, and citations therein) often choose to focus solely on two elements of recruitment limitation: seed limitation and microsite limitation. These two ideas have been well explored (Clark, Poulsen, Levey, & Osenberg, 2007; Turnbull et al., 2000; Zobel et al., 2000). These two elements are important, but they encompass many variables, and completely disregard the establishment limitation (seedlings do not survive). It is useful to consider challenges that are unique to each life stage in order gain a more holistic overview of the causes of establishment or mortality, rather than just two possible explanations (seed limitation or microsite limitation).

While there are many types of challenges or limits to establishment, I will examine three in detail. These three types of limitations are source, germination, and establishment. Below, I outline each limitation, its significance, and how it may influence my study of SPS prairie plant establishment

A. Source limitation

Source limitation, or the lack of healthy seeds in a given area, is the first key recruitment limitation. Source limitation can be broken into two parts: *fecundity*, or reproductive rate, of existing adult plants, and a reduction in *dispersal* of seeds.

Fecundity

The fecundity of native seeds is important because without healthy, viable seeds populations cannot sustain themselves. Fecundity could be reduced by a lack of sufficient pollination. At least one species the SPS prairies is known to be pollinator limited, *Balsamorhiza* *deltoidea* (Fazzino, Kirkpatrick, & Fimbel, 2011), although there may be others as well. In restoration seeds, however, the purity and viability of each species is typically known, and most seeds are of high quality. As such, fecundity is not likely to be a key limiting factor for this experiment.

Dispersal/seed limitations

Dispersal limitation, also known as seed limitation, has been a known limiting factor in SPS prairie restoration (Stanley et al., 2011). However, natural levels of seed rain are not known and probably highly variable due to patchy distributions of species. In seed addition experiments such as this one, seed limitations are overcome by adding seed to a given amount of space, rather than letting seed naturally disperse to that space. For this experiment we were both re-introducing species that were likely found in these areas historically, as well as augmenting existing populations. Some seed naturally dispersed into the study area in the same year as the seeding, but the control plots can help differentiate natural levels from our experimentally augmented ones. Higher seeding rates resulted in higher plant densities in another seed addition experiment in the SPS (Hamman et al., 2015). Generally speaking, the more seeds that are added to an area, the higher the plant establishment rate will be.

Dispersal limitation is an important and well-documented phenomenon. Tallgrass prairies in Iowa were found to be severely seed limited, and even the enhanced availability of microsites through ungulate grazing did not increase seedling emergence, likely because there was no seed of rare species available to germinate (Martin & Wilsey, 2006). Additionally, seed limitation, rather than lack of microsite availability, influenced species richness in a calcareous grassland (Zobel et al., 2000). Turnbull, Crawley, & Rees (2000) also found that seed limitation decreased from sand dune to woodland, to grassland ecosystems, which they correlated with an increase in bare ground, and thus competition-free microsites. In this review, Turnbull, Crawley, & Rees (2000) found that new ploughed and early/mid successional prairies had roughly equivalent proportion of seed limitation. These habitats were more seed limited than intact arid and intact mesic grasslands. The SPS prairies that I used for this study could be classified as early/mid successional rather than intact. However, even intact, high diversity prairies have been found to be seed limited, and in one case, the effect of seed addition increased species richness for eight growing seasons (Foster and Tilman, 2003). In reality, these theoretical arguments agree with Stanley et al. (2011) that even relatively high quality areas across the WPG ecoregion, including sites in the SPS, are limited by native seed availability.

Seed limitation is a principle component of community assemblage. Increasing native seed density increases the number of established plants, though not always in a linear fashion. There can be a decrease in establishment at extremely high seeding densities due to density dependent mortality (Burton, Burton, Hebda, & Turner, 2006). It is important to find the balance between overcoming seed limitation and wasting seeds by over sowing. Higher densities of seed may increase establishment of seeded species, though there may be a point at which additional seed does not have additional restoration value (Goldblum, Glaves, Rigg, & Kleiman, 2013). Native seeds are expensive, and in low supply, so it is important to maximize efficiency of seed use in restoration projects. In fact, “sites restored to native prairie and wetlands are frequently seed limited for several reasons: 1) the minimal extent of remnant habitat and vegetation remaining; 2) the substantial effort needed to harvest a diverse and large quantity of local genotype seed; and 3) degraded soil seed banks. In combination, these factors make it difficult to restore a diverse native plant community” (Goldblum et al., 2013). Community assemblage can also be altered through overcoming seed limitation. Higher seeding densities resulted in a rapid decrease in weeds, though even low seeding densities had similar results after two years (Stevenson, Bullock, & Ward, 1995). However, other findings suggest that while native seed addition may reduce the proportion of exotic species, the community dominance was not shifted from exotic to native (Martin & Wilsey, 2014). While this project’s findings may support the findings of Stanley et al., (2011) and others, the theory of seed limitation is tangential to the questions that I am attempting to answer with this study.

B. Germination limitation

Germination limitation, or failure of seed to become a seedling, is the second key recruitment limitation. Clark & Wilson (2003) state that seeds can either germinate to become seedlings, remain as seeds (enter dormancy), or die; thus germination limitation can be broken into three parts: inappropriate site conditions for germination, dormancy, and seed death. The first part, inappropriate site conditions, is best examined in the context of microsite availability.

Microsite

The microsite, or the small area where a seed lands, is a key factor involved in plant establishment. For example, a seed that lands upon rocks would have an inappropriate abiotic environment, and a seed that lands in an area occupied by other plants will likely have an inappropriate biotic environment. A recent study by Dunwiddie and Martin (2016) highlights the need for appropriate microsite placement of *Castilleja levisecta* plugs. *Castilleja levisecta* is a hemiparasitic plant endemic to the WPG ecoregion. Higher survival and flowering was correlated with higher native forb richness in the area around the plugs. Additionally, topography influenced survival of plugs, with those planted on mounds or in swales having an increased survival rate five years after planting (Dunwiddie & Martin, 2016). These findings highlight the need for suitable microsites not only for seed sowing, but plug planting as well.

Native seed addition following prescribed fire has been found to be more successful than additions after other site pre-treatments (Maret & Wilson, 2000, 2005; Stanley et al., 2011)**,** presumably due to the increased availability of appropriate microsites. Simply burning an area for restoration or sowing seeds alone would be counterproductive in an area without sufficient microsites or native seed bank (Maret & Wilson, 2005). Currently, prescribed fire is the restoration practice most preferred in the SPS, often in combination with other site preparation techniques.

In the SPS prairies buildup of moss, lichen, and thatch creates unfavorable microsites in the absence of burning (Hamman et al., 2011). Resumption of periodic burning may be especially beneficial for annual forbs that rely on these microsites between perennial bunch grasses and forbs (Dunwiddie et al., 2014). In other ecosystems, such as the tallgrass prairie of central Texas, the rates of germination and establishment depend on microsites that protect seeds from desiccation, in the form of either litter or rocks, compared to protections-free bare ground (Fowler, 1986). Other sources cite disturbances such as tilling, grazing, digging by fossorial animals, or other actions which create bare ground as the mechanisms responsible for the creation of appropriate microsites (Dunwiddie et al., 2014; Pfeifer-Meister et al., 2012; Bakker et al., 2003). Note that disturbances assist the establishment of species as long as they coincide with favorable abiotic conditions (Knappová, Knapp, & Münzbergová, 2013). Appropriate microsites are one important factor that may be limiting the germination of native species in the SPS prairies.

Dormancy

The second germination limitation, seed dormancy, is the only non-permanent stage of the three possible fates for a seed: germination, dormancy, or death. Most seeds have the ability to persist in this life stage until conditions become more favorable for germination, and thus growth and development. The lifespan of seeds varies greatly, even under favorable storage conditions such as low relative humidity and temperature (Justice and Bass, 1978). There are several different types of dormancy, and most species have unique requirements for breaking their dormancy (see Baskin and Baskin, 1998). Cold moist stratification has been shown to overcome dormancy in several WPG eco-regional species (Drake et al., 1998; Russell, 2011; Krock et al. 2016) and physical scarification such as heat shocking may or may not be necessary for some species (Elliott, Fischer, & LeRoy, 2011). Dormancy is not likely one of the main limiting factors in this experiment, or in general prairie restoration.

Seed death

The third and final type of germination limitation is increased seed death. Seed death is best examined at the scale of the individual seed which is undoubtedly difficult and time consuming. It makes sense then, that few scientists have tackled this problem. However, seed death by predation is widely acknowledged, and is investigated here in more detail.

Although a mysterious part of their life history, the seed stage of a plant’s lifecycle can only have a few general outcomes. Clark & Wilson (2003) found that for four western Washington prairie species, that seed death was the most common fate. I would assume that this phenomenon is not limited to merely four SPS species. This is likely at least one of the reasons that establishment rates have been so low.

Seed death is often driven by predation of some sort. Seed predation is difficult to study because predation can happen in several ways. For example, seeds can be eaten by an herbivore while still on the plant, by a bird or rodent once they have dispersed, or by pathogen such as fungi or bacteria at any stage of development. In some studies predation has not shown to influence seedling density (Henry et al., 2004), however models have shown that herbivores may have a larger impact on plant population dynamics than previously expected (Maron & Gardner, 2000). Seed herbivory by rodents has even shown impacts on community succession in prairies of southwestern Wisconsin (Howe & Brown, 2000). Predators may selectively consume seeds as well. Only one of four species was substantially preyed upon (21% reduction) in a seed-fate study of western Oregon (Clark and Wilson, 2003). Anecdotal evidence from CNLM’s seed production facilities suggests that mice preferentially prey upon *Viola adunca* seed, which results in low yields for this species (Angela Winter, CNLM, personal communications, May 2016). Unfortunately, little is known about the effect of predation on SPS prairie species in the field.

C. Establishment limitation

Establishment limitation, or seedling death, is the third and final key recruitment limitation. The three biggest challenges to seedling survival are drought, herbivory, and pathogens (Moles and Westoby, 2004). Another challenge to seedling survival is competition with other seedlings, but is generally less problematic than the first three challenges (Moles and

Westoby 2004). These four issues affecting seedling survival can be divided into biotic and abiotic factors.

Biotic

Biotic factors include herbivory and pathogens (see discussion above of seed predation), as well as competition with other seedlings and adult plants. While some would assume adult plants would act as nurse plant to small seedlings, this is not necessarily true. In a greenhouse experiment of three grasses in Central Texas, adult plants negatively impacted grass seedlings at least six cm away, and most of all natural microsites were found within six cm of an existing plant (Fowler, 1986). Litter from adult plants can either act in a positive way (retaining soil moisture) or a negative way (decreasing sunlight availability, and/or acting as physical barrier). Additionally, a large amount of litter has shown a negative impact on seedling survivorship of the three grass species of central Texas (Fowler, 1986). In western Oregon prairies, litter has been shown to inhibit seedling establishment (Maret & Wilson, 2005). Litter likely has the same negative effect in our SPS prairies, but this is not an issue addressed by this research because prescribed burning removed most above ground biomass before the experiment began.

Abiotic

Abiotic factors such as temperature, water and nutrient availability are very important for the survivorship of seedlings. Of these, it appears that nutrient availability is not as dynamic as the other two factors. It has been shown that most properties of prairie soils are static, or are difficult to measure over short time frames, such as less than five years (Brye, Norman, & Gower, 2002). Grassland restorations are complex, and it is important to consider treatment effects over time. For example, soil amendments to alter the nutrient availability have been shown to have different effects on plants during different years (Doll, Brink, Cates, & Jackson, 2009). There is a negative relationship between nitrogen availability and invasibility, the ability of non-native plants to invade an area (Tilman, 1997) which is counter-intuitive. Other studies have found the nitrogen fixing shrub, *Cytisus scoparius*, which invades SPS prairies elevates nitrogen levels in the soil and may facilitate the invasion by other non-native species (Kirkpatrick and Lubetkin, 2011). Today, remnant prairie is found most often on sites with the poorest quality soils, thus the least appealing for agriculture (Dunwiddie & Bakker, 2011). Low nutrient prairie soils may be one of the key abiotic factors influencing plant establishment in SPS prairies.

Annual variation can also affect the plant community, due to dynamic changes in temperature, moisture, and competition. The timing of precipitation and temperature fluctuation can influence which species may be successful in different years due to variability in germination time (Fowler, 1986). Unsurprisingly, lack of water may be one of the biggest enemies of seedlings. Establishment of native and non-native species increases with amount of precipitation they receive (Bakker et al., 2003). While abiotic factors are largely out of the control of restoration ecologists, these factors can be used in a predictive manner. Establishment may be increased if the timing of seeding is based on abiotic factors such as temperature and precipitation (Bakker et al., 2003; Westoby, Walker, & Noy-Meir, 1989). Maintaining flexibility in the seeding time could overcome unfavorable abiotic factors to increase establishment of native species. This also highlights the need to experimentally test seed sowing between years to understand the temporal variation as well as the spatial variation (Vaughn & Young, 2010)

Part 3: Theoretical Implications

Introduction to community assembly theory

It is common knowledge that plants can, and will, colonize an area after most types of disturbances. New communities of plants are assembled, sometimes quickly or sometimes more slowly, and often change over time. This phenomena is easily observed in cracks in the sidewalk, abandoned agricultural fields, or after a wild fire. Are the new colonizing plants products of random chance, or are they filling a specific niche created environmental conditions? Community assembly provides a framework for understanding which species, and how many, can coexist in a given area (Chase, 2003). Whether community assembly is more predetermined by biotic and abiotic filters or more stochastically developed is yet unknown and remains a controversial topic

(Fukami, Martijn Bezemer, Mortimer, & Putten, 2005; Weiher et al., 2011). One can trace the roots of the argument back to the beginning of the field of ecology with Clements' (1916) analysis of deterministic climax communities versus Gleason's (1927) view of random species assemblages influenced by historical factors. Today the argument continues in terms of niche versus neutral assembly theory. Niche theory focuses on the biotic and abiotic filters that create a local community out of a subset of a regional species pool, while neutral theory focuses on how stochastic forces such as historical inertia, dispersal, and ecological drift influence community assembly (Weiher et al., 2011). Today the core arguments for each theory have been thoroughly investigated and slightly rebranded (see Chase and Leibold (2003) for niche theory, and Hubbell (2001) for neutral theory). Although the vocabulary has shifted, the questions remain unresolved. Recent work has shown that in coral reef community dynamics are non-neutral, overturning a decade of assumptions that stochastic processes drive biodiversity (Connolly et al., 2014). The ongoing debate is not likely to be resolved in the near future. It is likely that both processes are acting simultaneously, and thus the degree to which they are occurring may be more useful to investigate (Weiher et al., 2011). Understanding these drivers of community composition may have practical implications in addition to theoretical ones.

Roadmap

First I will investigate niche theory, especially how this widely accepted concept of biotic and abiotic environmental conditions is prevalent in the literature, and yet often overlooked in restoration. Then I will describe the counter-argument of neutral theory in more detail and pinpoint the specific mechanism, priority effects, which is most applicable to this study. Priority effects have been well studied in laboratory and natural settings, including grasslands. These findings have potentially useful application in the restoration of SPS prairies. Finally, I will conclude this section with a discussion of the relative significance of these competing theories, and the overlap between practical and theoretical work.

Niche theory- Ecological Filtering

In contrast to the neutral theory, niche theory suggests that biotic and abiotic conditions influence how communities re-establish after a disturbance. Community assemblage proceeds in predictable, deterministic fashion due to ecological filtering. Ecological filters are the environmental conditions such as soil type, water availability, or interactions with other species. Ecological filters create a niche which can only be filled by a subset of species from a larger regional species pool (Weiher et al., 2011). Plants that can colonize and persist in a given niche create a somewhat predictable community. Some have even gone so far as to propose a search for "assembly rules" (Diamond, 1975). While generally, the concept of niches has gone out of favor, a semi-recent re-investigation of the niche theory by Chase and Liebold (2003) has renewed interest in this concept as a unifying theory in ecology. Additionally, recent work in coral reef community dynamics overturns a decade of assumptions that stochastic processes drive biodiversity (Connolly et al., 2014) and exemplifies the need for further research for this and other ecological theories. Generally, the idea that site conditions are appropriate or inappropriate for species establishment is well recognized in the literature. Fewer studies delve into the reasons why plants do not establish in certain areas. These challenges to establishment are discussed in the practical section under site conditions.

Neutral Theory- Priority Effects

There are several proposed mechanisms of stochastic, or neutral community assemblage processes, including site history, competitive asymmetry, and priority effects (Ejrnaes, Bruun, & Graae, 2006). I will be focusing only on priority effects because I think it can be easily incorporated into restoration planning. Priority effects were originally defined as the competitive boost that an early-establishing species gets from reaching a large size before its competitors arrive (Wilbur & Alford, 1985). Alternative definitions state that priority effects could have a positive or negative effect on later occurring species, thus early arriving species may either impede or facilitate the establishment of later arriving species (Ejrnaes et al., 2006; Vannette & Fukami, 2014). Regardless, evidence of priority effects can be considered a historical and stochastic process driving community assemblages, supporting the neutral assembly theory (Weiher et al., 2011). The timing of sowing and priority effects have been shown to be persistent, and important for developing a stable native state rather an exotic state (Martin & Wilsey, 2014), which is among the ultimate goals of prairie restoration.

Priority effects have been demonstrated in a variety of different ecosystems with many different species. Priority effects have been well tested in plant communities in natural settings such as grasslands and prairies (Dickson, Hopwood, & Wilsey, 2012; Fukami et al., 2005; Grman & Suding, 2010; Helsen et al., 2012; Hooper & Dukes, 2010; Plückers et al., 2013; von Gillhaussen et al., 2014; Larson et al., 2011; Martin & Wilsey, 2012) wetlands (Pfeifer-Meister et al., 2012) and shrub steppe (Schantz et al., 2014) as well as in microcosm experiments (Ejrnaes et al., 2006; Körner, Stöcklin, Reuther-Thiébaud, & Pelaez-Riedl, 2008; Ross & Harper, 1972). Other species that have been tested include frogs (Wilbur & Alford, 1985), fungi (Fukami et al., 2010), phytoplankton (Robinson & Edgemon, 1988) multi-trophic aquatic systems (Drake, 1991) dragon flies (Amoroso & Chalcraft, 2015) and yeasts (Vannette & Fukami, 2014). While priority effects are not a new or understudied idea, their practical application to prairie restoration in the south Puget Sound has yet to be determined.

Priority effects in greenhouse studies

Priority effects have been observed in greenhouse studies to have long lasting implications for plant community development, which is often the target of restoration ecology. These effects are found both within the arrival times of seeded species versus the existing community into which they are sown, and the equal start given to faster or slower developing species (Körner, Stöcklin, Reuther-Thiébaud, & Pelaez-Riedl, 2008). In a greenhouse study, a three week earlier arrival time of certain plant functional groups resulted in lasting community composition and biomass effects even after several harvests and two growing seasons (Körner et al., 2008). Priority effects act quickly, even a few weeks delay in sowing time substantially alters the resulting community. Certain plant functional groups can dominate over others when given a six week head start, but more later sown functional groups are represented when there is only a three week gap (von Gillhaussen et al., 2014). Likewise, in a greenhouse study, native Australian grasses were able to suppress growth of a competitive non-native grass when given a three week head start (Firn, MacDougall, Schmidt, & Buckley, 2010). In an outdoor microcosm experiment the species composition was determined more by priority effects than by traits and preferred habitat type of the species tested (Ejrnaes et al., 2006). The relative arrival times of species and/or functional groups can influence their successional trajectories.

Priority effects in field studies

Priority effects may have long-term implications for restoration. Species sown first may have future implications for community diversity and composition (Bullock, Pywell, & Walker, 2007; Hoelzle, Jonas, & Paschke, 2012). A sowing experiment in the dry, acidic grassland of Germany showed that after four years priority effects were still evident in the above ground productivity, community cover, and functional group composition, though not on total species number, nor target species number (Plückers et al., 2013). Priority effects are a complex and important part of many restoration processes, the practical application of which has been largely overlooked in SPS prairie restoration.

Some studies have found that other mechanisms are more responsible for community assembly than priority effects. A study by (Amoroso & Chalcraft, 2015) found that the duration (length of time) that available habitat was open for colonization was more indicative of patch biodiversity than variation (when) the window of time (early vs late season) was open for colonization in a study of ephemeral ponds and dragonflies. Others have found that propagule pressure (amount of seeds) may be more indicative of community assemblage than priority effects (Schantz et al., 2014). The species richness of phytoplankton was caused by invasion rate (i.e. propagule pressure), invasion timing, and invasion order, with invasion order explaining the least of the variation (Robinson & Edgemon, 1988). In another example, the convergence of community assembly in a wetland restoration was attributed to both inhibitory priority effects and competitive dominance by perennial grass species (Pfeifer-Meister et al., 2012). Fukami, Martijn Bezemer, Mortimer, & Putten (2005) found that priority effects and “trait-based assembly rules” were simultaneously responsible for community assembly in abandoned agricultural fields. These studies indicate that further testing is needed to determine the relative importance of priority effects within the larger context of community assembly theory.

Overlap of Niche and Neutral Theories

Of course, there is considerable overlap between these two theoretical frameworks. For example, the strength of priority effects may be dependent upon niche components (Vannette & Fukami, 2014) or ecological filters, such as drought (Chase, 2007). This suggests that priority effects are not acting alone as the sole mechanism of community assembly, but they are one piece of a larger puzzle. This highlights the idea that there is a relative influence between priority effects, and ecological filtering, just as there is a middle ground between neutral and niche theory. Some researchers have found that community assembly is generally deterministic (niche theory), but that the actual species composition is historically influenced (neutral theory) (Fukami et al., 2005; Helsen et al., 2012). Thus, while all prairies will look structurally similar to each other, they may be made up of different species. These findings have implications or theoretical insights and for the practical application prairie restoration- whichever species occupies a niche first may persist so long as there is an appropriate niche available for it. Predictability would be a useful tool for the restoration ecologist, but to date standard ‘assembly rules’ have been elusive despite patterns in some ecosystems (Weiher, Clarke, & Keddy, 1998). Hopefully this experiment will shed some light on whether community assembly is driven more by neutral or niche processes, as well as the applicability of these theories to on the ground restoration practices in the SPS prairies.

Application to SPS prairies

My theoretical research question is: *To what degree is plant community assembly driven by neutral or niche processes?* The sown seeds are arriving in an environment where some native and non-native species already occur, and may be arriving before or after the propagules of these and other species. Presumably, the earlier the sown seeds arrive the better chance they will have of competing for resources and achieving establishment, demonstrating priority effects, a neutral process. Simultaneously, these seeds are affected by the biotic and abiotic conditions of three different locations. The relative quality of each location is a rough proxy describing ecological filtering processes. Presumably ecological filters only allowing a subset of the seeds or species to establish in each location, thus demonstrating niche processes. I hypothesized that both neutral and niche processes are likely acting on this restoration experiment. Better understanding practical research questions in the context of theoretical frameworks potentially broadens the usefulness of such research.

Sufficiently testing any community assembly theory in the field setting with native plants will likely require more than one growing season. The first growing season's data presented here only offers a preliminary snapshot into what will be influencing the establishment and long term community composition. A longer study period for this experiment may show population dynamics and trends within plant community assembly and coexistence, thus shedding more light on priority effects, ecological filtering, and overall community assembly theory. Understanding community assembly theory and its drivers may determine the success of restoration projects (Chase, 2003). Testing ecological theory while simultaneously doing prairie restoration seems like a mutually beneficial relationship between theory and practice, the results of which not only benefit local ecosystems, but broader audiences as well.

Conclusion of Literature Review

This study has many potential benefits to both science and the ecosystem. In the scientific community, restoration ecology has been viewed as the testing grounds of ecological theory (Cairns and Heckman, 1996), thus a natural fit for both theoretical and practical learning. This study provides benefits to the ecosystem in multiple ways, as it increases our understanding, but as a field experiment, it actually is a small-scale restoration project. Seed addition experiments often increase the native species richness. This study both re-introduces species that were likely found in these areas historically but have since been extirpated, and augments other populations that are currently found in and near the study areas but at a lower densities. Increasing native biodiversity through re-introduction and augmentation can have an impact on ecosystem health and resiliency to invasion. Restoration of vegetative communities may have positive implications for arthropod community assemblage (Déri et al., 2011; Krauss, Steffan-Dewenter, & Tscharntke, 2003; Summerville, 2008). Overall, this study is currently benefitting the ecosystem in the small scale, but the lessons that can be learned are applicable to large-scale restorations.

Although prairie restoration can happen much more quickly than restoration of an old growth forest, it still takes a considerable amount of time. Without active restoration efforts it takes a long time, perhaps 50 years or more, for an ex-arable field to regain the species richness of a semi-natural grassland even in areas where seeds naturally disperse from adjacent semi-natural grasslands (Öster, Ask, Cousins, & Eriksson, 2009). Even with active restoration effort such as seed addition, it may take over a decade to reach target objectives. Unfortunately, some studies have shown that seed addition may not result in long-term persistent populations (Rinella, Mangold, Espeland, Sheley, & Jacobs, 2012). Other long term studies have shown unanticipated results such as the dominance of seeded native grass species to the exclusion of seeded native forbs (Sluis, 2002). Regardless, seed addition and other types of experiments can improve decision making on the amount of seed needed to reach target populations, as well as species selection (Sayuti & Hitchmough, 2013). Some studies have shown successful restoration, and persistent communities eight years after a one time seed addition (Foster & Tilman, 2003**).** There is much to be learned about the long term, short term, and transient coexistence of native and exotic species in grassland ecosystems.

METHODS

Site Description

The experiment was conducted from September 2014 until July 2015 at Joint Base Lewis-McChord's Rainier Training Area (RTA) in western Washington (46°54' N, -122°43'W). The RTA lies within the Willamette Valley-Puget Trough- Georgia Basin Ecoregion which is a long, narrow stretch of lowlands between the Cascades and coastal mountain ranges. More specifically, the RTA is part of the south Puget Sound (SPS) prairies, which were formed when glaciers retreated across this landscape approximately 12,000 years ago. The soils where study plots were located are Spanaway gravelly sandy loam, 0-3% slopes, created from parent materials of volcanic ash over gravelly outwash (Natural Resources Conservation Service, 2015). These soils are 10% organic matter and "somewhat excessively drained," though it is classified as "prime farmland if irrigated" (Natural Resources Conservation Service, 2015). The mean annual precipitation for the study site is 40-60 inches, and the mean annual air temperature is 48-52 degrees F (Natural Resources Conservation Service, 2015). The climate is temperate maritime, with mild wet winters, and warm dry summers (LandScope America, 2015). Frost action for soils of study site are ranked low. The frost-free period is 200-240 days (Natural Resources Conservation Service, 2015).

In 1943 Fort Lewis (now Joint Base Lewis-McChord) acquired the 18,000 acres south of the Nisqually River, which became the RTA (Lewis History Museum, 2014). Currently, the land is used for military training exercises and public recreation. Mowing has been used at this site to reduce tree and shrub encroachment and maintain native prairie species. Prescribed fire has been used at this size for at least the last six to eight years. No records could be found describing the burn history prior to 2008.

Locations on Upper Weir, Lower Weir, and South Weir prairie were selected (Figure 1). These prairies have relatively high levels of access for setup and monitoring, and they are at little risk of being impacted by military training. Each of the three prairie represents a different quality category.

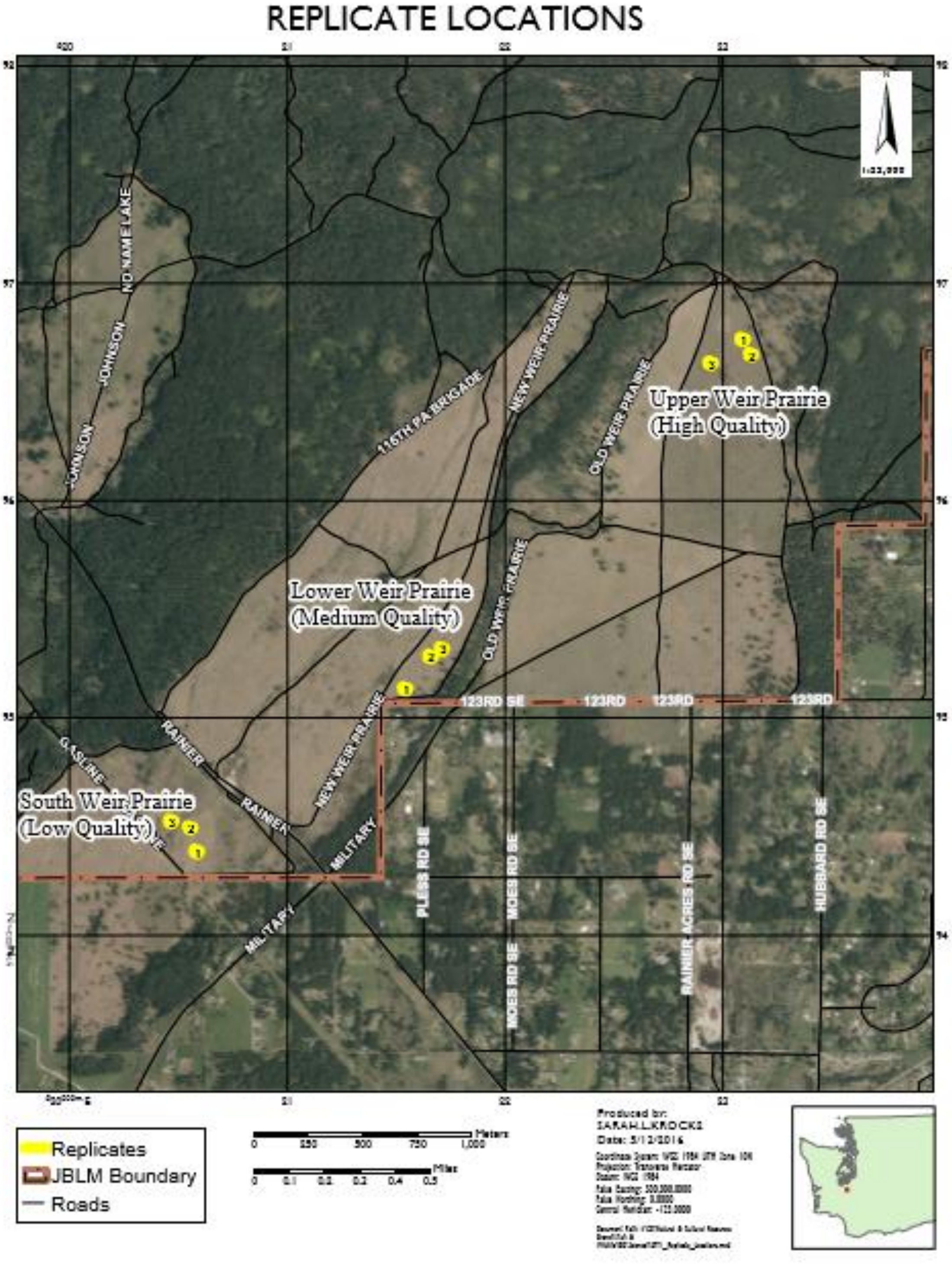

Figure 1: Map of replicate locations

Map shows locations of Upper Weir prairie (high quality), Lower Weir prairie (medium quality) and South Weir prairie (low quality) replicates in relation to one another. Each prairie contains three replicates (n=3). Each replicate contains one array of plots.

Each of the three prairies has a unique burn history (Table 1), though all three locations were burned in summer 2014 before experiment began. During site selection an effort was made to choose only areas with relatively homogeneous burn effects. Future studies should include a pre-burn survey, minimally for species richness, to help tease apart the confounding factors of naturally occurring (extant populations) and seeded species.

Location of Replicates	**Recent Burn History**
Upper Weir	8/12/2008, 8/30/2011, 9/8/2014
Lower Weir	9/14/2009, 9/21/2012, 7/17/2014, 8/5/2015*
South Weir	7/14/2010, 9/17/2012, 9/4/2014

Table 1. Burn history of study sites
Replicates locations on Upper, Lower, and South Weir prairies have had unique, but generally similar management in the recent past. Replicates on each prairie where positioned within the same burn unit so that they would have likely received a similar burn history. Burning before 2008 could have occurred, but there are no written records of such treatments. There was likely a large gap in burn history due to the cessation of Native American burning following European American settlement in the 1850's, and the initiation of ecological prescribed fire in the 2000's.
*8/5/2015 burn date occurred after the completion of data collection for this project. However, this may impact the results of continued monitoring efforts of this research.

The quality of prairies can be rather subjective. The structure and function of a prairie can be evaluated by looking at the types and abundances of native and non-native vegetation, the amount of woody vegetation present, and the ground cover types, among other ecological cues. Comparing these ecological cues to high quality remnant prairies offer a rough comparison between sites. Personal observation and data from this experiment show the three locations selected in this experiment are different from one another despite some similarities. Data collected during the monitoring of this experiment suggest that the three locations are comprised of different quantities of native and non-native species (Figure 2).

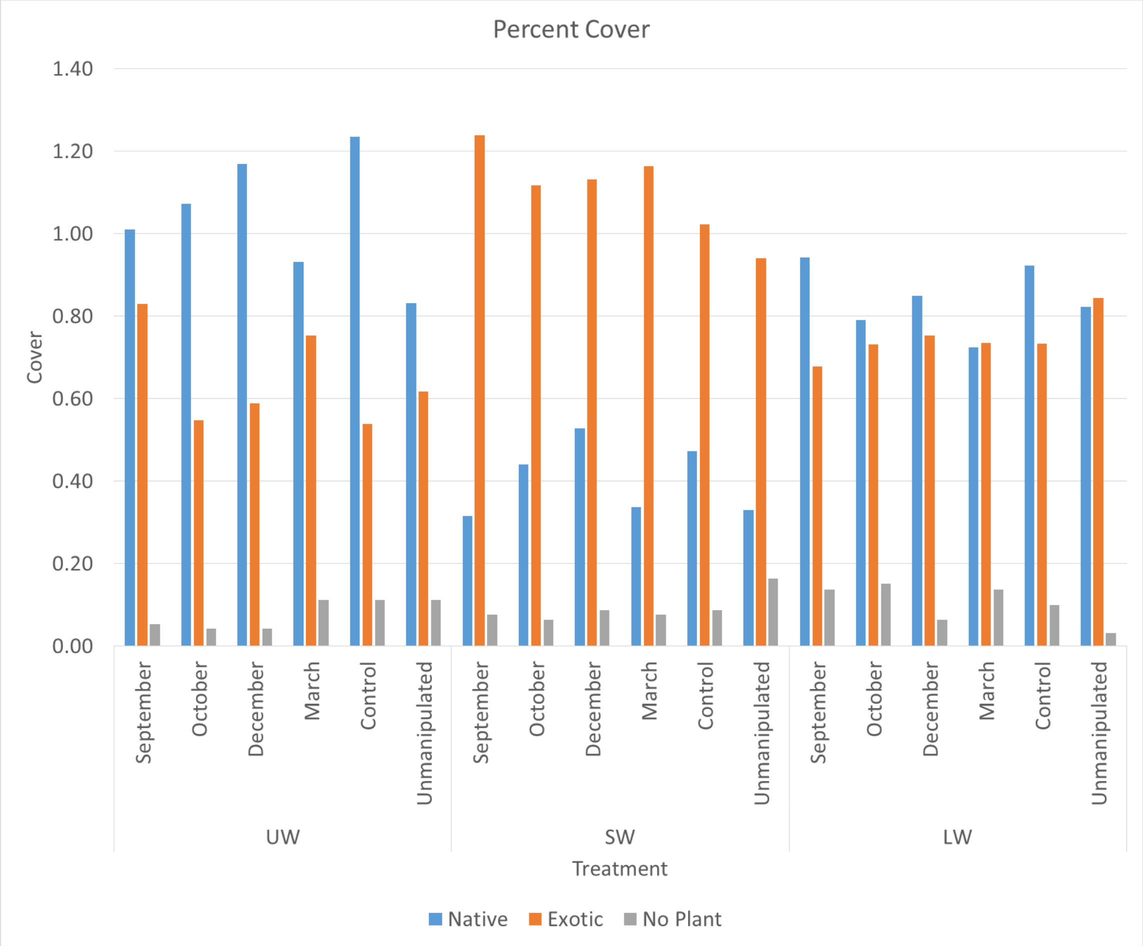

Figure 2: Percent cover of native and exotic plants for each study site

Cover of native, exotic (non-native) and no plant is shown as an average of each replicate (n=3). UW, SW, and LW are Upper Weir, South Weir, and Lower Weir, respectively. Coverage over 1.00 (100%) is possible due to overlapping of plants.

Upper Weir had 83-124% native cover, hereafter “high quality,” South Weir had 32-53% hereafter “low quality,” and Lower Weir had 72-94% native cover, hereafter “medium quality.” Percent cover is often over 100% due to overlapping plants. Native perennial species may take several years to attain a large size that would skew the results of coverage calculations. Likewise, the annual species selected for this experiment are typically very small in these growing conditions, and were not likely to skew the results coverage calculations. With these considerations in mind, the circularity of the argument "which came first the seed addition or relative site quality?" is partially avoided. Unfortunately, due to the techniques used in this study it is impossible to entirely separate the pre-existing species and their abundance, with those that established as a result of the experimental treatments. An additional step, preliminary vegetation monitoring prior to site preparation (i.e. burning) and seed addition, would have been extremely useful in this situation.

Upper Weir prairie replicates were in the highest quality prairie of the three locations, and the control plots contained 11 of 23 seeded species (Table 2). Lower Weir prairie replicates were in medium quality prairie which contained nine of 23 seeded species. South Weir prairie replicates were located in the lowest quality prairie, relative to the other two sites, but still nine of 23 seeded species persisted in the control plots. Currently, the dominant vegetation on the site is exotic colonial bentgrass (*Agrostis capillaris*), and native Roemer's fescue (*Festuca idahoensis* subsp. *roemeri*), as well as other exotic and native graminoids, forbs, and occasionally shrubs such as exotic Scot's broom (*Cytisus scoparius*). South Weir and Upper Weir have had targeted restoration efforts for Mazama pocket gopher. South Weir has had some habitat enhancement in preparation for proposed Taylor's checkerspot butterfly release on adjacent CNLM owned land (Prairie Habitat Enhancement Report on JBLM, Annual Report, 2014). These restoration efforts do not include the areas where the plots are located, but may contribute to the overall health of the prairies.

Species	**Low Quality (South Weir)**	**Medium Quality (Lower Weir)**	**High Quality (Upper Weir)**
Achillea millefolium	Y	Y	Y
Armeria maritima			
Balsamorhiza deltoidea			
Cerastium arvense		Y	
Clarkia amoena			
Collinsia grandiflora			
Collinsia parviflora			
Danthonia californica	Y	Y	Y
Eriophyllum lanatum	Y	Y	Y
Erigeron speciosus			
Festuca idahoensis subsp. *roemeri*	Y	Y	Y
Koeleria macrantha	Y		Y
Lomatium utriculatum	Y		Y
Lupinus albicaulis	Y	Y	Y
Lupinus bicolor			Y
Microseris laciniata		Y	Y
Plectritis congesta			
Potentilla gracilis			
Ranunculus occidentalis	Y	Y	Y
Sericocarpus rigidus	Y	Y	Y
Sisyrinchium idahoense			
Solidago simplex			
Viola adunca			
Number of sown species present in control plots	**9/23**	**9/23**	**11/23**

Table 2: Presence of seeded species in control plots
Seeded species are listed in alphabetical order, and the presence of the species in at least one of the control plots per prairie indicated by “Y.” This gives the reader a glimpse of the species found in the prairie prior to the initiation of this experiment. While the control plots do not explain all of the variation found within the replicates on each prairie, it provides an overview of the most common species.

Experimental Design

In September 2014, a systematic block array in which each set of replicates was spatially segregated from the others was established in the RTA prairies. Within each of the relative qualities of prairie (high, medium, and low) there were three replicates for each sowing time (n=3). Each replicate was placed on a roughly homogeneous 5x5m area with a 5m buffer zone between each seeded treatment. Each plot was raked by hand with standard garden rakes prior to sowing in order to mimic a tractor-pulled harrow’s soil and moss disturbance. This pre-sowing raking created more available microsites that seeds require for germination, and increased likelihood of seed-soil contact.

At each of four treatment time points, a seed mix of 23 native species was mixed with vermiculite to enable more even distribution, and sown via drop seeder into each of nine plots. Sowing time treatments were September 29, 2014; October 29, 2014; December 17, 2014, and March 16, 2015. Control plots were raked and vermiculite was added, while seeds were withheld. Additionally, un-manipulated control plots were established within the plot array, and these were not raked, and vermiculite and seeds were withheld. The un-manipulated control was added to make sure that the soil disturbance (micro-site preparation) did not influence the establishment of seeds already present in the soil-seed bank. Array set up is shown in Figure 3. Each treatment plot is 5 x 5 meters with a 5-meter buffer zone around each, with the exception of the un-manipulated controls, which were set up in a representative, untouched block within array. These un-manipulated controls were added after the arrays were set up when further questions were raised about the effects of disturbance, and potentially activating the soil seed bank. There are a total of 54 plots, which were monitored in spring 2015.

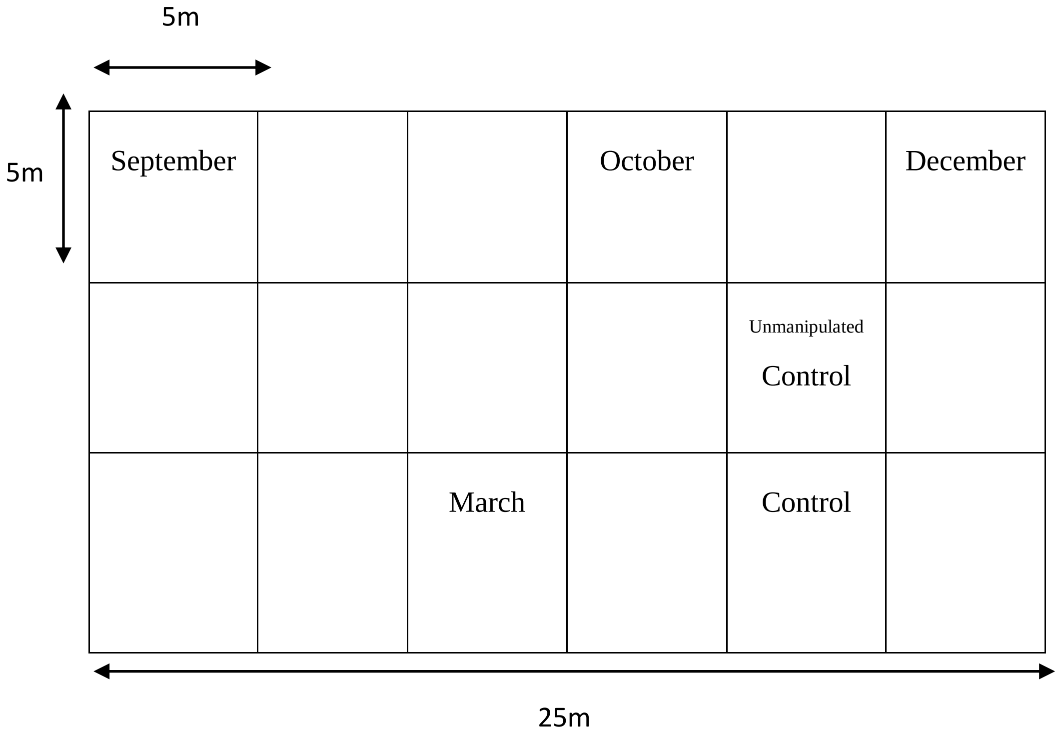

Figure 3: Experimental design

Typical array set up is shown. Each treatment plot is 5 x 5 meters. Sowing time treatments were September 29, 2014; October 29, 2014; December 17, 2014, and March 16, 2015. Control plots were raked and vermiculite was added, while seeds were withheld. Unmanipulated control plots were established within the plot array, and these were not raked, and vermiculite and seeds were withheld. Three arrays were set up per prairie.

Species selection

There are 190 past and present native herbaceous species (Dunwiddie, Alverson, Martin, & Gilbert, 2014) it would be logistically challenging to test all of them. A subset consisting of 23 species was selected based on availability of a sufficient quantity of seed, time, and resources. An effort was made to select a broad spectrum of plants including perennial grasses, perennial forbs, and annual forbs (Table 3). Some species are resources for threatened and endangered species (e.g., *Plectritis congesta* is a Taylor's checkerspot butterfly nectar resource) but most are relatively common and widespread. A broad range of plant families are represented and this may allow some transferability to other species not tested here. Seeds were obtained from the Center for Natural Lands Management (Olympia, Washington, USA) and were not stratified or otherwise pre-treated before sowing. Seeds were grown at Webster's Nursery and were of "A" grade (highest quality) clean seed. A restoration seed mix for upland prairie was calculated using Center for Natural Lands Management's 2014 Seed Mix Calculator. The seed mix calculator calculates the weight of bulk seed need to meet specific restoration targets using the latest seed purity and viability information and the best available science for field establishment rates. See Table 4 for more information about seed mix calculations.

Scientific Name	**Common Name**	**Family**	**Growth Habit**	**Duration**
Achillea millefolium L.	common yarrow	Asteraceae	F	P
Armeria maritima (Mill.) Willd.	thrift seapink	Plumbaginaceae	F	P
Balsamorhiza deltoidea Nutt.	deltoid balsamroot	Asteraceae	F	P
Cerastium arvense L.	field chickweed	Caryophyllaceae	F	P
Clarkia amoena (Lehm.) A. Nelson & J.F. Macbr.	farewell to spring	Onagraceae	F	A
Collinsia grandiflora (Lindl.)	giant blue eyed Mary	Scrophulariaceae	F	A
Collinsia parviflora (Lindl.)	Blue eyed Mary	Scrophulariaceae	F	A
Danthonia californica Bol.	California oatgrass	Poaceae	G	P
Eriophyllum lanatum (Pursh) Forbes	common woolly sunflower	Asteraceae	F	P
Erigeron speciosus (Lindl.) DC.	aspen fleabane	Asteraceae	F	P
Festuca idahoensis Elmer subsp. *roemeri* (Pavlick) S. Aiken	Roemer's fescue	Poaceae	G	P
Koeleria macrantha (Ledeb.) Schult.	prairie Junegrass	Poaceae	G	P
Lomatium utriculatum (Nutt. Ex Torr. & A. Gray)	common lomatium	Apiaceae	F	P

Lupinus albicaulis Douglas	sicklekeel lupine	Fabaceae	F	P*
Lupinus bicolor Lindl.	miniature lupine	Fabaceae	F	A
Microseris laciniata (Hook.) Sch. Bip.	cutleaf silverpuffs	Asteraceae	F	P
Plectritis congesta (Lindl.) DC.	shortspur seablush	Valerianaceae	F	A
Potentilla gracilis Douglas ex Hook.	slender cinquefoil	Rosaceae	F	P
Ranunculus occidentalis Nutt.	western buttercup	Ranunculaceae	F	P
Sericocarpus rigidus (Lindl.)	Columbia whitetop aster	Asteraceae	F	P
Sisyrinchium idahoense E.P. Bicknell	Idaho blue-eyed grass	Iridaceae	F	P
Solidago simplex Kunth	Mt. Albert goldenrod	Asteraceae	F	P
Viola adunca Sm.	Hookedspur violet	Violaceae	F	P

Table 3: Species selected
Species are listed with their common name, family, functional group where F is forb and G is grass, and life history, where A is annual and P is perennial. Information from USDA, NRCS Plants Database (2016). P*= perennial plant in SPS prairies, but is listed as an annual plant in USDA, NRCS Plants Database (2016).

Species	**Target density (plants/ m^2)**	**Target cover**	**Approx. number of seeds/gram**	**Grams/ replicate (5mx5m plot)**	**Seeds/ replicate (5mx5m plot)**	**Seeds/ m^2 sowing rate**	**Seeds/ $3m^2$ sowing rate**
Achillea millefolium	2	1%	6455	0.05	322.75	1 2.91	38.73
Armeria maritima	2	1%	465	0.38	176.7	7.07	21.20
Balsamorhiza deltoidea	0.5	10%	138	1.81	249.78	9.99	29.97
Cerastium arvense	4	2%	5704	0.04	228.16	9.13	27.38
Clarkia amoena	4	2%	2152	0.64	1377.28	55.09	165.27
Collinsia grandiflora	3	0.50%	268	1.12	300.16	12.01	36.02
Collinsia parviflora	4	1%	653	0.61	398.33	15.93	47.80
Danthonia californica	3	2%	250	1	250	10.00	30.00
Eriophyllum lanatum	1	2%	2710	0.03	81.3	3.25	9.76
Erigeron speciosus	2	2%	5240	0.07	366.8	14.67	44.02
Festuca idahoensis subsp. *roemeri*	5	40%	1123	1.25	1403.75	56.15	168.45
Koeleria macrantha	2	1%	8132	0.2	1626.4	65.06	195.17
Lomatium utriculatum	4	2%	631	0.71	448.01	17.92	53.76
Lupinus albicaulis	1	2%	33	8.24	271.92	10.88	32.63
Lupinus bicolor	2	2%	169	5.32	899.08	35.96	107.89
Microseris laciniata	3	1%	924	0.49	452.76	18.11	54.33
Plectritis congesta	4	2%	1699	0.24	407.76	16.31	48.93
Potentilla gracilis	2	2%	2901	0.18	522.18	20.89	62.66
Ranunculus occidentalis	3	2%	419	3.46	1449.74	57.99	173.97
Sericocarpus rigidus	7	3%	2941	0.54	1588.14	63.53	190.58
Sisyrinchium idahoense	2	0.50%	763	0.79	602.77	24.11	72.33
Solidago simplex	4	2%	3446	0.49	1688.54	67.54	202.62

Viola adunca	6	3%	1293	2.51	3245.43	129.82	389.45
Total:	**70.5**	**86%**	**n/a**	**30.17**	**18357.74**	**734.31**	**2202.93**

Table 4: Seed Mix Calculations
Each species is listed with restoration target densities and target cover, approximate number of seeds per gram of bulk seed weight, the quantity of seed that was weighed out for each 5x5m replicate, the average seeding rate per square meter, and finally the average seeding rate per 3 square meters. 3 square meters is amount of area monitored for this study, for easy comparison. These numbers were calculated using Center for Natural Lands Management’s 2014 Seed Mix Calculator which takes into account the most recent restoration targets and seed viability information.

Monitoring Methods

Monitoring within each replicate was done using two different methods. Point intercept method was done every half meter along three randomly selected transects per replicate. The identity of any species (native or exotic) was recorded in order to calculate percent cover. These point intercept data were used to verify the relative quality of each of the three prairies. The second method, density of plants per 1m^2 quadrats was done to determine count of individual species per unit area. These count data were collected for seeded species only within three randomly selected samples per replicate, these samples were later summed to the plot level. These density count data were used to determine the effects of sowing time and relative prairie quality on the first year establishment of the seeded native species. All data were recorded by hand on data sheets and later entered into Excel.

Statistical Analysis

To compare the raked control with the un-manipulated control a two tail t-test with unequal variances was performed in Excel. The mean density between these two treatments were not significantly different (α=0.05) for each species, so only the control was used in further analysis.

To test the effects of sowing time and relative prairie quality on the overall diversity of sown native species in the plots, a Shannon-Wiener diversity index was calculated in Excel. This diversity index takes into consideration both the species richness (defined as the number of different species) and abundance (defined here as the count of individuals in each species) (Spellerberg & Fedor, 2003). Count data were summed for each sowing time and prairie quality combination. A total of 15 different Shannon's H' values were calculated.

To test the effects of sowing time and site quality on each species individually, a generalized regression model, a type of general linear model, was developed in JMP. A number of considerations went into making this decision because these data were over-dispersed meaning that variance was greater than mean for each species, and most closely fit a negative binomial distribution. A factorial cross of sowing time and relative prairie quality was used as the predictor variables, and count data were the response variable. Maximum likelihood was the estimation method and the mean model link was logarithmic. General linear models are often used for analyzing non-parametric data, the product of random variation in ecology and evolution studies (Bolker et al., 2008). General linear models have been used in experiments similar to this one (see Bakker, Colasurdo, & Evans, 2012; Dunwiddie & Martin, 2016; Zeiter, Stampfli, & Newbery, 2006) though other analyses such as hurdle models, may be more appropriate in certain circumstances (Potts & Elith, 2006; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). If the generalized regression demonstrated an effect ($p<0.05$) from either sowing time or relative prairie quality on each species then a post-hoc Steel-Dwass all pairs multiple comparisons test was performed. The Steel-Dwass test is similar to a Tukey's honestly significantly different test, but is for non-parametric data, and is more conservative.

RESULTS

Overall establishment rates were low for most species, with 13 of 22 species showing less than 5% establishment (Table 5). Some species (five of 22) had modest establishment rates of 6-30%. Two species had greater than 30% establishment, though this was likely due to experimental design flaw, rather than as a result of the treatments. One species, *Festuca idahoensis* subsp. *roemeri*, had a relatively high rate of establishment, 55%, presumably due to large number of already established plants and/or large number of small seedlings. The second species, *Eriophyllum lanatum*, had an unrealistic establishment rate of 887% primarily due to the way plants were counted and the background presence of several adult plants. *Eriophyllum lanatum* is rhizomatous so stems were counted because it was impossible to positively identify individual plants without digging them up. See “suggestions for future research” section for ideas of ways to better test the establishment rates of these species.

Species	**Target density (plants/ m^2)**	**Target cover (%m^2)**	**Sowing rate (seeds/ m^2)**	**Observed Average density (plants/m^2)**	**Difference between observed and target densities (plants/m^2)**	**Establish-ment rate (plants/seeds)**
Achillea millefolium	2	1%	12.91	1.33	-0.67	10%
Armeria maritima	2	1%	7.07	0.00	-2.00	0%
Balsamorhiza deltoidea	0.5	10%	9.99	0.09	-0.41	1%
Cerastium arvense	4	2%	9.13	0.39	-3.61	4%
Clarkia amoena	4	2%	55.09	0.06	-3.94	0%
Collinsia grandiflora	3	0.5%	12.01	5.56	-1.44	20%
Collinsia parviflora	4	1%	15.93			
Danthonia californica	3	2%	10	0.09	-2.91	1%
Eriophyllum lanatum	1	2%	3.25	28.84	27.84	887%
Erigeron speciosus	2	2%	14.67	0.00	-2.00	0%
Festuca idahoensis subsp. *roemeri*	5	40%	56.15	30.86	25.86	55%
Koeleria macrantha	2	1%	65.06	1.10	-0.90	2%
Lomatium utriculatum	4	2%	17.92	0.15	-3.85	1%
Lupinus albicaulis	1	2%	10.88	2.69	1.69	25%
Lupinus bicolor	2	2%	35.96	1.06	-0.94	3%
Microseris laciniata	3	1%	18.11	1.40	-1.60	8%

Plectritis congesta	4	2%	16.31	0.84	-3.16	5%
Potentilla gracilis	2	2%	20.89	0.19	-1.81	1%
Ranunculus occidentalis	3	2%	57.99	4.96	1.96	9%
Sericocarpus rigidus	7	3%	63.53	19.34	12.34	30%
Sisyrinchium idahoense	2	0.5%	24.11	0.17	-1.83	1%
Solidago simplex	4	2%	67.54	0.00	-4.00	0%
Viola adunca	6	3%	129.82	0.00	-6.00	0%

Table 5: Overall establishment rates
Species are listed with target density, target percent cover, calculated sowing rate, observed average density of plants, difference between observed and target counts of plants, with negative numbers in red, and establishment rate. Observed average density (plants/m2) was calculated by averaging counts of all sowing times except the control plots. Establishment rates highlighted in green are those species not found in any control plot.

All species showed a unique response to the treatments in the study. For various reasons not all species were analyzed. Three species which were not encountered at all during monitoring: *Armeria maritima*, *Solidago simplex*, and *Viola adunca.* A fourth species, *Erigeron speciosus* is notoriously difficult to identify as a seedling, so this species was also considered “not encountered.” These four species were excluded from all analysis, and further research should be done to determine their unique establishment requirements. Two congeneric species--*Collinsia grandiflora* and *Collinsia parviflora*--were often indistinguishable from each other during monitoring and were combined under the label *Collinsia* spp.. *Collinsia* spp. was treated as a single species for analysis.

The Shannon-Weiner diversity index included sixteen sown native species: *Achillea millefolium*, *Balsamorhiza deltoidea*, *Cerastium arvense*, *Clarkia amoena*, *Collinsia* spp., *Danthonia californica*, *Koeleria macrantha*, *Lomatium utriculatum*, *Lupinus albicaulis*, *Lupinus bicolor*, *Microseris laciniata*, *Plectritis congesta*, *Potentilla gracilis*, *Ranunculus occidentalis*, *Sericocarpus rigidus*, and *Sisyrinchium idahoense*. Meanwhile, six total species were excluded from this analysis. Of these, two species, *Festuca idahoensis* subsp. *roemeri* and *Eriophyllum* *lanatum* were excluded from this analysis because the majority of the plants counted were not a result of the seed addition. Additionally, the four species not encountered were excluded from this analysis: *Armeria maritima*, *Erigeron speciosus*, *Solidago simplex,* and *Viola adunca.*

The general linear model analysis was run on thirteen species independently. The thirteen species were: *Achillea millefolium*, *Cerastium arvense*, *Collinsia* spp., *Danthonia californica*, *Eriophyllum lanatum*, *Festuca idahoensis* subsp. *roemeri*, *Koeleria macrantha*, *Lupinus albicaulis*, *Lupinus bicolor*, *Microseris laciniata*, *Plectritis congesta*, *Ranunculus occidentalis*, and *Sericocarpus rigidus*. A total of nine species were excluded from this analysis. The four species not encountered were obviously excluded. Additionally, five species were excluded because they were found in too low abundance, typically fewer than 30 individual plants were found across all treatment combinations. The plants found in too low of abundance were: *Balsamorhiza deltoidea*, *Clarkia amoena*, *Lomatium utriculatum*, *Potentilla gracilis*, and *Sisyrinchium idahoense*.

Community Response

The Shannon-Weiner diversity index takes into account both richness and abundance of all seeded species (Figure 4). The higher the H' value, the more types and abundances of sown species. The H' value was highest for the September treatment in the high quality prairie with H'=2.05, followed by October treatments in medium and high quality prairies with H'=2.03 and H'=1.93 respectively. For reference, highly diverse, unharvested tropical forests in Papua New Guinea showed a Shannon's diversity index of 4.9 ± 0.21 standard deviation (Yosi, Keenan, & Fox, 2011), meanwhile forest stands in Oklahoma ranged from 0.72-1.48 and had a maximum of 32 species (Risser & Rice, 1971). Only the native, sown species were included in this analysis, with the exception of the two most common species that were found in high numbers. A Shannon's diversity index that included other native species and non-native species would have resulted in a much higher H' values.

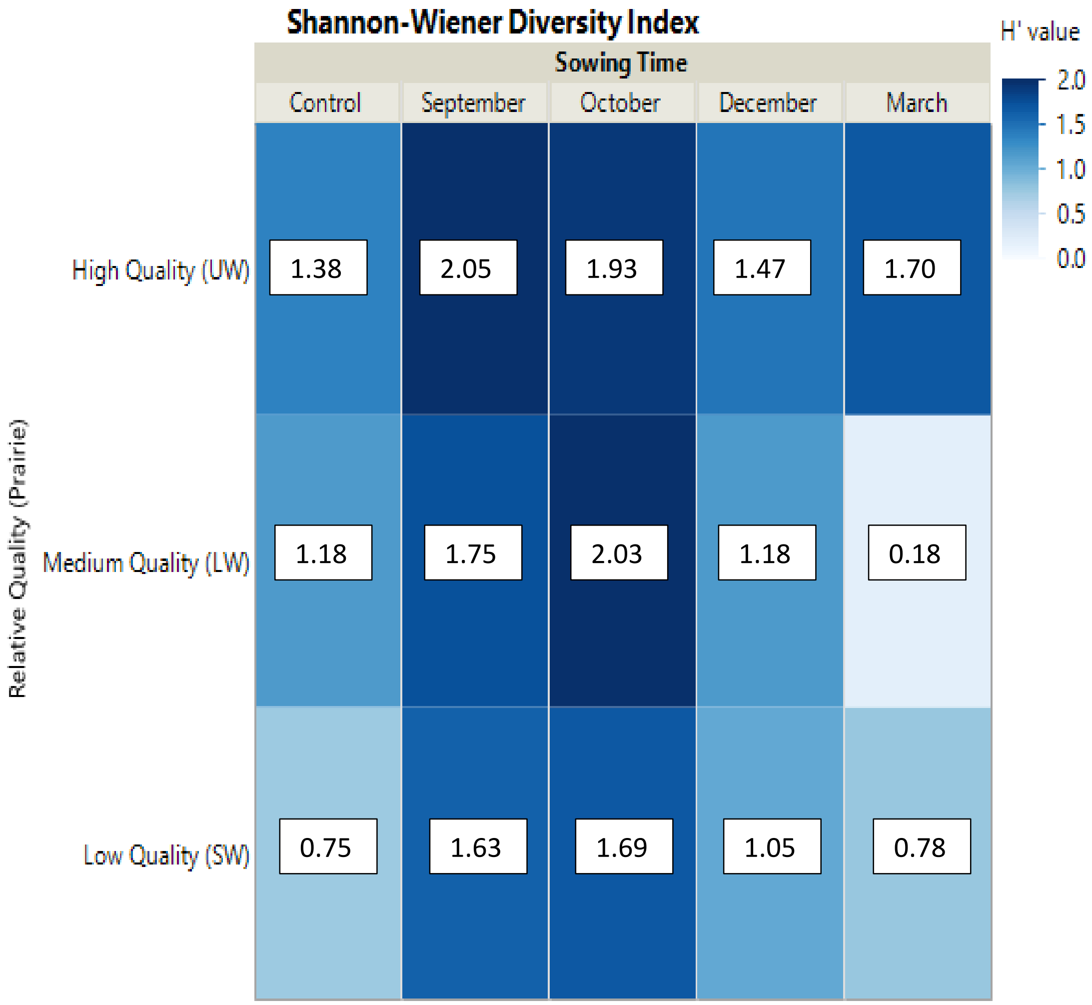

Figure 4: Community diversity
Shannon Weiner Diversity Index calculated on only seeded species, and summed to the plot level. Festuca idahoensis subsp. roemeri and Eriophyllum lanatum were excluded from this analysis due to high numbers and relatively large plants which suggests that most of the plants counted were already established before seeding took place.

Individual Species Response

Individual species responded uniquely to both sowing time treatments and varying prairie qualities. Three species, *Collinsia* spp., *Lupinus bicolor*, and *Plectritis congesta* were statistically significantly affected by treatment time (α=0.05). Initially, five species: *Achillea millefolium*, *Danthonia californica*, *Eriophyllum lanatum*, *Koeleria macrantha*, and *Ranunculus occidentalis*, were statistically significantly affected by prairie quality (α=0.05). However, upon further analysis (post hoc Steel-Dwass multiple comparisons test, α=0.05) *Koeleria macrantha* showed that it was not actually significantly influenced by quality. One species, *Lupinus albicaulis*, was initially affected by both treatment and quality, but upon further analysis (post hoc Steel-Dwass multiple comparisons test, α=0.05) was found to not actually be significantly influence by quality. The other four analyzed species, *Cerastium arvense*, *Festuca idahoensis* subsp. *roemeri*, *Microseris laciniata*, and *Sericocarpus rigidus* were not significantly affected by treatment or prairie quality.

Each species is grouped by type of response, and results are described in more detail below. Where appropriate, generalized regression and Steel-Dwass all pairs multiple comparisons test results are considered and general trends are also discussed.

Species significantly influenced by sowing time

Collinsia spp., which includes both *C. parviflora* and *C. grandiflora*, commonly known as blue-eyed Mary and giant blue-eyed Mary respectively, were strongly influenced by sowing time ($p<0.0001$), but not by site quality ($p<0.39$). These annual forbs responded more positively to September and October sowing times than December sowing times (Figure 5). Of the total 600 individual plants found across all relative prairie qualities, there were 324 in September, 223 in October, and 53 in December. No plants were found in the March or Control plots. Plants were found across all three site conditions. Of the 600 total plants found, 273 were in medium quality, 197 were found in low quality, and 130 in high quality. These plants are rare in SPS prairies, and were likely extirpated from the area. In order to accurately distinguish these congeneric species one must monitor multiple times during the year, since they can only reliably be distinguished by their flower sizes.

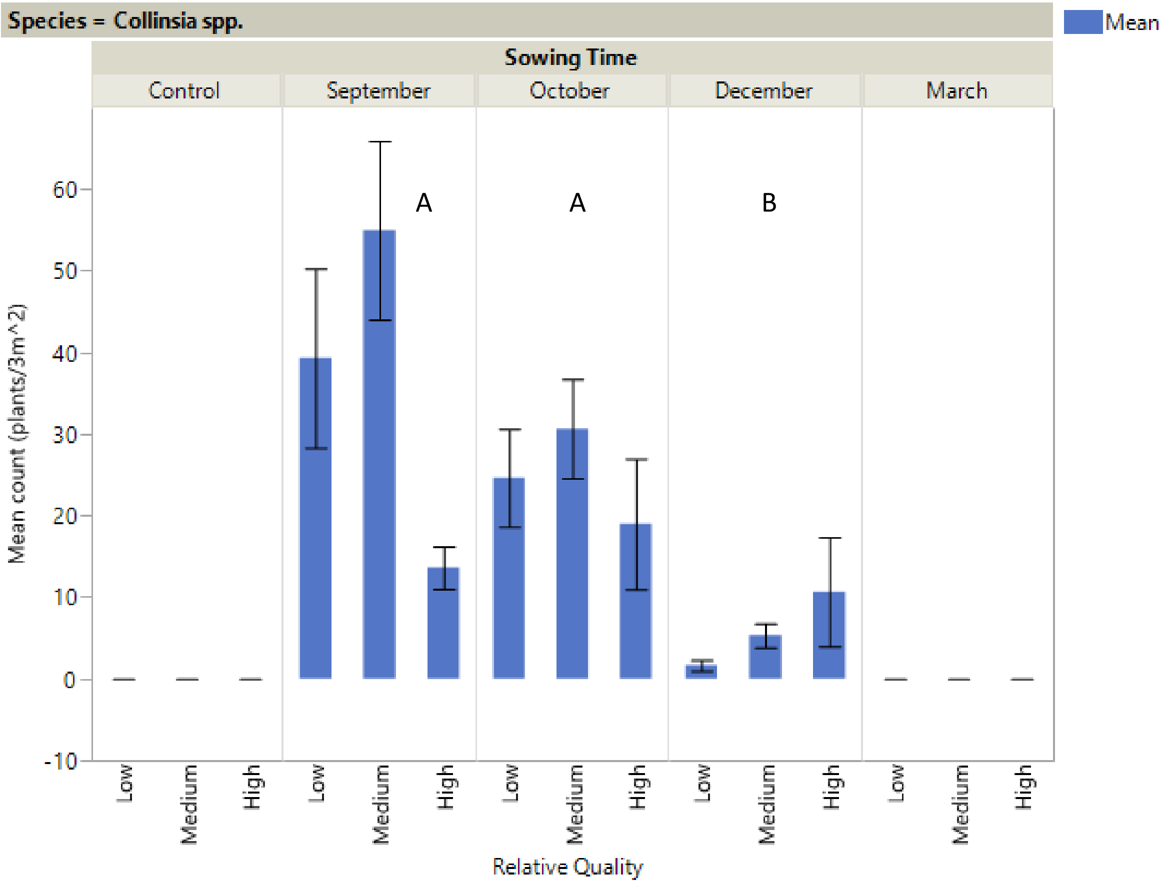

Figure 5: *Collinsia* spp. results

Different letter (A, B, C, etc.) indicate that each sowing time is significantly different from one another (α = 0.05). Letters that are shared between two sowing times indicate that they are not significantly different from one another. Error bars represent standard error.

Lupinus bicolor, commonly known bicolor lupine or miniature lupine, was influenced by seed sowing time ($p<0.0001$) but not by relative site quality ($p<0.67$). This species responded positively to all sowing times equally, except the control (Figure 6). Of the total 115 individual plants found across all relative prairie qualities, the highest counts were found in September (47) followed by October (32) and December (28) and very few were found in March (7) and in Control (1). This annual forb is fairly common across restored SPS prairies, and was observed in medium quality (48), high quality (40), and low quality (27) prairies.

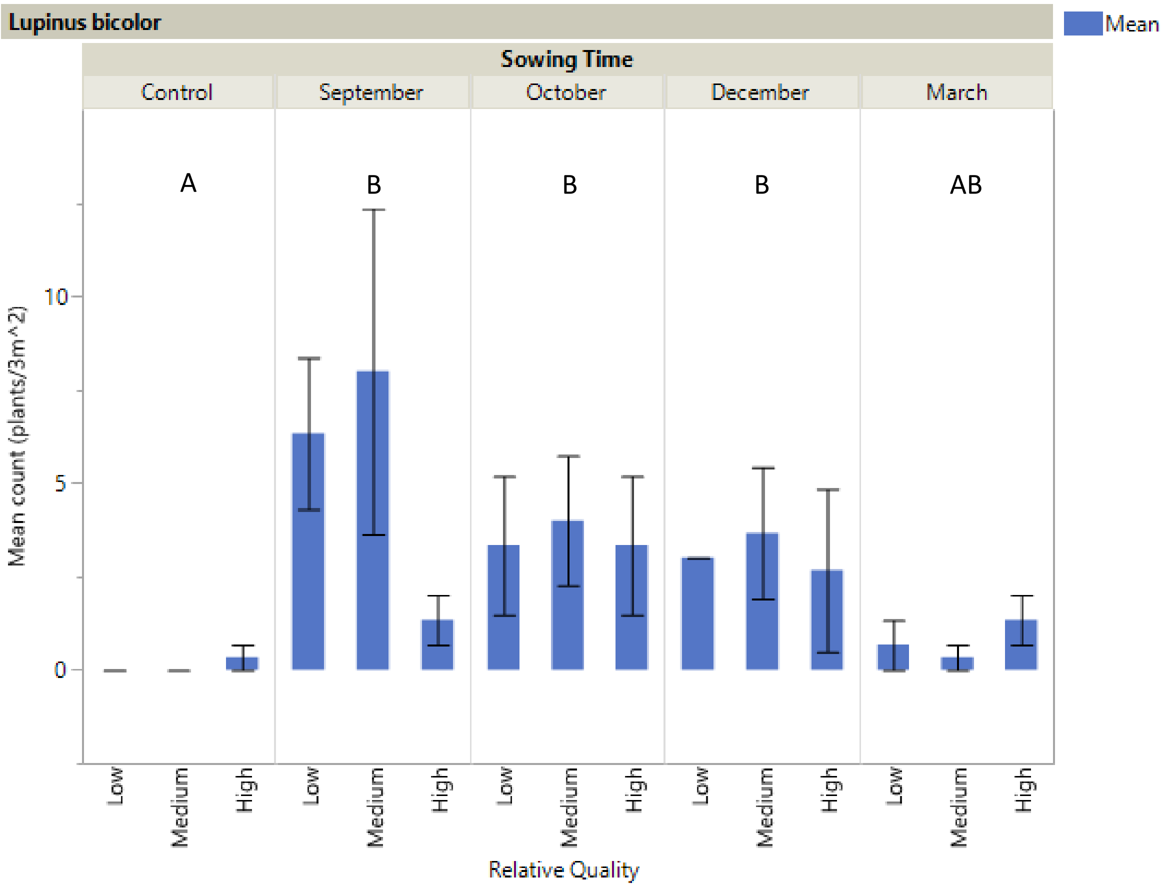

Figure 6: *Lupinus bicolor* results

Different letters (A, B, C, etc.) indicate that each sowing time is significantly different from one another (α = 0.05). Letters that are shared between two sowing times indicate that they are not significantly different from one another. Error bars represent standard error.

Plectritis congesta, commonly known as shortspur seablush, was influenced by seed sowing time ($p<0.0001$) but not relative site quality (0.052). It was found in three of five sowing times across all three site conditions. *Plectritis congesta* responded positively to earlier sowing times than later sowing times (Figure 7). Of the total 91 individual plants found across all relative prairie qualities, the highest count of was found in September (64), followed by October (23), and finally December (4). No plants were found in March or Control plots. The highest count of plants was found in high quality (45) followed by medium (28) and low quality (18). This annual forb is rare in SPS prairies, and was likely extirpated from some areas.

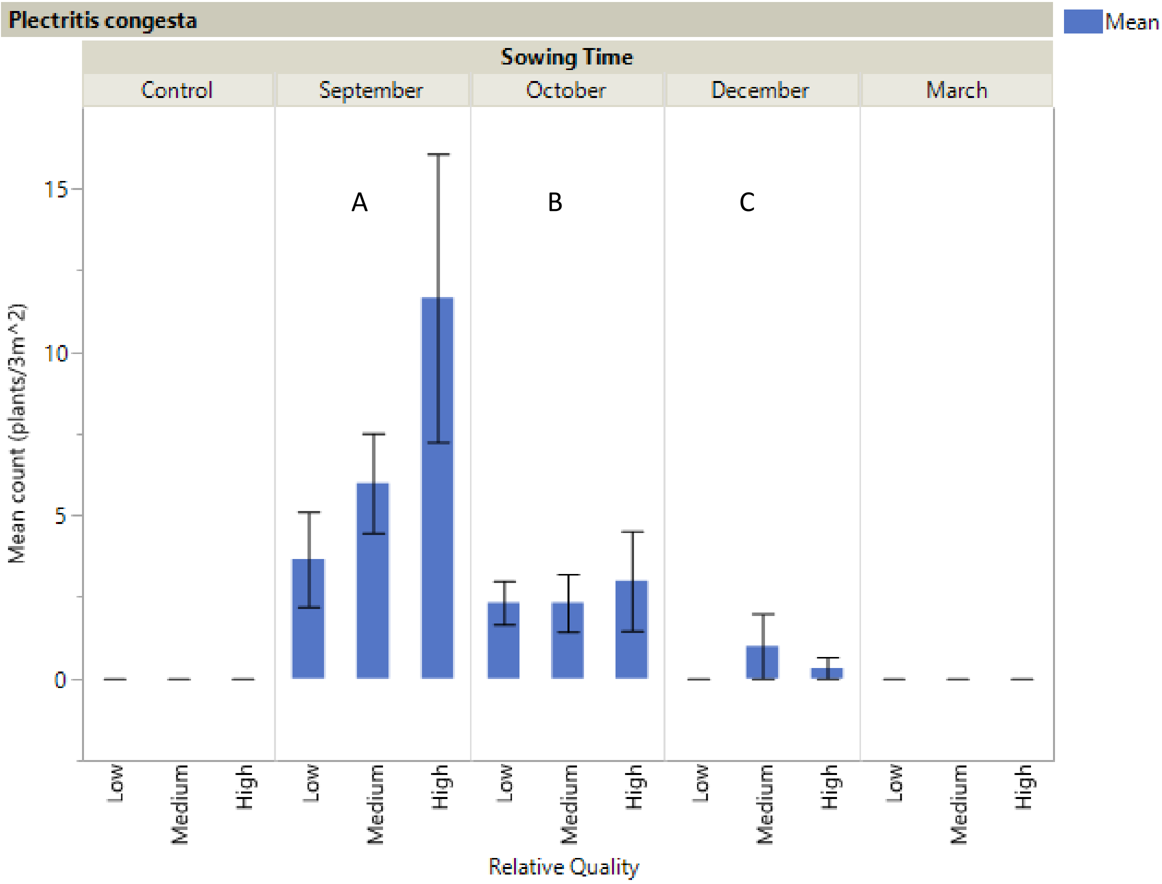

Figure 7: *Plectritis congesta* results

Different letters (A, B, C, etc.) indicate that each sowing time is significantly different from one another ($\alpha = 0.05$). Letters that are shared between two sowing times indicate that they are not significantly different from one another. Error bars represent standard error.

Lupinus albicaulis, commonly known as sicklekeel lupine, was initially influenced by both seed sowing time ($p<0.0001$) and relative site quality ($p<0.0001$). It responded positively to fall sowing times rather than spring or the control (Figure 8). However, upon further investigation, a Steel-Dwass test showed that none of the site conditions were statistically significantly different from each other at α=0.05 (**Error! Reference source not found.**). While igh quality and medium quality had similar means (p=1.00), the low quality mean was not statistically significantly different from medium quality (p=0.12). Likewise, the low quality mean was not statistically significantly different from the high quality mean (p=0.07). While these results are not statistically significant they also show a pattern that this species prefers or is found more often in high and medium quality prairie rather than low quality prairie. These results should be further investigated. Of 319 total individual plants found across all relative qualities, the highest abundances were found in October (112) and September (99) with fewer plants found in December (67), Control (28) and March (13). Of 319 total plants across all treatment times more were observed in medium quality (139) and high quality (130) than in low quality (50). This perennial forb is fairly common in SPS prairies, thus found in the control plots, but seed sowing likely greatly augmented this population.

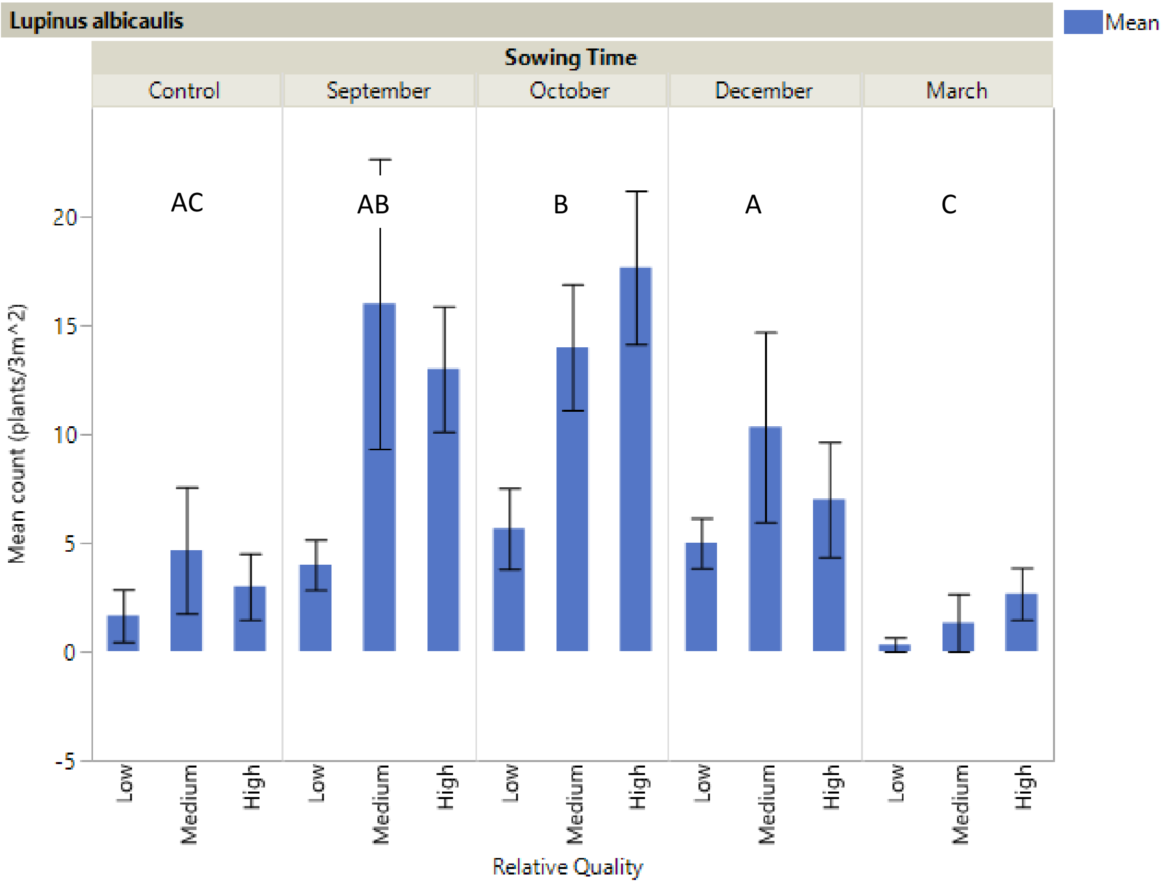

Figure 8: *Lupinus albicaulis* results 1

Different letters (A, B, C, etc.) indicate that each sowing time is significantly different from one another (α = 0.05). Letters that are shared between two sowing times indicate that they are not significantly different from one another. Error bars represent standard error.

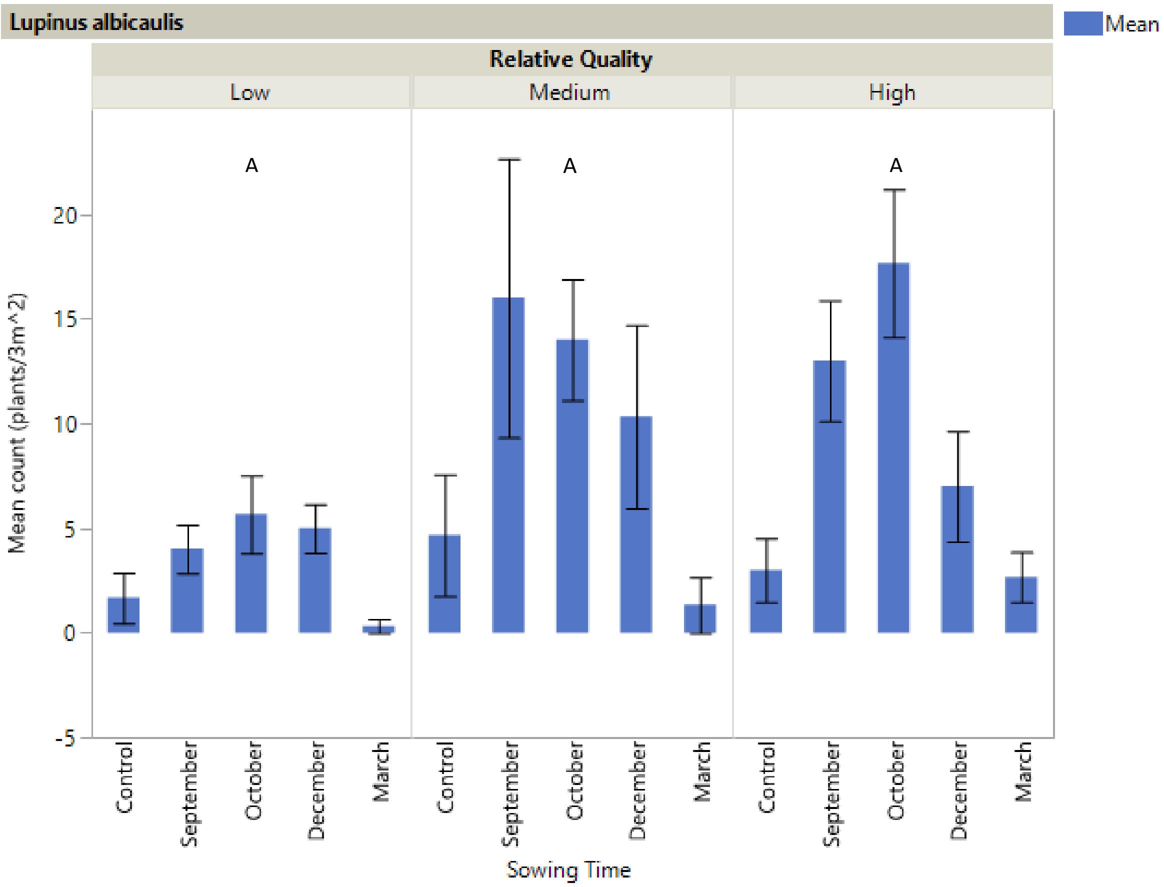

Figure 9: *Lupinus albicaulis* results 2

Different letters (A, B, C, etc.) indicate that each relative quality is significantly different from one another (α = 0.05). Letters that are shared between two relative qualities indicate that they are not significantly different from one another. Error bars represent standard error.

Species significantly influenced by site quality

Achillea millefolium, commonly known as yarrow, was not influenced by seed sowing time ($p<0.75$), but was influenced by site quality ($p<0.04$). This perennial forb responded most positively to high and medium quality site conditions (**Error! Reference source not found.**). cross all sowing times, of the total 167 individual plants, 112 of them were found in high relative quality prairie. Of the total 167 individuals, fewer plants were found in medium quality (37) and low quality (18). *Achillea millefolium* is a common SPS prairie species, and can be weedy in certain circumstances. *Achillea millefolium* was found in all five sowing time treatments, including the control. Of the total 167 individual plants, most plants were found in September (51 total plants), and the fewest plants were found in the control (23 total plants). *Achillea millefolium* spreads by rhizomes as well as reproduces by seed, and monitoring protocols did not discern between the two forms of reproduction. The count of plants likely overestimates the number of genetically distinct individuals.

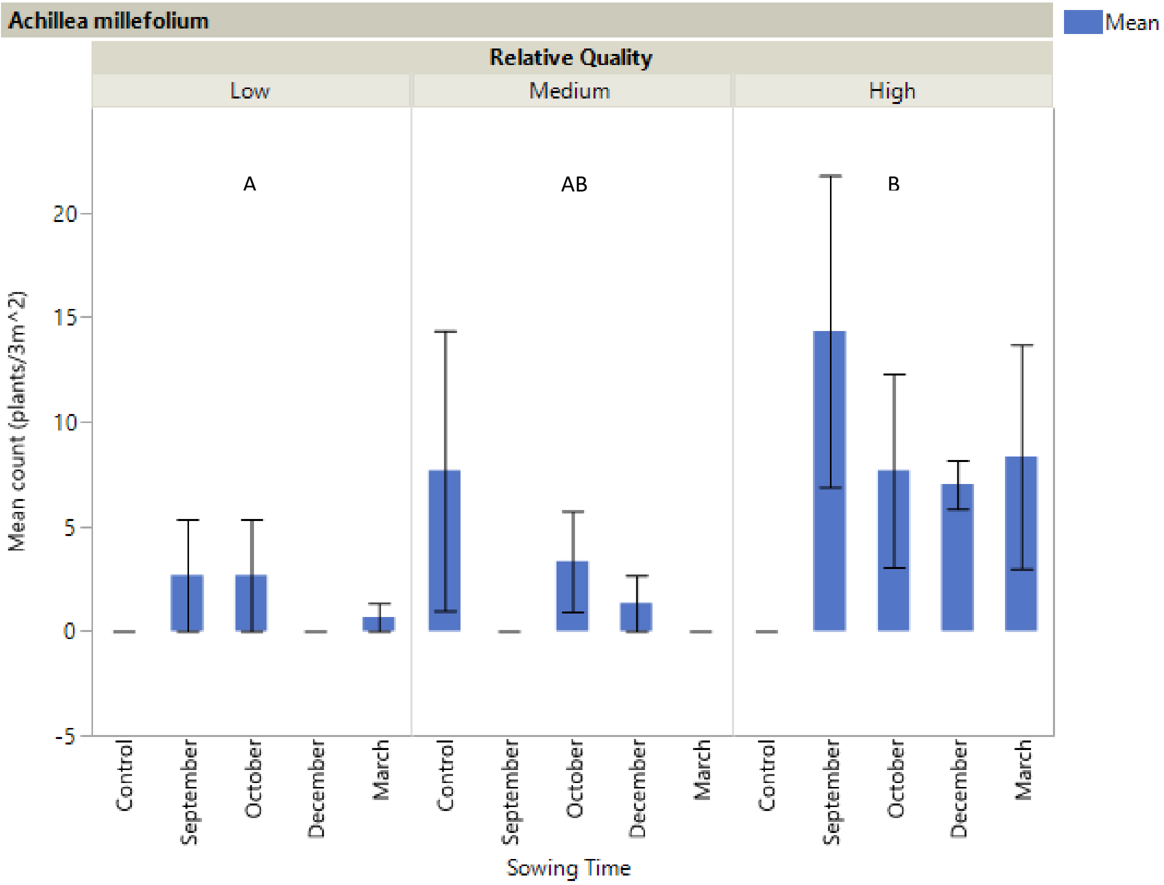

Figure 10: *Achillea millefolium* results

Different letters (A, B, C, etc.) indicate that each relative quality is significantly different from one another ($\alpha = 0.05$). Letters that are shared between two relative qualities indicate that they are not significantly different from one another. Error bars represent standard error.

Danthonia californica, commonly known as California oatgrass, was not influenced by seed sowing time (p<0.58), but was influenced by site quality (p<0.02). It responded most positively to high and medium quality sites than to low quality sites (Figure 11). Of the total 145 individual plants found across all sowing times, 66 were found in medium quality, 58 in high quality, and 21 in low quality. This common perennial grass was found in all five sowing time treatments, including the control. The highest count occurred in October (35 total plants) and the lowest count occurred in Control and December (both had 22 total plants). Like many grasses, they are difficult to identify, especially when very small or when intermixed with other grass species, so the actual count of this species may be higher than what was found during monitoring.

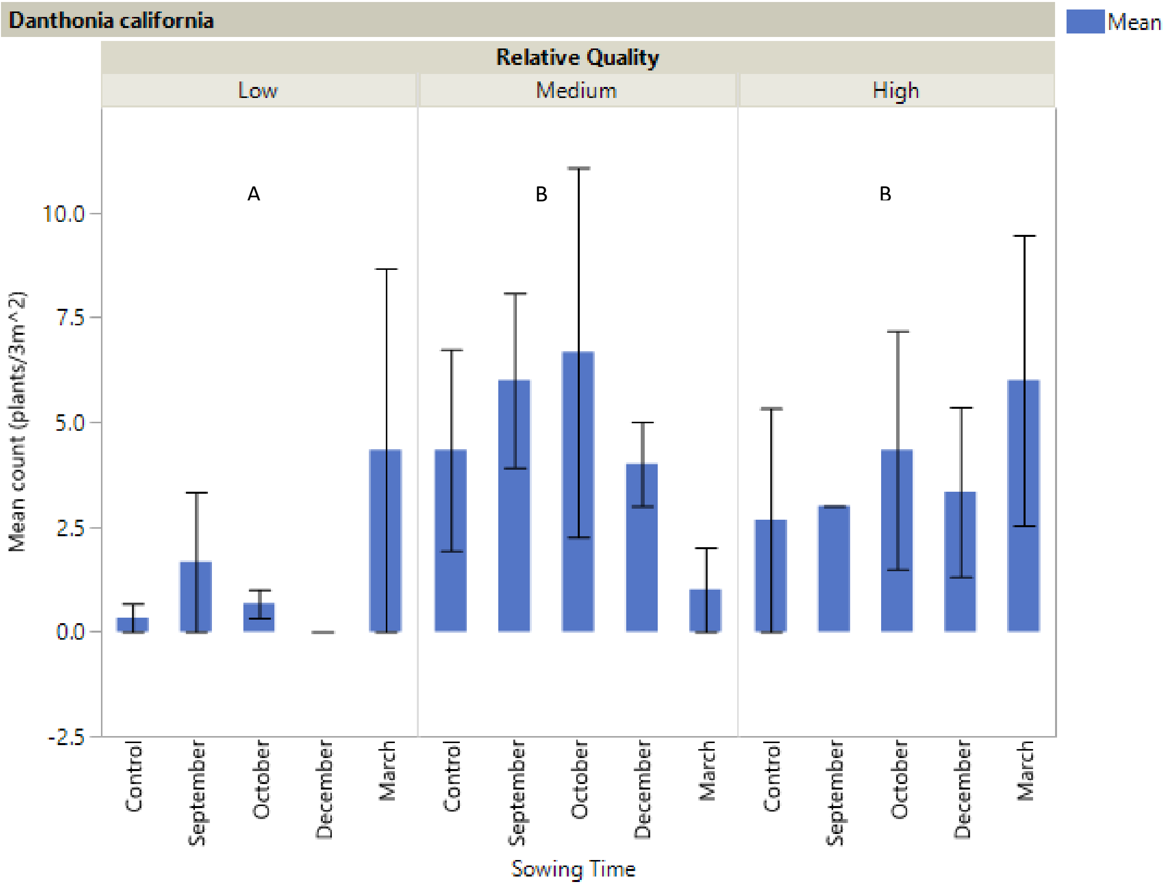

Figure 11: *Danthonia californica* results
Different letters (A, B, C, etc.) indicate that each relative quality is significantly different from one another (α = 0.05). Letters that are shared between two relative qualities indicate that they are not significantly different from one another. Error bars represent standard error.

Eriophyllum lanatum, commonly known as woolly sunflower or Oregon sunshine, was not influenced by seed sowing time (p<0.42), but was strongly influenced by site quality (p<0.0001). This species responded most positively to medium quality rather than high or low quality (Figure 12). Of 3,923 total stems found across all sowing times, most (3026) were found in medium quality, while fewer (866) were found in high quality, and very few (21) in low quality. This perennial forb is very common in SPS prairies and was found in all five sowing time treatments, including the control. Of the total stems counted across all relative prairie qualities, the highest count of stems was observed in September (970) and the lowest in October (658) This plant was counted by stems rather than by plants because it was very difficult to determine independent plants without destructively sampling. This plant reproduces by rhizomes as well as by seed, so the count of genetically distinct individual plants may be much lower.

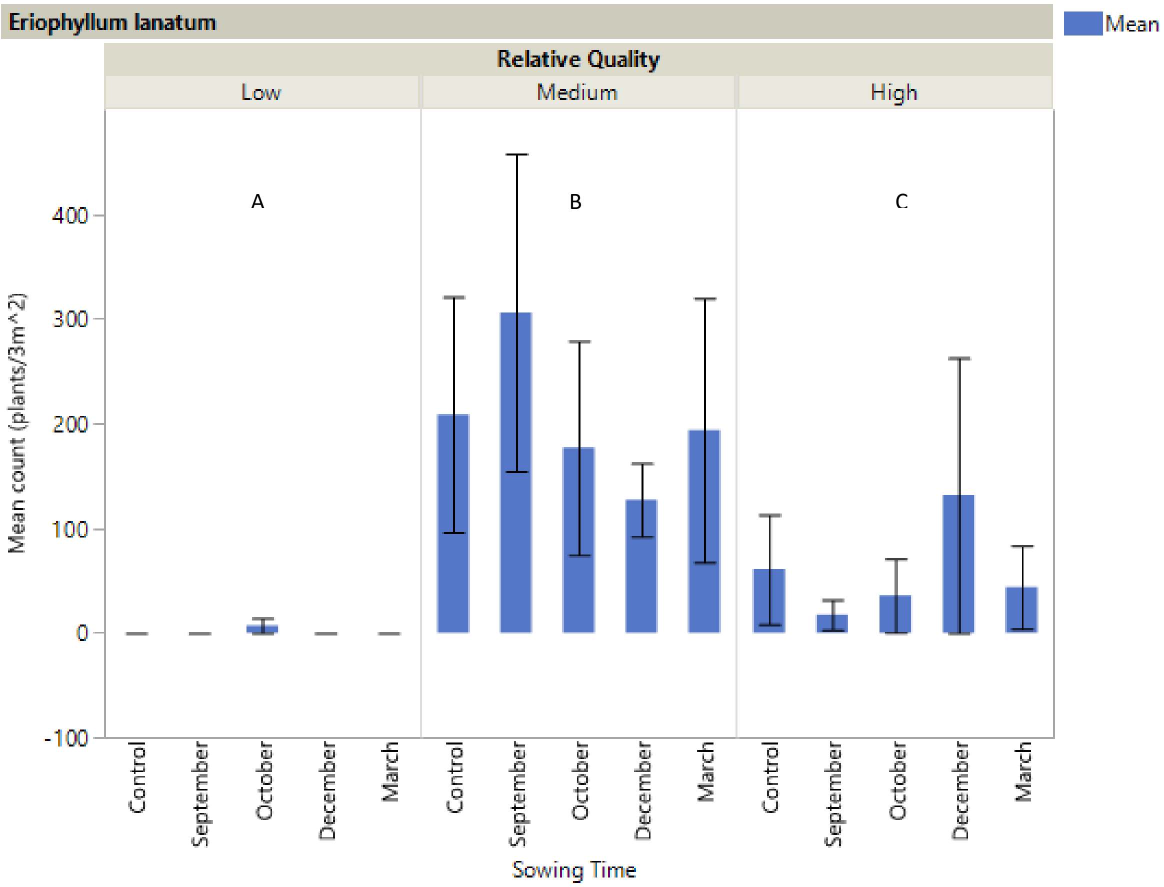

Figure 12: *Eriophyllum lanatum* results

Different letters (A, B, C, etc.) indicate that each relative quality is significantly different from one another (α = 0.05). Letters that are shared between two relative qualities indicate that they are not significantly different from one another. Error bars represent standard error.

Ranunculus occidentalis, commonly known as western buttercup, was not influenced by seed sowing time ($p<0.29$), but was influenced by relative site quality ($p<0.01$). This species responded positively to both high and low quality sites rather than medium quality (Figure 13). Of the total 793 individual plants found, across all of the sowing times, the greatest number of plants were found in high quality (455) followed by low quality (258) and medium quality (80). This perennial forb is very common in SPS prairies and was found in all five sowing time treatments, including the control. Of the total 793 plants found across all relative prairie qualities, the most plants were found in the control (257) while the lowest count was found in March (85). The highest count is probably skewed due to a much higher on average count (119 plants) in one quadrat in one of the control plots within the low quality site. This exceptionally high density of *Ranunculus occidentalis* may be due to recording error during monitoring or due to the patchy distribution of the species.

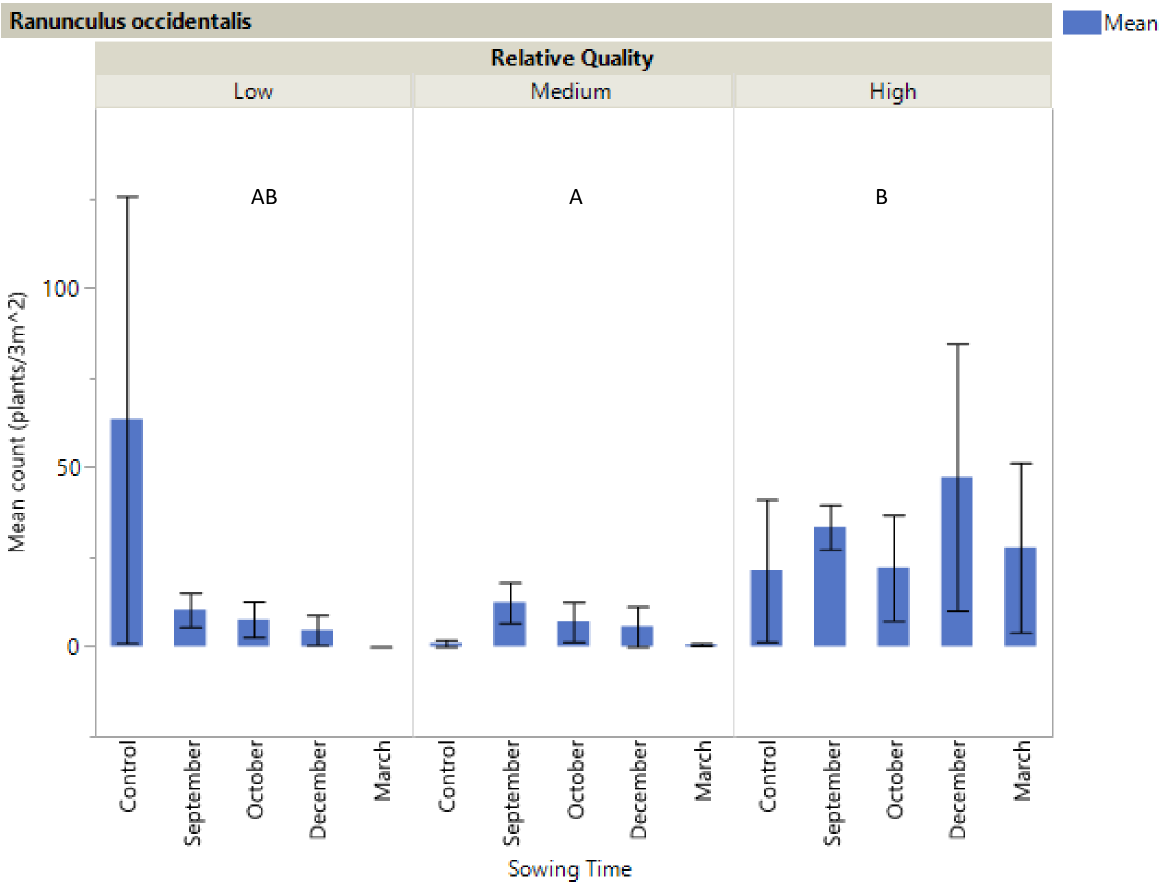

Figure 13: Ranunculus occidentalis results

Different letters (A, B, C, etc.) indicate that each relative quality is significantly different from one another ($\alpha = 0.05$). Letters that are shared between two relative qualities indicate that they are not significantly different from one another. Error bars represent standard error.

Species not significantly influenced by either sowing time or site quality

Koeleria macrantha, commonly known as prairie Junegrass, was not influenced by seed sowing time ($p<0.85$), but was initially influenced by relative site quality ($p< 0.02$). However, upon further investigation, Steel-Dwass all pairs test showed that none of the site qualities were actually different from each other (Figure 14). The means of low and medium qualities were very similar ($p=1.00$). The means of medium quality and high quality were not significantly different ($p=0.056$). Likewise, the means of low and high quality were not significantly different ($p=0.053$). While these results are not statistically significant they show a pattern that this species prefers or is found in higher quality prairie more than low quality prairie. Of 160 total plants found across all sowing times, most of them were found in high quality prairie (135), while fewer were found in medium (16) and low qualities (9). This perennial grass is a fairly common species in SPS prairies, and it was found across all five sowing time treatments, including the Control. Of the 160 total plants found across all relative prairie qualities, the most total plants were found in September (43) and the fewest total plants were found in March (7). Like many grasses, they are difficult to identify, especially when very small or when intermixed with other grass species, so the actual count of this species may be higher than what was found during monitoring.

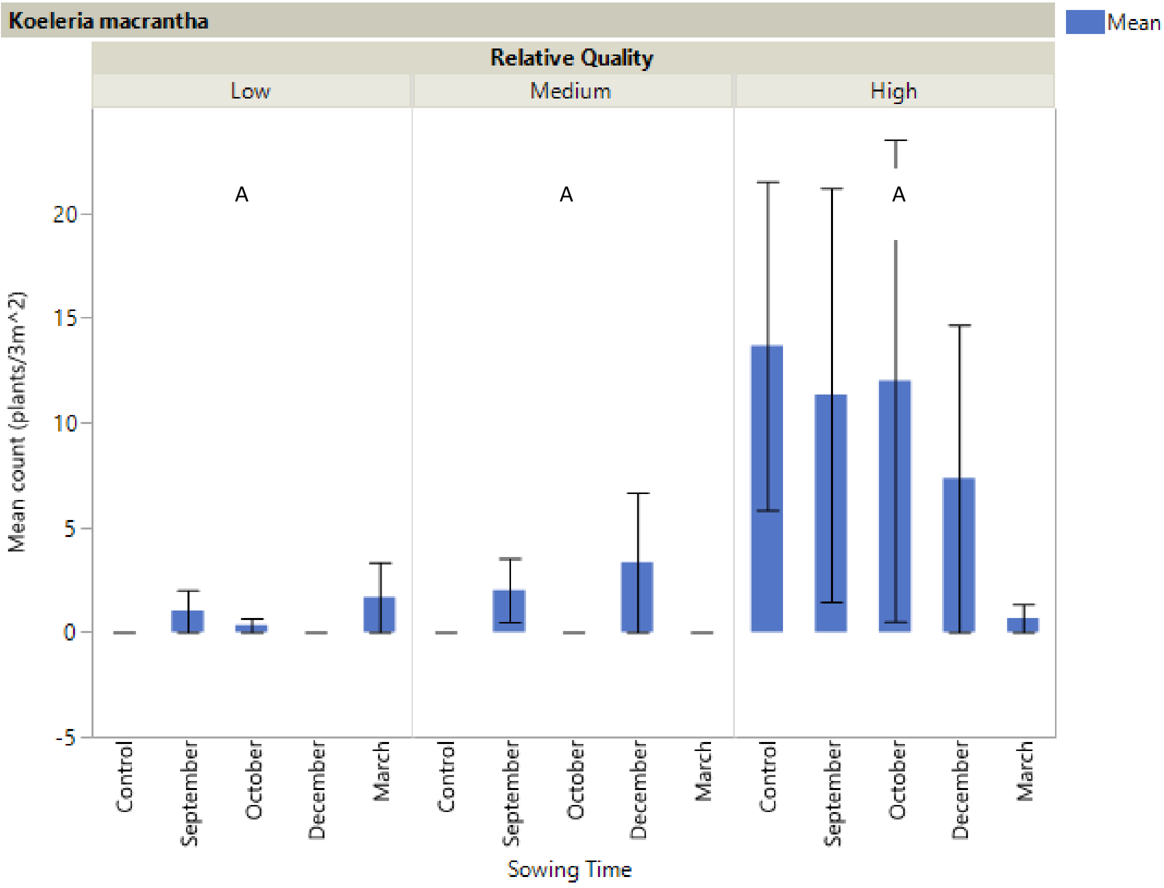

Figure 14: *Koeleria macrantha* results

Different letters (A, B, C, etc.) indicate that each relative quality is significantly different from one another ($\alpha = 0.05$). Letters that are shared between two relative qualities indicate that they are not significantly different from one another. Error bars represent standard error.

Cerastium arvense, commonly known as field chickweed, was not influenced by seed sowing time ($p<0.89$) or site quality ($p<0.18$). However, this fairly common perennial forb was found in all three site qualities and in all five time treatments, including the control (Figure 15). Of 47 total plants, 28 were found in medium quality, 16 were found in high quality, and three were found in low quality. The highest count of plants was found in December with 15 total plants and the lowest in the control with five plants. It reproduces by rhizomes as well as by seed, so the count of genetically distinct individual plants may be much lower.

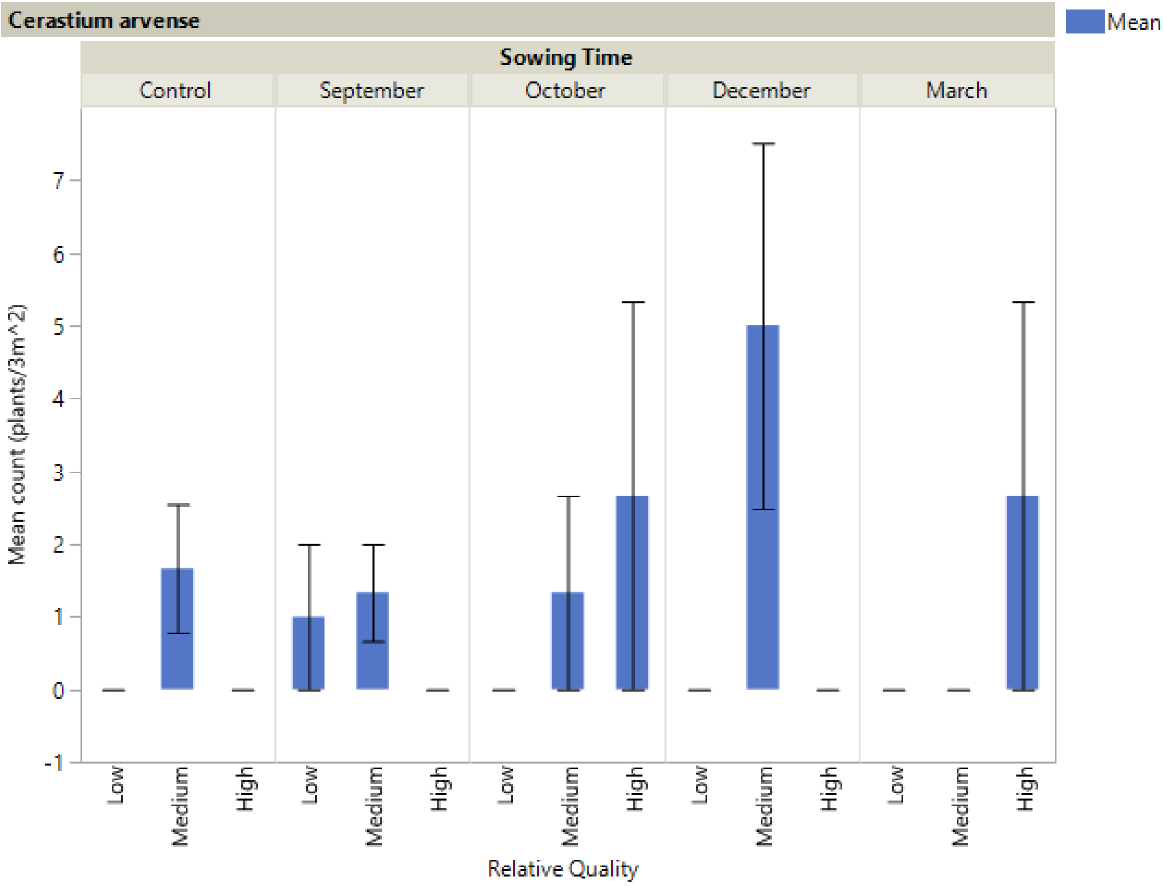

Figure 15: *Cerastium arvense* results

Species did not respond to either sowing time or relative prairie quality. Error bars represent standard error.

Festuca idahoensis subsp. *roemeri*, commonly known as Roemer's fescue, was not influenced by seed sowing time (p<0.63) or site quality (p<0.21). Of 4183 total plants, the highest number was found in the medium quality prairie (1782) followed by high quality (1376) and low quality (1025). *Festuca idahoensis* subsp. *roemeri* is the most common plant in SPS prairies, and was found high abundances in all five time treatments, including the control (Figure 16). The highest count of plants was observed in March (1139), and the lowest in December (616). Identifying individual plants can be challenging in areas that were recently burned. Often the plant will re-sprout along the outside edges of the original bunch only, thus it will look like many small plants when in reality it is sourced from one large plant, which could have affected the count data for this species.

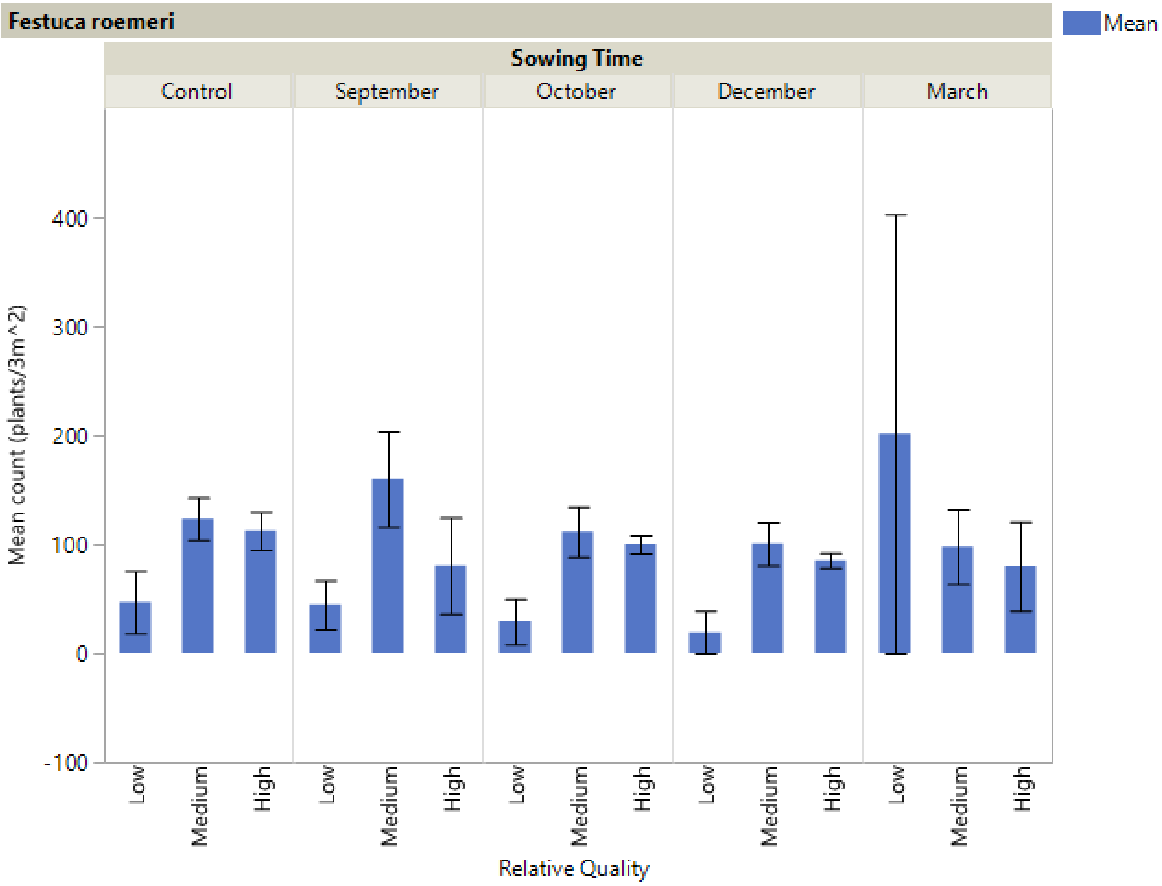

Figure 16: *Festuca idahoense* subsp. *roemeri* results

Species did not respond to either sowing time or relative prairie quality. Error bars represent standard error.

Microseris laciniata, commonly known as cutleaf silverpuffs, was not influenced by seed sowing time (p<0.77) or relative site quality (p<0.82). This is a fairly common perennial forb in SPS prairies, and was found in all 5 of the sowing time treatments, and in high and medium quality but not in low quality prairie (Figure 17). Of 191 total plants more than twice as many were found in high quality (129) than medium quality (62). The highest total count was found in September (63) and the lowest in March (19).

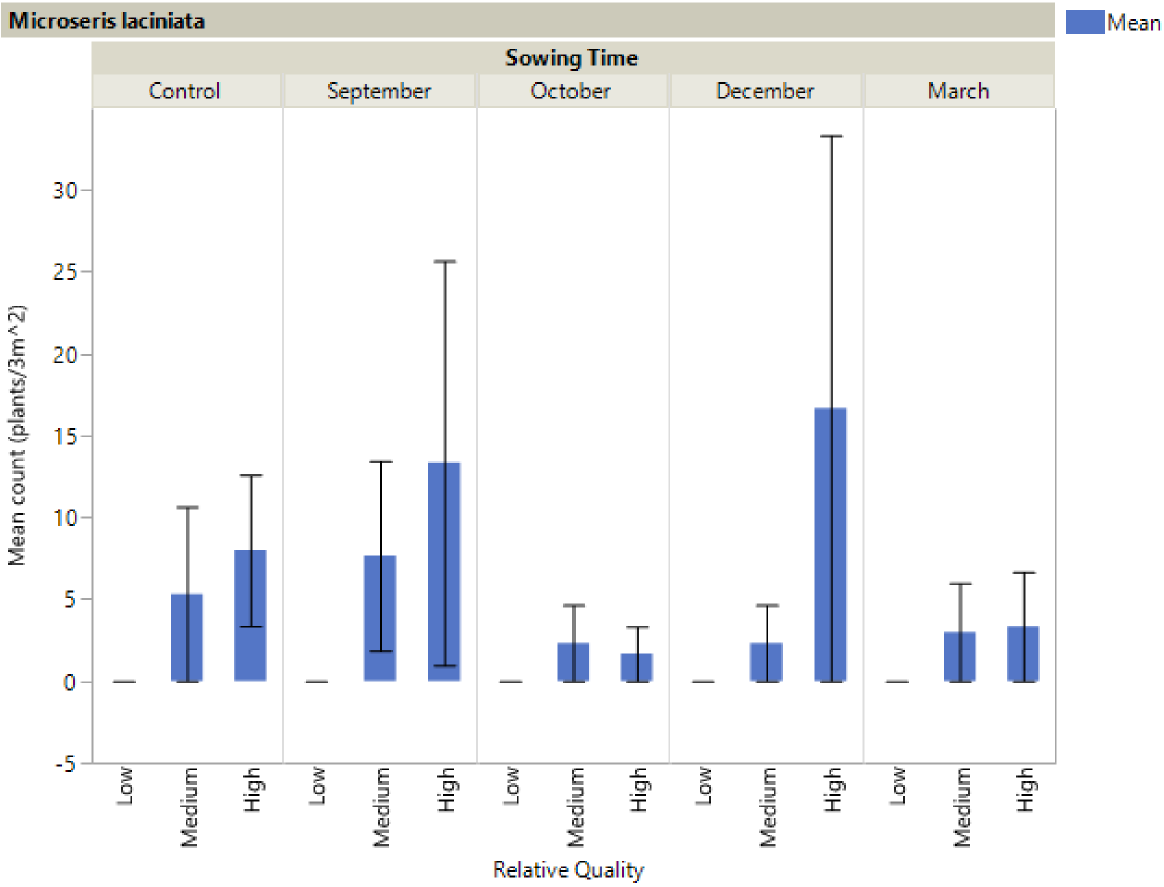

Figure 17: *Microseris laciniata* results

Species did not respond to either sowing time or relative prairie quality. Error bars represent standard error.

Sericocarpus rigidus, commonly known as white-topped aster, was not influenced by seed sowing time (p<0.71) or relative site quality (p<0.65). This perennial forb is common in SPS prairies and was found in all five sowing treatments, including the control, as well as across all three site conditions (Figure 18). Of 2483 total plants, the highest count was found in the medium quality (1225) followed by high quality (784) and low quality (474). The highest counts were found in December (854) and the lowest were found in September (150). It reproduces by rhizomes as well as by seed, so the count of genetically distinct individual plants may be much lower.

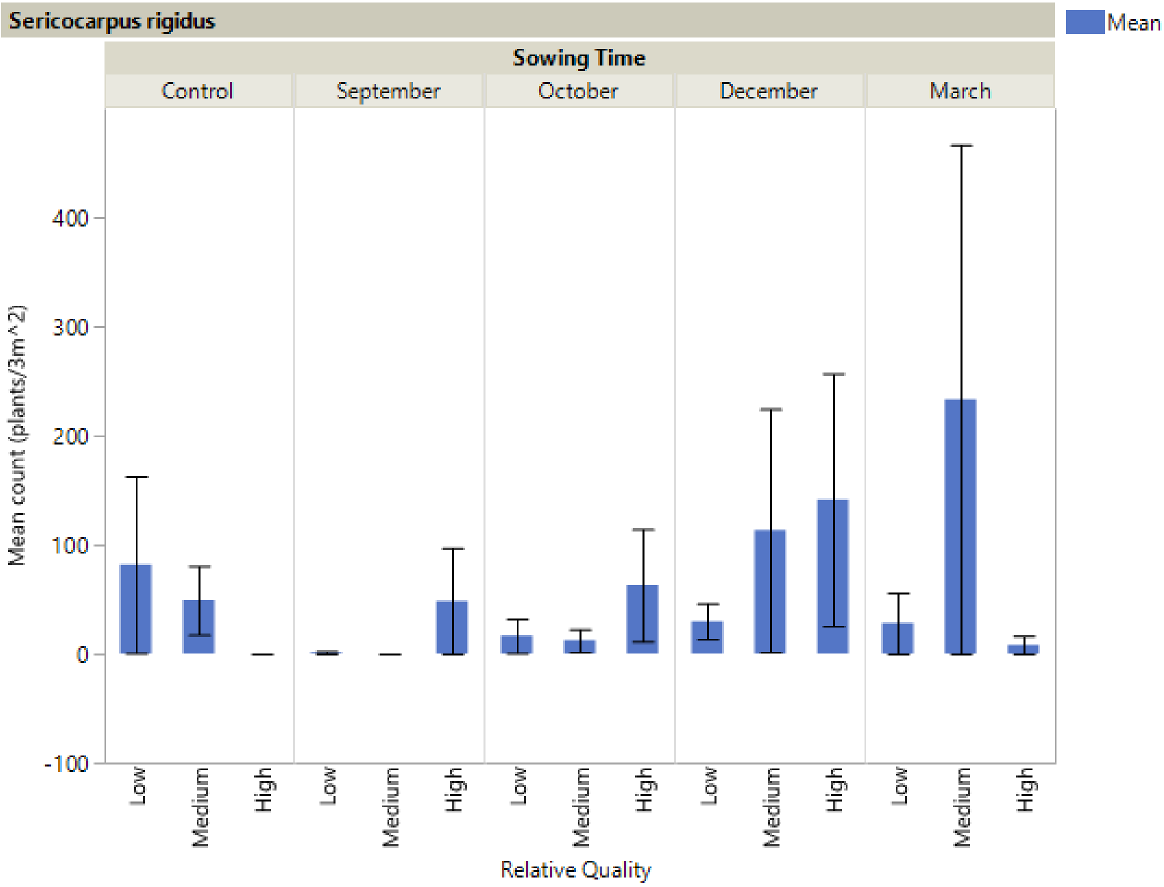

Figure 18: *Sericocarpus rigidus* results

Species did not respond to either sowing time or relative prairie quality. Error bars represent standard error.

Species excluded from analysis due to low abundance

Balsamorhiza deltoidea, commonly known as deltoid balsamroot, was found in very low quantities: a total of eight plants were found. This plant is relatively rare in the SPS prairies, but seedlings were found across all three prairie qualities. Due to low sample size this species was excluded from analysis, but it is interesting that all eight seedlings encountered were in September seeding time treatments (Figure 19). No seedlings were found in October, December, March, or Control plots.

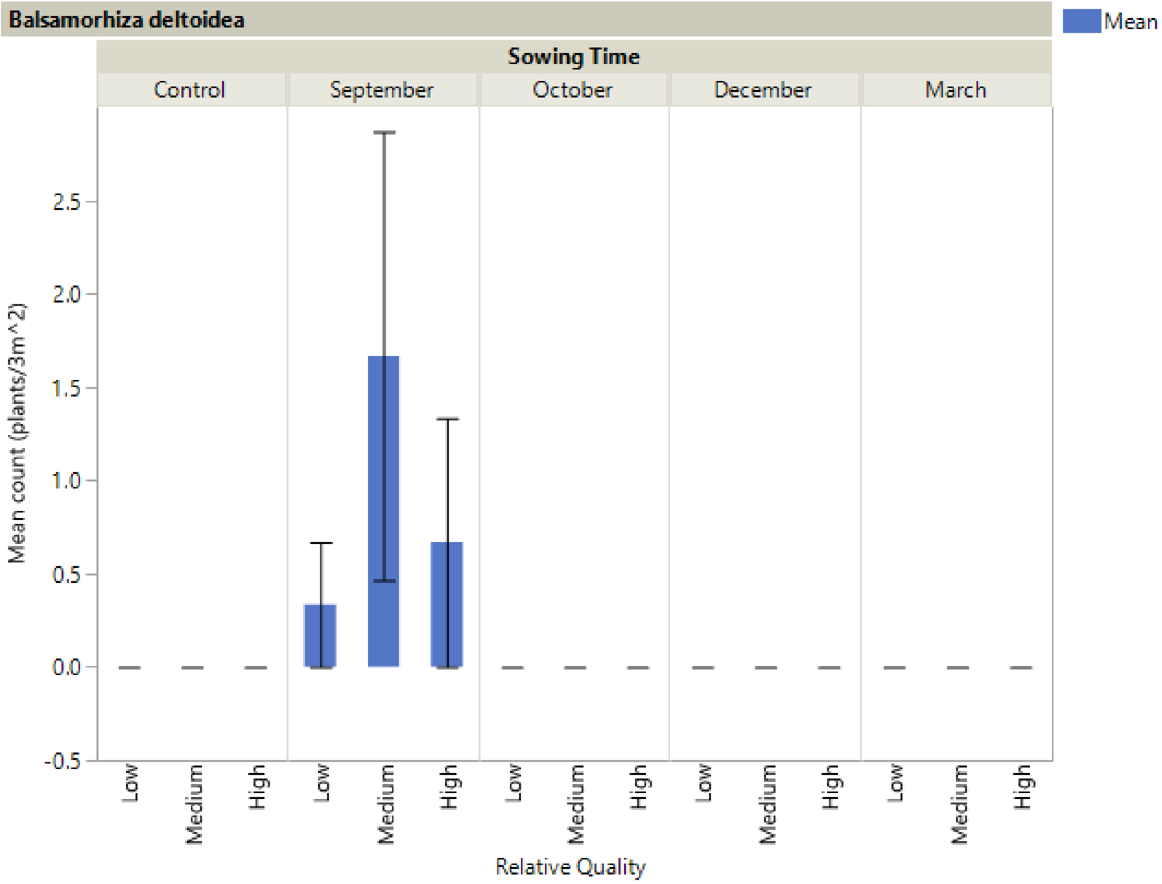

Figure 19: *Balsamorhiza deltoidea* results

Species was excluded from generalized regression analysis due to low abundance. Error bars represent standard error.

Clarkia amoena, commonly known as farewell to spring, was found in very low quantities: a total of six individuals were found. Due to low sample size this species was excluded from analysis. This annual forb is very rare in SPS prairies, and was likely extirpated from some areas. Plants were found in only medium (1) and low qualities (5). No plants were found in high quality site conditions. Interestingly, of the six total plants, four were found in September plots, and two were found in October plots. No plants were found in December, March, or Control plots (Figure 20*Figure 20*).

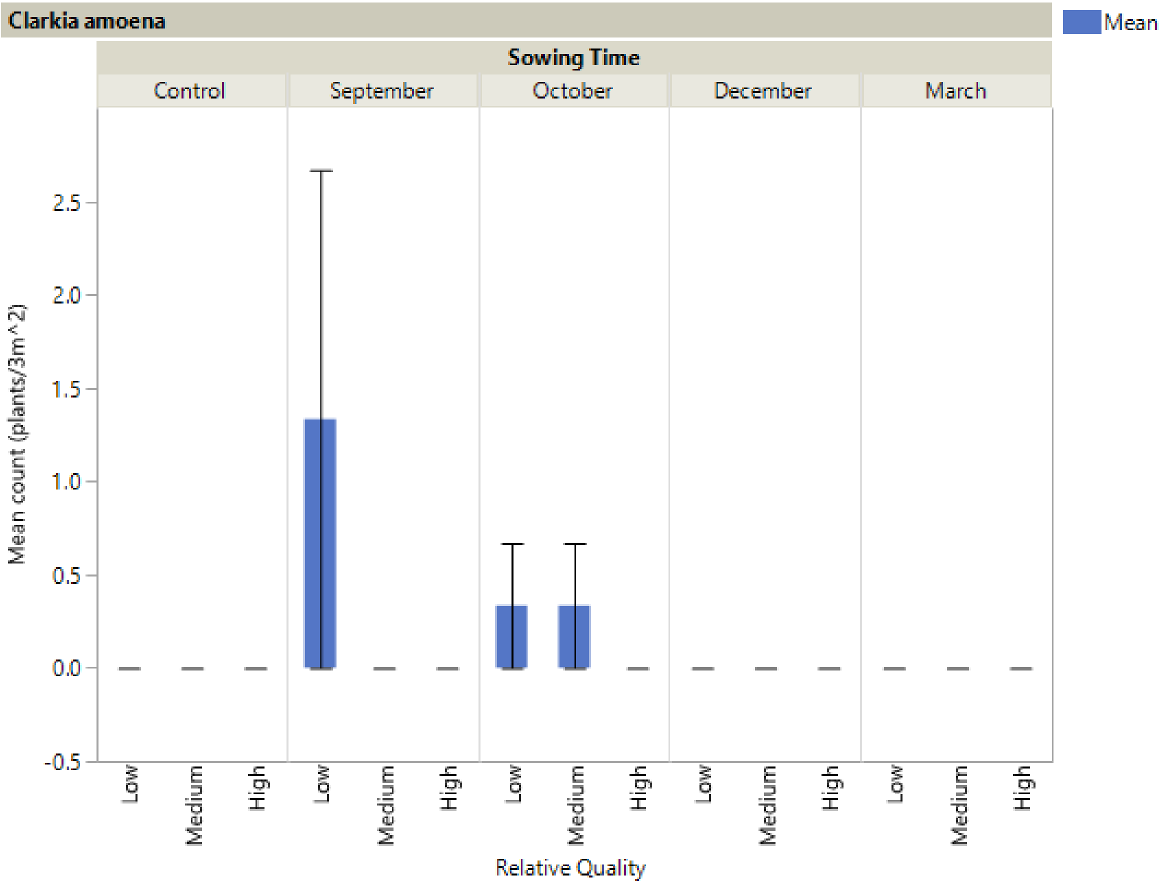

Figure 20: *Clarkia amoena* results

Species was excluded from generalized regression analysis due to low abundance. Error bars represent standard error.

Lomatium utriculatum, commonly known as spring gold or common lomatium, was found in very low quantities: a total of 16 individuals were found. Due to low sample size this species was excluded from analysis. This perennial forb is very common in SPS prairies, but interestingly was not found in low quality prairie, or in the control plots across any of the three site conditions (Figure 21). Of the 16 total plants, nine of them were found in high quality, and seven were found in medium quality. Half of the plants were found in the September sowing time treatment, while only one plant was found in December treatment plots.

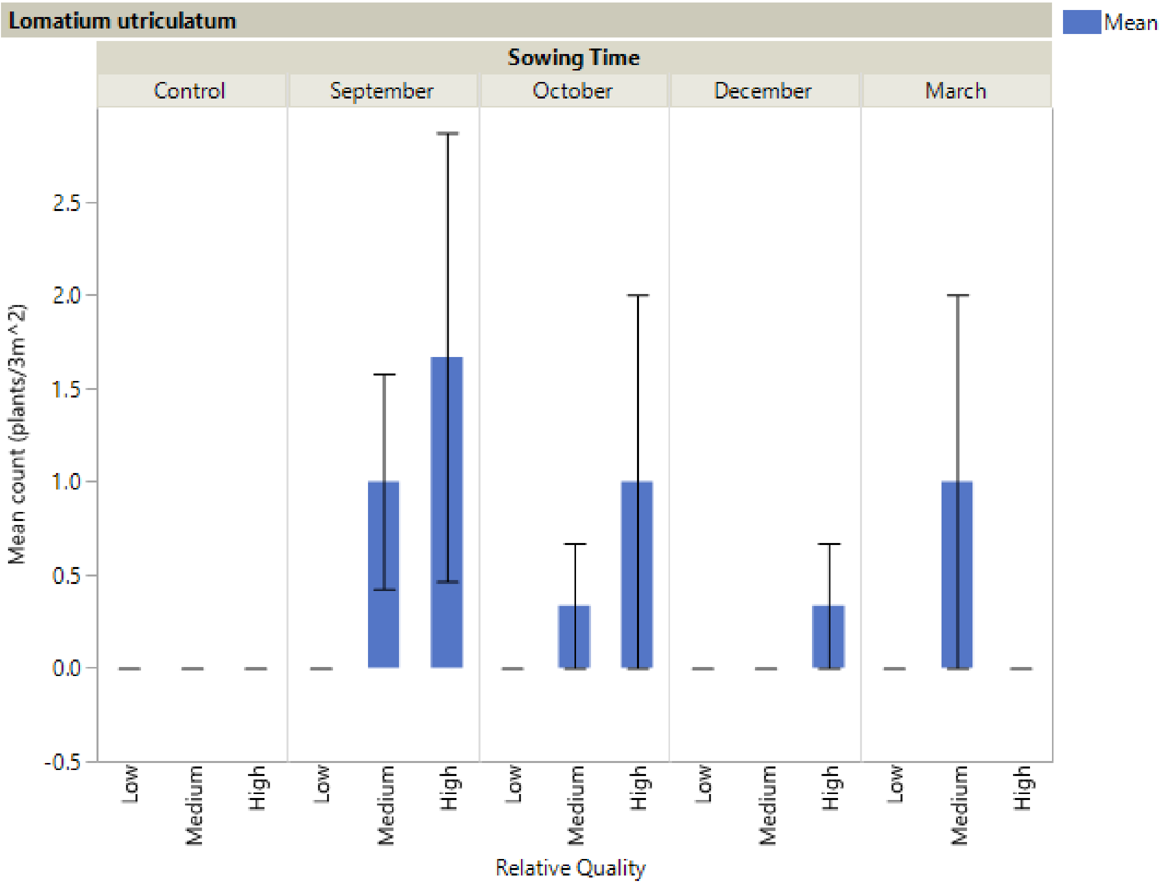

Figure 21: *Lomatium utriculatum* results

Species was excluded from generalized regression analysis due to low abundance. Error bars represent standard error.

Potentilla gracilis, commonly known as slender cinquefoil, was found in very low quantities, with a total of 20 individuals. This species was excluded from analysis. This plant is fairly common in SPS prairies, but it was not found in the control plots, or in September or March (Figure 22). It was mostly found in October (17) and a few in December (3). It was not found in the low quality site, but was found in the medium quality (15) and high quality (5).

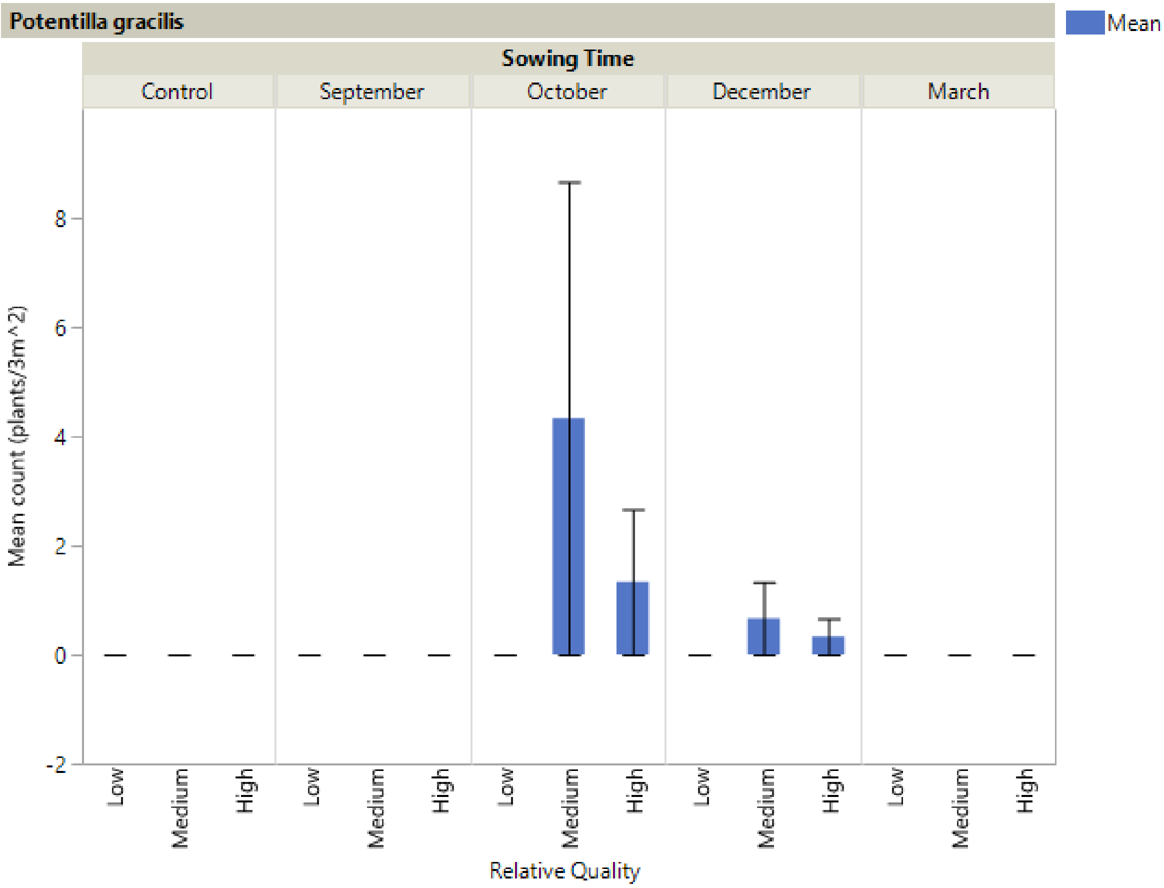

Figure 22: Potentilla gracilis results

Species was excluded from generalized regression analysis due to low abundance. Error bars represent standard error.

Sisyrinchium idahoense, commonly known as Idaho blue-eyed grass, was found in very low quantities, with a total of 18 individuals. This perennial forb was excluded from analysis. This plant is rare in SPS prairies, and was not found in the control plots. Most of them were found in December (17) and one in October. All 18 plants were found in the high quality site, and none were found in the medium or low quality sites (Figure 23). This forb it looks very much like a grass before it flowers, so small individuals or individuals intermixed with grass species may have been overlooked. The actual count of this species may be higher than results presented here.

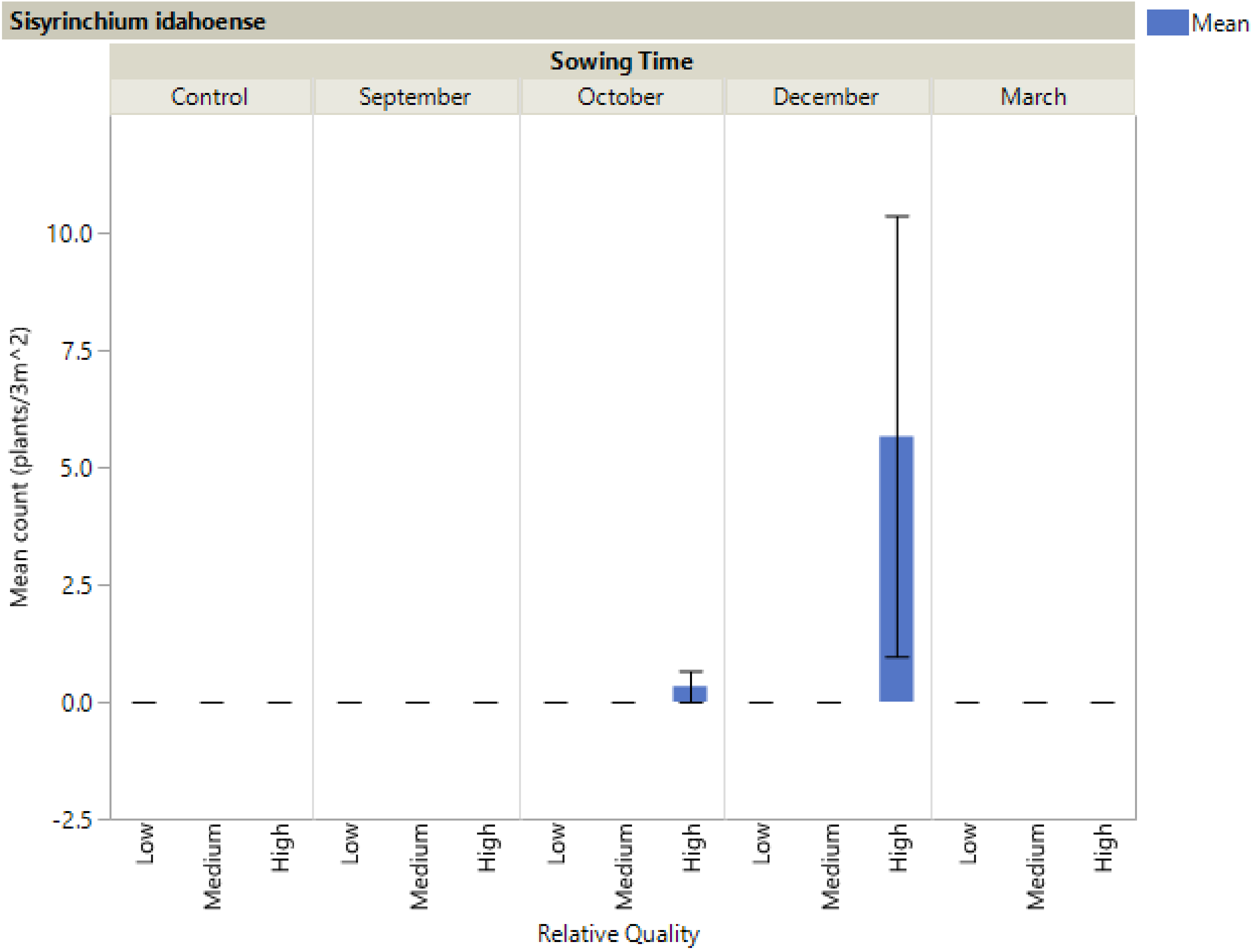

Figure 23: *Sisyrinchium idahoense* results

Species was excluded from generalized regression analysis due to low abundance. Error bars represent standard error.

Species not encountered

Armeria maritima, commonly known as sea thrift or sea pink, was not found in any treatment plot in any of the site conditions. This plant is very rare in SPS prairies and was likely extirpated from some areas.

Erigeron speciosus, commonly known as aspen fleabane, is notoriously difficult to identify, and was excluded from analysis. This plant is very rare in SPS prairies and was likely extirpated from some areas.

Solidago simplex, commonly known as sticky goldenrod, or Mt. Albert goldenrod, was not found in any treatment plot in any of the site conditions. This plant is very rare in SPS prairies and was likely extirpated from some areas.

Viola adunca, commonly known as early blue violet or other names, was not found in any treatment plot in any of the site conditions. This plant is fairly common in SPS prairies, and was likely extirpated from some areas. In the past the viability of the seeds of this species has been highly variable due to a combination of improper drying and storage techniques as well as some natural variability.

DISCUSSION

While sowing time and relative prairie quality affected a few species, many other factors may have influenced these results, such as precipitation, seed distribution, seed-soil contact, dormancy, predation, seedling death prior to monitoring, or other factors. Despite the complexity of these interactions I feel confident in these experiments results. Restoration ecology is a messy science, full of unexpected surprises and complicated natural phenomena. The lessons learned in this experiment are worthwhile, and it demonstrates the kinds of interesting questions and patterns that can be observed in a relatively simple experiment. This experiment also serves as a pilot project for future studies on these practical questions of when and where seeds should be sown in order to achieve the greatest restoration success.

Community response

The community of sown species showed some interesting trends. The total plot diversity was highest for September sowing in high quality prairie, H’=2.05. The lowest Shannon-Weiner diversity index number was found in March treatment in medium quality prairie at H’= 0.18. Low diversity in March suggests that raking may be having some negative impacts on the existing native vegetation, or that the seeds did not germinate. Continued monitoring of this experiment may be able to determine if December or March sown seeds do better the following year, resulting in delay in diversity. General trends shown by the Shannon’s diversity index indicate that fall sowing is better than winter or spring sowing, and the overall diversity of the prairies, despite their relative qualities, increases with seed addition, compared to the unsown controls.

In response to the practical question (*Does temporal variation of seed sowing affect the first year establishment of 23 native prairie species across a gradient of prairie quality?),* I hypothesized that sowing time and relative prairie quality would affect the establishment of these species. The Shannon’s diversity index results support this hypothesis, showing that both sowing time and relative prairie quality increase native community diversity. As expected, this research shows that seed addition generally overcomes the dispersal/seed limitation. This finding agrees with the findings of Stanley et al. (2008, 2011). This research suggests that fall sowing and higher relative quality prairie tends to result in higher richness and abundance of native plants than winter or spring sowing or medium and low qualities.

Individual species response

When considered individually, the sown species demonstrated an incredible amount of variability. Some species responded to sowing time, others to site condition, and some were not affected by either treatment. No plant responded to both sowing time and site conditions ($\alpha = 0.05$). In response to the theoretical question (*To what degree is plant community assembly driven by neutral or niche processes?),* I hypothesized that both neutral and niche processes are acting upon these plants. In order to study community assembly theory I used seed sowing time as a proxy for priority effects, which is a mechanism of neutral theory, and relative prairie quality as a proxy for ecological filtering, which is a mechanism of niche theory. The individual species responses do not support my hypothesis that both neutral and niche processes are influencing community assembly. Several species were excluded from the generalized regression analysis due to low abundance. Species that were not influence by any treatment or were excluded due to low abundance, or were not encountered all support the hypothesis is that none of the species respond to either the sowing time treatments or the relative site qualities.

Sowing time

If priority effects were the most influential mechanism driving community assemblage, one would expect species to respond more positively to sowing time, rather than to any of the relative site qualities. Specifically, I hypothesize that the earlier the arrival time, the better a species chances of survival would be. Based on this neutral theory of community assemblage September should have the highest count of plants, followed by October, December, March, and finally the control. *Plectritis congesta* was the only tested species that responded to seeding time entirely as I had hypothesized. Additionally two species which were excluded from analysis due to low abundance, *Balsamorhiza deltoidea* and *Clarkia amoena* showed similar patterns of positive response to September sowing. Two species, *Collinsia* spp. and *Lupinus albicaulis* showed partial support for my hypothesis that early seed sowing times would result in higher establishment, as they responded positively to both September *and* October sowing times. For the theoretical question the null hypothesis stated no difference in the mean counts of plants in any sowing time treatment, thus the count of plants found in any of the treatments would not be different from one another. *Lupinus bicolor* performed well in every sowing time treatment except the control, which supports the null hypothesis, although still demonstrates that this species is dispersal/seed limited.

Generally speaking, the species that responded to variation in sowing time preferred earlier fall sowings (September and October) over later sowings (December and March). Three of the four species that responded to the fall sowing were annual forbs (*Collinsia* spp., *Lupinus* *bicolor*, and *Plectritis congesta*) suggesting that annual prairie species would benefit from fall sowing in restoration sites. *Lupinus albicaulis*, a perennial forb, also responded to earlier sowing times; this result suggests that earlier sowing times may be beneficial for other perennial forbs as well, though more research is needed. This research also does not take into consideration the health, longevity, or size of the seedlings found in each of the sowing time treatments, though typically fall sown plants seemed more robust (author's personal observation).

Relative Quality

If ecological filtering is the most influential mechanism driving community assemblage, one would expect species to respond more positively to the relative prairie quality, rather than to any of the sowing times. The high, medium, and low relative prairie qualities are proxies for biotic and abiotic site conditions. Specifically, I hypothesized that the higher quality the site, the higher the native species establishment. Based on this niche theory of community assemblage, the high quality site should have the highest count of plants, followed by the medium quality site, and finally the low quality site. Two of the four species that responded to site quality, *Achillea millefolium* and *Danthonia californica*, performed best in high or medium quality prairie. These two species partially support my hypothesis that higher quality prairie will have higher establishment. The null hypothesis would be that there is no difference in the mean counts of plants in any relative prairie quality, thus the count of plants found in any of site conditions would not be different from another. One of the four species, *Eriophyllum lanatum*, had the highest mean count of plants in medium quality. This species does not necessarily support my hypothesis that the higher quality prairie would have higher first year establishment rates. The cause of this phenomenon may be partially due to the protocol for counting this species. Since *E. lanatum* is rhizomatous, stems were counted as a proxy for plants, while the actual genetically unique number of plants is likely much lower than represented in this research, though it is difficult to tell for sure without destructive sampling techniques. The fourth and final species that responded to relative prairie quality, *Ranunculus occidentalis*, performed well in both high and low quality prairies but less so in medium quality prairie. This species does not necessarily support my hypothesis that higher quality prairie would result in higher establishment rates. The causes of this phenomenon are unknown, but perhaps that microsite conditions were not favorable, or some influence of pre-existing plants/seeds influence this result. In the future, preliminary site monitoring could help de-tangle all of the background noise caused by pre-existing species, though it would still be difficult to know that this common plant was not present in the seedbank.

Generally speaking, the species that responded to site conditions seemed to prefer better site conditions (medium or high quality) rather than poor site conditions (low quality). No species responded solely to relatively low quality prairie, which is unfortunate for the restoration of badly degraded sites. Three perennial forbs (*Achillea millefolium*, *Eriophyllum lanatum*, and *Ranunculus occidentalis*) and one perennial grass (*Danthonia californica*) responded to site conditions. However, it is difficult to attribute these trends entirely to causation and not correlation. Was the site considered high quality because these species were present there, or were the seeded species actually responding to some element of the high quality? Further research could better answer this question.

Some of the five species that were excluded from the generalized regression analysis due to low abundances showed patterns of response to relative prairie quality. I had hypothesized that higher quality prairie would result in higher establishment rates. One species, *Sisyrinchium idahoense* was only found in high quality prairie, which supports this hypothesis. Two other species, *Lomatium utriculatum* and *Potentilla gracilis*, show partial support for this hypothesis, as they were found in only high and medium quality prairie. It is unclear if the results for these three species were due to the seeding treatments or they were already present prior to this experiment. Regardless, these three species either show preference for high quality prairie, or they are more persistent in higher quality sites. Another species, *Balsamorhiza deltoidea*, showed a small amount of support for my hypothesis: of eight individual seedlings found, five of them were in medium quality prairie, two in high quality prairie, and one in low quality prairie. While this is much too small of a sample size to say anything definitively about the condition preferences for *Balsamorhiza deltoidea*, continued monitoring of these long-lived individuals could shed some light on the patterns. Another species, *Clarkia amoena,* supported the null hypothesis. Of six individual plants found, five were in low quality, one in medium quality, and zero in high quality. A larger sample size is need to determine if this is an actual effect, or due to random chance. More research is need on the species that were found in low abundances in order to determine if they truly support the hypotheses.

Suggestions for future research

Some of the species used in this research are common in SPS prairies, or are patchily distributed. This makes interpretation of results difficult, especially when species are found in the control plots or in higher abundances that are possible due to seeding rate. Increasing the seeding rate and selecting sites with few native species could be potential strategies for separating causation from correlation. Alternatively, monitoring the plot areas a year prior to sowing, selecting species that don't occur in or nearby the plot area, and adding more replicates could be ways to improve an experiment similar to this one. In addition, increasing the monitoring effort to include more samples, or monitoring at several times throughout the growing season could help with identification of seedlings, and identifying any species that sprout and then die/senesce early in the season. Removal of dominant grasses has been shown to increase forb productivity, cover, and species richness (McCain, Baer, Blair, & Wilson, 2010). Use of grass-specific herbicide to control non-native grasses should be considered for future experiments.

Native species may have unique germination and establishment limitations that were not examined here. These limitations could explain low abundance or complete absence of some species. Seed predation is another factor that this experiment did not take into consideration, which could be a very important variable. For example, rodent predation of *Viola adunca* seeds impacted production at native seed nurseries (Angela Winter, CNLM, personal communications, May 2016), though impacts of rodent predation in the field is unknown. Greenhouse studies with these or similar species could be useful to tease apart these variables, though controlled field studies may be more immediately practicable.

Future research on these plots could help us understand if first-year establishment of these species results in successful prairie restoration. Additionally, future research could shed light on the persistence of multiple generations of annual species. Many annual species have been largely extirpated from the SPS prairies (Dunwiddie et al., 2014), so understanding where and how to re-introduce them should be a high priority of restoration in this area. Presumably, the seed addition in this experiment could have contributed to the soil seedbank, which could increase establishment in subsequent years, under the right conditions. For instance the seeds sown in March could positively respond after a year of natural stratification, and establish in the spring of the second year.

CONCLUSION

Of the four species that responded positively to sowing time, three support the idea of priority effects, and therefore, the theory of neutral assemblage. These three species are *Collinsia* spp., *Lupinus albicaulis*, and *Plectritis congesta*. For these three species, the earlier sowing times result in higher establishment rates. On the other hand, three of the four species that responded positively to relative prairie quality support the idea of ecological filtering. These three species are *Achillea millefolium, Danthonia californica,* and *Ranunculus occidentalis*. For these three species the higher quality biotic and abiotic conditions of site influenced the establishment rates. Other species that responded positively to site conditions support the idea of ecological filtering, and therefore the theory of niche assemblage. While six species showed some amount of support for either neutral or niche theories, no species supported both theories. The remaining sixteen species did not support these theories, had no measurable response, were found in too low of numbers, or were not found at all. Therefore, it is difficult to draw conclusions about the relative influence of neutral and niche processes for the native plant community as a whole. It is interesting that only one species (*Lupinus albicaulis*) initially showed support for both theories, but upon further investigation only supported priority effects theory. Intuitively, one would expect that both neutral and niche theory are both acting upon community assembly and are not mutually exclusive. However, this study's results indicate that these two theories do not overlap as much as previously assumed, at least for the few species tested. Further testing of the relative importance of these theories in restoration ecology is warranted.

This research demonstrates some of the challenges in ecological studies, especially those due to variability in species responses. There is still a lot to learn about restoration, and how to harness natural processes to help meet restoration goals. It remains difficult to get native prairie plants to establish through direct seeding. While a cost-benefit analysis is outside the scope of this project, future studies could investigate the long-term cost of direct seed sowing, plug planting, or other methods. This research suggests that SPS prairies are native seed limited, corroborating the findings of Stanley et al. (2011). Adding seeds of native species increased the diversity in all three relative qualities of prairie, relative to the unseeded control plots. Interestingly, even the Upper Weir site, which was the highest quality tested in this study, showed an increase in diversity after seed sowing. Other studies have found that the most species rich locations are more resistant to invasion (Naeem et al., 2000; Tilman, 1997; Tilman et al., 2014), thus seed addition of native or non-native species to a species-rich site should not show an increase in diversity. On a positive note, many species were found in the control plots, suggesting higher than anticipated native richness, despite obvious non-native cover.

A one size fits all approach to restoration is more likely to fail than a carefully planned restoration project that is tailored to fit the site conditions. That is to say, sowing seed at the right time in the right place will have a positive effect on the species. It is difficult to pinpoint the optimal time and conditions for each unique species. In total, there were over 13,000 individual plants counted in this research. It is difficult to unpack all of the patterns of 23 different species amongst the complexity of the natural world. There is still a lot to be learned about how to do prairie restoration well, and how to do it more efficiently. This research demonstrates that, among other things, first year establishment rates of native prairie plants are typically very low, and that there is a lot of room for improvement. However, the patterns seen here for several species can provide guidance for managers when deciding when and where to sow particular species to meet restoration goals. This research also attempts to bridge the gap between practical and theoretical research in restoration ecology. These results indicate a few species that support either niche theory or neutral theory, but not necessarily both theories, though more research is needed. There is a synergistic relationship between practical and theoretical fields of study that could lead to important scientific discoveries in the future.

PRACTICAL RECOMMENDATIONS

1. Sow seeds of native prairie species (especially annuals forbs) as soon as possible after sites have been prepared in the summer or fall. More closely aligning restoration sowing with natural seed dispersal times could improve native plant establishment. Priority effects can be used to favor native species, and help them compete with non-native species. Four out of five tested annual forb species responded positively to sowing time, so for these species sowing time is especially important. One perennial forb, *Lupinus albicaulis,* also responded positively to earlier sowing times. If sowing seeds is not logistically possible until late fall or winter, consider storing seeds until the following summer or fall, and then seeding into newly prepared sites.
2. Sow species in sites where they are known to occur in low abundance, or were historically known to occur. Persistence of a species in a given site suggests that the biotic and abiotic site conditions are favorable for growth and persistence. The relative prairie quality had a significant influence on three perennial forbs and one perennial grass, though it is difficult to determine if the seed addition was the true cause of these species' establishment.

3. Try sowing common species, or less expensive seeds, in low quality sites, and/or be prepared for more intensive follow up work after the initial seeding. Consider using herbicides to help control non-native pasture grasses and other invasive species, and mitigate low establishment rates by increasing the seeding rates, if possible.
4. Sow rare species, which are typically more expensive, in medium and high quality sites only. Consider targeting areas of bare ground or lightly disturbed soil to improve seed-soil contact, which could help increase establishment rates. Even the relatively high quality prairie showed an increase in overall species diversity after fall sowing, suggesting that there is seed limitation present in relatively healthy prairie.
5. This research suggests sowing seeds at a higher rate than currently prescribed is warranted, though it is difficult to predict long-term restoration success from first year results. Generally speaking, over half of the species used in this study had 0-5% establishment rates. Consider using both plugs and direct seeding in restoration efforts. Repeated monitoring of this and other restoration projects will shed some light on the long-term success of restoration using direct seeding techniques.

Bibliography

Agee, J. K. (1996). Achieving conservation biology objectives with fire in the Pacific Northwest. *Weed Technology*, *10*(2), 417–421.

Amoroso, N., & Chalcraft, D. R. (2015). Duration of colonization and interactions between early and late colonists determine the effects of patch colonization history on patch biodiversity. *Oikos*, *124*(10), 1317–1326. http://doi.org/10.1111/oik.01922

Bakker, J. D., Colasurdo, L. B., & Evans, J. R. (2012). Enhancing Garry oak seedling performance in a semiarid environment. *Northwest Science*, *86*(4), 300–309. http://doi.org/10.3955/046.086.0406

Bakker, J. D., Wilson, S. D., Christian, J. M., Li, X., Ambrose, L. G., & Waddington, J. (2003). Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*, *13*(1), 137–153. http://doi.org/10.1890/1051-0761(2003)013[0137:COGROY]2.0.CO;2

Baskin, C. C. & Baskin, J. M. (1998). Seeds: ecology biogeography, and evolution of dormancy and germination. 1st Edition. San Diego (CA): Academic Press. 666p.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. (2008). Generalized linear mixed models: a practical guide for ecology and evolution, (Table 1). http://doi.org/10.1016/j.tree.2008.10.008

Brye, K. R., Norman, J. M., & Gower, S. T. (2002). Assessing the progress of a tallgrass prairie restoration in Southern Wisconsin. *The American Midland Naturalist*, *148*(2), 218–235. http://doi.org/10.1674/0003-0031(2002)148[0218:ATPOAT]2.0.CO;2

Bullock, J. M., Pywell, R. F., & Walker, K. J. (2007). Long-term enhancement of agricultural production by restoration of biodiversity. *Journal of Applied Ecology*, *44*(1), 6–12. http://doi.org/10.1111/j.1365-2664.2006.01252.x

Burton, C. M., Burton, P. J., Hebda, R., & Turner, N. J. (2006). Determining the optimal sowing density for a mixture of native plants used to revegetate degraded ecosystems. *Restoration Ecology*, *14*(3), 379–390. http://doi.org/10.1111/j.1526-100X.2006.00146.x

Cairns, J., & Heckman, J. R. (1996). Restoration ecology: the state of an emerging field. *Annual Review of Energy and the Environment*, *21*(1), 167–189. http://doi.org/10.1146/annurev.energy.21.1.167

Carter, D. L., & Blair, J.M. (2011). Recovery of native plant community characteristics on a chronosequence of restored prairies seeded into pasture in west-central Iowa. *Restoration Ecology, 20*(2), 170 – 179.

Chase, J. M. (2003). Community assembly: When should history matter? *Oecologia, 136*(4), 489–498. http://doi.org/10.1007/s00442-003-1311-7

Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(44), 17430–17434. http://doi.org/10.1073/pnas.0704350104

Chase, J. M., & Leibold, M. A. (2003). Ecological niches: Linking classical and contemporary approaches. Chicago, IL: University of Chicago Press.

Clark, A. C. J., Poulsen, J. R., Levey, D. J., & Osenberg, C. W. (2007). Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Midland Naturalist*, *170*(1), 128–142. http://doi.org/10.1086/518565

Clark, D. L., & Wilson, M. V. (2003). Post-dispersal seed fates of four prairie species. *American Journal of Botany*, *90*(5), 730–735.

Clements, F. E. (1916). *Plant Succession. An Analysis of the Development of Vegetation*. Carnegie Institutue of Washington. http://doi.org/10.1126/science.45.1162.339

Connolly, S. R., MacNeil, M. A., Caley, M. J., Knowlton, N., Cripps, E., Hisano, M., Wilson, R. S. (2014). Commonness and rarity in the marine biosphere. *Proceedings of the National Academy of Sciences*, *111*(23), 8524–8529. http://doi.org/10.1073/pnas.1406664111

Delvin, E. G. (2013). Restoring abandoned agricultural lands in Puget lowland prairies: a new approach, 150.

Déri, E., Magura, T., Horváth, R., Kisfali, M., Ruff, G., Lengyel, S., & Tóthmérész, B. (2011). Measuring the short-term success of grassland restoration: the use of habitat affinity indices in ecological restoration. *Restoration Ecology*, *19*(4), 520–528. http://doi.org/10.1111/j.1526-100X.2009.00631.x

Diamond, J.M. (1975). Assembly of Species Communities. In M.L. Cody and J.M. Diamond (Eds.) *Ecology and Evolution of Communities* (342-444). Cambridge, MA: Harvard University Press.

Dickson, T. L., Hopwood, J. L., & Wilsey, B. J. (2012). Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. *Biological Invasions*, *14*(12), 2617–2624. http://doi.org/10.1007/s10530-012-0257-2

Doll, J. E., Brink, G. E., Cates, R. L. J., & Jackson, R. D. (2009). Effects of native grass restoration management on above- and belowground pasture production and forage quality. *Journal of Sustainable Agriculture*, *33*(5), 512–527. http://doi.org/10.1080/10440040902997702

Doll, J. E., Haubensak, K. A., Bouressa, E. L., & Jackson, R. D. (2011). Testing disturbance, seeding time, and soil amendments for establishing native warm-season grasses in non-native cool-season pasture. *Restoration Ecology*, *19*(101), 1–8. http://doi.org/10.1111/j.1526-100X.2010.00687.x

Drake, J. A. (1991). Community-Assembly Mechanics and the Structure of an Experimental Species Ensemble. *The American Naturalist*, *137*(1), 1–26.

Drake, D., Ewing, K., & Dunn, P. (1998). Techniques to promote germination of seed from Puget Sound prairies. *Ecological Restoration*, *16*(1), 33–40.

Dunwiddie, P., Alverson, E., Martin, R., & Gilbert, R. (2014). Annual species in native prairies of South Puget Sound, Washington. *Northwest Science*, *88*(2), 94–105. http://doi.org/10.3955/046.088.0205

Dunwiddie, P. W., & Bakker, J. D. (2011). The future of restoration and management of prairie-oak ecosystems in the Pacific Northwest. *Northwest Science*, *85*(2), 83–92. http://doi.org/10.3955/046.085.0201

Dunwiddie, P. W., & Martin, R. A. (2016). Microsites matter: Improving the success of rare species reintroductions. *Plos One*, *11*(3), e0150417. http://doi.org/10.1371/journal.pone.0150417

Ejrnaes, R., Bruun, H. H., & Graae, B. J. (2006). Community assembly in experimental grasslands: suitable environment or timely arrival? *Ecology*, *87*(5), 1225–1233.

Elliott, C. W., Fischer, D. G., & LeRoy, C. J. (2011). Germination of three native *Lupinus* species un response to temperature. *Field and Ecosystem Ecology*, *85*(2), 403–410. http://doi.org/10.3955/046.085.0223

Eriksson, O. & Ehrlén, J. (2008). Seedling recruitment and population ecology. In: Leck, M. A., Parker, V. T., & Simpson, R. L. (eds.) *Seedling Ecology and Evolution*. pp. 239-254. [Online]. Cambridge: Cambridge University Press. Available from: Cambridge Books Online <http://dx.doi.org/10.1017/CBO9780511815133.013>

Ewing, K. (2002). Effects of initial site treatments on early growth and three-year survival of Idaho fescue. *Restoration Ecology*, *10*(2), 282–288. http://doi.org/10.1046/j.1526-100X.2002.02039.x

Fazzino, L., Kirkpatrick, H. E., & Fimbel, C. (2011). Comparison of hand-pollinated and naturally-pollinated Puget balsamroot (*Balsamorhiza deltoidea* Nutt.) to determine pollinator limitations on South Puget Sound lowland prairies. *Northwest Science*, *85*(2), 352–360. http://doi.org/10.3955/046.085.0220

Firn, J., MacDougall, A. S., Schmidt, S., & Buckley, Y. M. (2010). Early emergence and resource availability can competitively favour natives over a functionally similar invader. *Oecologia*, *163*(3), 775–784. http://doi.org/10.1007/s00442-010-1583-7

Foster, B. L., & Tilman, D. (2003). Seed limitation and the regulation of community structure in oak savanna grassland. *Journal of Ecology*, *91*, 999–1007. http://doi.org/10.1046/j.1365-2745.2003.00830.x

Fowler, N. L. (1986). Microsite requirements for germination and establishment of three grass species. *The American Midland Naturalist*, *115*(1), 131–145.

Frischie, S. L., & Rowe, H. I. (2012). Replicating life cycle of early-maturing species in the timing of restoration seeding improves establishment and community diversity. *Restoration Ecology*, *20*(2), 188–193. http://doi.org/10.1111/j.1526-100X.2010.00770.x

Fukami, T., Martijn Bezemer, T., Mortimer, S. R., & Putten, W. H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, *8*(12), 1283–1290. http://doi.org/10.1111/j.1461-0248.2005.00829.x

Gleason, H. A. (1927). Further Views on the Succession. *Ecology*, *8*(3), 299–326.

Goldblum, D., Glaves, B. P., Rigg, L. S., & Kleiman, B. (2013). The impact of seed mix weight on diversity and species composition in a tallgrass prairie restoration planting, Nachusa Grasslands, Illinois, USA. *Ecological Restoration, 31*(2), 154–167. http://doi.org/10.1353/ecr.2013.0026

Grman, E., & Suding, K. N. (2010). Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology*, *18*(5), 664–670. http://doi.org/10.1111/j.1526-100X.2008.00497.x

Hamman, S. T., Dunwiddie, P. W., Nuckols, J. L., & McKinley, M. (2011). Fire as a restoration tool in Pacific Northwest prairies and oak woodlands: Challenges, successes, and future directions. *Northwest Science*, *85*(2), 317–328. http://doi.org/10.3955/046.085.0218

Hamman, S. T., Smith, S. & Bakker, J. (2015). Final Report for Center for Natural Lands Management Budget G1005. Prepared for the U.S. Fish and Wildlife Service. Regional prairie native seed project. Olympia, WA.

Hedberg, P., & Kotowski, W. (2010). New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead. *Journal for Nature Conservation*, *18*(4), 304–308. http://doi.org/10.1016/j.jnc.2010.01.003

Helsen, K., Hermy, M., & Honnay, O. (2012). Trait but not species convergence during plant community assembly in restored semi-natural grasslands. *Oikos*, *121*(12), 2121–2130. http://doi.org/10.1111/j.1600-0706.2012.20499.x

Henry, M., Stevens, H., Bunker, D. E., Schnitzer, S. a., & Carson, W. P. (2004). Establishment limitation reduces species recruitment and species richness as soil resources rise. *Journal of Ecology*, *92*(2), 339–347. http://doi.org/10.1111/j.0022-0477.2004.00866.x

Hitchmough, J., de la Fleur, M., & Findlay, C. (2004). Establishing North American prairie vegetation in urban parks in northern England. *Landscape and Urban Planning*, *66*(2), 75–90. http://doi.org/10.1016/S0169-2046(03)00096-3

Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters*, *8*(1), 23–29. http://doi.org/10.1111/j.1461-0248.2004.00686.x

Hoelzle, T. B., Jonas, J. L., & Paschke, M. W. (2012). Twenty-five years of sagebrush steppe plant community development following seed addition. *Journal of Applied Ecology*, *49*(4), 911–918. http://doi.org/10.1111/j.1365-2664.2012.02154.x

Holl, K. D., Hayes, G. F., Brunet, C., Howard, E. A., Reed, L. K., Tang, M., & Vasey, M. C. (2014). Constraints on direct seeding of coastal prairie species: Lessons learned from restoration. *Grasslands, 24,* 8 – 12.

Hooper, D. U., Chapin, E. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., & Lawton, J. H. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, *75*(1), 3–35. http://doi.org/10.1890/04-0922

Hooper, D. U., & Dukes, J. S. (2010). Functional composition controls invasion success in a

California serpentine grassland. *Journal of Ecology*, *98*(4), 764–777. http://doi.org/10.1111/j.1365-2745.2010.01673.x

Howe, H. F., & Brown, J. S. (2000). Early effects of rodent granivory on experimental forb communities. *Ecological Applications*, *10*(3), 917–924.

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography.* Princeton, NJ: Princeton University Press.

Justice, O. L., & Bass L. N., Science and Education Administration (1978). *Principles and practices of seed storage*. (U.S. Department of Agriculture Handbook No. 506). Washington DC: U.S. Government Printing Office.

Kirkpatrick, H. E., & Lubetkin, K. C. (2011). Responses of native and introduced plant species to sucrose addition in Puget lowland prairies. *Northwest Science, 85*(2), 255–268. http://doi.org/10.3955/046.085.0214

Knappová, J., Knapp, M., & Münzbergová, Z. (2013). Spatio-temporal variation in contrasting effects of resident vegetation on establishment, growth and reproduction of dry grassland plants: Implications for seed addition experiments. *PLoS ONE*, *8*(6), e65879. http://doi.org/10.1371/journal.pone.0065879

Körner, C., Stöcklin, J., Reuther-Thiébaud, L., & Pelaez-Riedl, S. (2008). Small differences in arrival time influence composition and productivity of plant communities. *New Phytologist*, *177*(3), 698–705. http://doi.org/10.1111/j.1469-8137.2007.02287.x

Krauss, J., Steffan-Dewenter, I., & Tscharntke, T. (2003). Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia*, *137*(4), 591–602. http://doi.org/10.1007/s00442-003-1353-x

Krock, S., Smith, S., Elliot, C., Kennedy, A., Hamman, S. (2016). Using smoke-water and cold-moist stratification to improve germination of native prairie species. *Native Plants Journal 17*(1), 19-27.

LandScope America. (2015). Willamette Valley-Puget Trough-Georgia Basin Ecoregion. http://www.landscope.org/explore/natural_geographies/ecoregions/Puget%20Trough%20-%20Willamette%20Valley%20-%20Georgia%20Basin/ accessed 12/27/15.

Larson, D. L., Bright, J., Drobney, P., Larson, J. L., Palaia, N., Rabie, P. A., Wells, D. (2011). Effects of planting method and seed mix richness on the early stages of tallgrass prairie restoration. *Biological Conservation*, *144*(12), 3127–3139. http://doi.org/10.1016/j.biocon.2011.10.018

Lawson, C. S., Ford, M. a, & Mitchley, J. (2004). The influence of seed addition and cutting regime on the success of grassland restoration on former arable land. *Applied Vegetation Science*, *7*(2), pp. 259–266. http://doi.org/10.1111/j.1654-109X.2004.tb00618.x

Lewis Army Museum (2014). World War II, 1939-1949. Joint Base Lewis-McChord, DPTMS. http://www.lewis-mcchord.army.mil/dptms/museum/wwii.htm. (Accessed 6/4/2016).

Maret, M. P., & Wilson, M. V. (2000). Fire and seedling population dynamics in western Oregon prairies. *Journal of Vegetation Science*, *11*(2), 307–314. http://doi.org/10.2307/3236811

Maret, M. P., & Wilson, M. V. (2005). Fire and litter effects on seedling establishment in western Oregon upland prairies. *Restoration Ecology*, *13*(3), 562–568. http://doi.org/10.1111/j.1526-100X.2005.00071.x

Maron, J. L., & Gardner, S. N. (2000). Consumer pressure, seed versus safe-site limitation, and plant population dynamics. *Oecologia*, *124,* 260–269. http://doi.org/10.1007/s004420000382

Martin, L. M., & Wilsey, B. J. (2006). Assessing grassland restoration success: relative roles of seed additions and native ungulate activities. *Journal of Applied Ecology*, *43*(6), 1098–1109. http://doi.org/10.1111/j.1365-2664.2006.01211.x

Martin, L. M., & Wilsey, B. J. (2012). Assembly history alters alpha and beta diversity, exotic-native proportions and functioning of restored prairie plant communities. *Journal of Applied Ecology*, *49*(6), 1436–1445. http://doi.org/10.1111/j.1365-2664.2012.02202.x

Martin, L. M., & Wilsey, B. J. (2014). Native-species seed additions do not shift restored prairie plant communities from exotic to native states. *Basic and Applied Ecology*, *15*(4), 297–304. http://doi.org/10.1016/j.baae.2014.05.007

McCain, K. N. S., Baer, S. G., Blair, J. M., & Wilson, G. W. T. (2010). Dominant grasses suppress local diversity in restored tallgrass prairie. *Restoration Ecology*, *18*(SUPPL. 1), 40–49. http://doi.org/10.1111/j.1526-100X.2010.00669.x

Moles, A. T., & Westoby, M. (2004). What do seedlings die from and what are the implications for evolution of seed size? *Oikos*, *106*(1), 193–199.

Naeem, S., Knops, J. M., Tilman, D., Howe, K. M., Kennedy, T., & Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, *91*(1), 97–108. http://doi.org/10.1034/j.1600-0706.2000.910108.x

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, *15*(7), 278–285. http://doi.org/10.1016/S0169-5347(00)01874-7

Native Plant Network, Reforestation, Nurseries, and Genetic Resources Propagation Protocol Database. (2016). http://npn.rngr.net/npn/propagation accessed 1/11/2016.

Natural Resources Conservation Service. (2015). Web Soil Survey. http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx accessed 12/27/2015.

Öster, M., Ask, K., Cousins, S. A. O., & Eriksson, O. (2009). Dispersal and establishment limitation reduces the potential for successful restoration of semi-natural grassland communities on former arable fields. *Journal of Applied Ecology*, 1266–1274. http://doi.org/10.1111/j.1365-2664.2009.01721.x

Pfeifer-Meister, L., Roy, B. a., Johnson, B. R., Krueger, J., & Bridgham, S. D. (2012). Dominance of native grasses leads to community convergence in wetland restoration. *Plant Ecology*, *213*(4), 637–647. http://doi.org/10.1007/s11258-012-0028-2

Pielou, E. C. (1991). *After the ice age: The return of life to glaciated North America.* Chicago, IL: University of Chicago Press.

Plückers, C., Rascher, U., Scharr, H., von Gillhaussen, P., Beierkuhnlein, C., & Temperton, V. M. (2013). Sowing different mixtures in dry acidic grassland produced priority effects of varying strength. *Acta Oecologica*, *53*, 110–116. http://doi.org/10.1016/j.actao.2013.09.004

Potts, J. M., & Elith, J. (2006). Comparing species abundance models. *Ecological Modelling*, *199*(2), 153–163. http://doi.org/10.1016/j.ecolmodel.2006.05.025

Rinella, M. J., Mangold, J. M., Espeland, E. K., Sheley, R. L., & Jacobs, J. S. (2012). Long-term population dynamics f seeded plants in invaded grasslands. *Ecological Applications*, *22*(4), 1320–1329.

Robinson, J. V, & Edgemon, M. A. (1988). An experimental evaluation of the effect of invasion history on community structure. *Ecology*, *69*(5), 1410–1417. http://doi.org/10.2307/1941638

Ross, D. a., & Harper, J. L. (1972). Occupation of biological space during seedling establishment and growth. *Ecology*, *60*(1), 77–88. http://doi.org/10.2307/2258041

Rowe, H. I. (2010). Tricks of the Trade: Techniques and Opinions from 38 Experts in Tallgrass Prairie Restoration. *Restoration Ecology*, *18*(November), 253–262. http://doi.org/10.1111/j.1526-100X.2010.00663.x

Russell, M. (2011). Dormancy and Germination Pre-Treatments in Willamette Valley Native Plants. *Northwest Science*, *85*(2), 389–402. http://doi.org/10.3955/046.085.0222

Sayuti, Z., & Hitchmough, J. D. (2013). Effect of sowing time on field emergence and growth of South African grassland species. *South African Journal of Botany*, *88*, 28–35. http://doi.org/10.1016/j.sajb.2013.04.008

Schantz, M. C., Sheley, R. L., & James, J. J. (2014). Role of propagule pressure and priority effects on seedlings during invasion and restoration of shrub-steppe. *Biological Invasions*, *17*, 73–85. http://doi.org/10.1007/s10530-014-0705-2

Sinclair, M., Alverson, E., Dunn, P., Dunwiddie, P., & Gray, E. (2006). Bunchgrass prairies. In

Apostol, D. & Sinclair, M. (Eds.), *Restoring the Pacific Northwest: the art and science of ecological restoration in Cascadia* (29-59).Washington DC: Island Press.

Sluis, W. J. (2002). Patterns of species richness and composition in re-created grassland. *Restoration Ecology*, *10*(4), 677–684. http://doi.org/10.1046/j.1526-100X.2002.01048.x

Smith, S. & Elliot, C. (2015). South Sound prairie conservation nursery 2014 annual report. Center for Natural Lands Management and Sustainability in Prisons Project. Olympia, WA.

Spellerberg, I. F., & Fedor, P. J. (2003). A tribute to Claude-Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the “Shannon-Wiener” Index. *Global Ecology and Biogeography, 12*(3), 177–179. http://doi.org/10.1046/j.1466-822X.2003.00015.x

Stanley, A. G., Dunwiddie, P. W., & Kaye, T. N. (2011). Restoring invaded Pacific Northwest prairies: management recommendations from a region-wide experiment. *Northwest Science*, *85*(2), 233–246. http://doi.org/10.3955/046.085.0212

Stanley, A. G., Kaye, T. N., & Dunwiddie, P. W. (2008). Regional strategies for restoring invaded prairies: Observations from a multisite, collaborative research project. *Native Plants Journal*, *9*(3), 247–254. http://doi.org/10.2979/NPJ.2008.9.3.247

Stevenson, M. J., Bullock, J. M., & Ward, L. K. (1995). Re-creating semi-natural communities: Effect of sowing rate on establishment of calcareous grassland. *Restoration Ecology*, *3*(4), 279–289. http://doi.org/10.1111/j.1526-100X.1995.tb00095.x

Sullivan, A. T., & Howe, H. F. (2009). Prairie forb response to timing of vole herbivory. *Ecology*, *90*(5), 1346–1355.

Summerville, K. S. (2008). Species diversity and persistence in restored and remnant tallgrass prairies of North America: a function of species’ life history, habitat type, or sampling bias? *Journal of Animal Ecology*, *77*(3), 487–494. http://doi.org/10.1111/j.1365-2656.2008.01356.x

Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, *78*(1), 81–92.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 471–493. http://doi.org/10.1146/annurev-ecolsys-120213-091917

Turnbull, L. a, Crawley, M. J., & Rees, M. (2000). Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, *88*(August 1999), 225–238. http://doi.org/10.2307/3547018

U.S. Fish and Wildlife Service. 2015. Listed species believed to or known to occur in Washington (updated 2/13/2015). *Environmental Conservation Online System, Conserving the Nature of America.* http://ecos.fws.gov/tess_public/reports/species-listed-by-state-report?state=WA (accessed 10/24/2015)

USDA, NRCS. (2016). The PLANTS Database (http://plants.usda.gov). National Plant Data Team, Greensboro, NC 27401-4901 USA. (Accessed 5/19/2016).

Vannette, R. L., & Fukami, T. (2014). Historical contingency in species interactions: Towards niche-based predictions. *Ecology Letters*, *17*(1), 115–124. http://doi.org/10.1111/ele.12204

Vaughn, K. J., & Young, T. P. (2010). Contingent conclusions: Year of initiation influences ecological field experiments, but temporal replication is rare. *Restoration Ecology*, *18*(SUPPL. 1), 59–64. http://doi.org/10.1111/j.1526-100X.2010.00714.x

von Gillhaussen, P., Rascher, U., Jablonowski, N. D., Plückers, C., Beierkuhnlein, C., & Temperton, V. M. (2014). Priority effects of time of arrival of plant functional groups override sowing interval or density effects: A grassland experiment. *PLoS ONE*, *9*(1), e86906. http://doi.org/10.1371/journal.pone.0086906

Walsh, M. K., Pearl, C. A., Whitlock, C., Bartlein, P. J., & Worona, M. A. (2010). An 11,000 - year-long record of fire and vegetation history at Beaver Lake, Oregon, central Willamette Valley. *Quaternary Science Reviews*, *29*, 1093–1106.

Weiher, E., Clarke, P., & Keddy, P. A. (1998). Community assembly rules, morphological dispersion, of plant species the coexistence. *Oikos*, *81*(2), 309–322.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2403–2413. http://doi.org/10.1098/rstb.2011.0056

Weiser, A., & Lepofsky, D. (2009). Ancient land use and management of Ebey's Prairie, Whidbey Island, Washington. *Journal of Ethnobiology*, *29*(2), 184–212. http://doi.org/10.2993/0278-0771-29.2.184

Westoby, M., Walker, B., & Noy-Meir, N. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, *42*(4), 266–274. http://doi.org/10.2307/3899492

Wilbur, H. M., & Alford, R. A. (1985). Priority effects in experimental pond communities: Responses of *Hyla* to *Bufo* and *Rana*. *Ecology*, *66*(4), 1106–1114.

World Health Organization. (2005). Ecosystems and human well-being. *Ecosystems*, *5*(281), 1–100. http://doi.org/10.1196/annals.1439.003

Zavaleta, E. S., Pasari, J. R., Hulvey, K. B., & Tilman, G. D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(4), 1443–1446. http://doi.org/10.1073/pnas.0906829107

Zeiter, M., Stampfli, A., & Newbery, D. M. (2006). Recruitment limitation constrains local species richness and productivity in dry grassland. *Ecology*, *87*(4), 942–51. http://doi.org/10.1890/0012-9658(2006)87[942:RLCLSR]2.0.CO;2

Zobel, M., Otsus, M., Liira, J., Moora, M., & Mols, T. (2000). Is small-scale species richness limited by seed availability or microsite availability? *Ecology*, *81*(12), 3274. http://doi.org/10.2307/177492

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models and Extensions with R*. New York, NY: Springer.