AN ABSTRACT OF THE DISSERTATION OF

Merilynn C. Schantz for the degree of Doctor of Philosophy in Rangeland Ecology and Management presented on May 27, 2014.

Title: Role of Propagule Pressure and Priority Effects on Plant Establishment during Restoration of Invaded Shrub-Steppe

Abstract approved: ____

Roger L. Sheley Michael M. Borman

Biological plant invasions are diminishing the ecological integrity and function of ecosystems worldwide. A primary example of this is in the Great Basin of the United States, where invasive annual grasses, like cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski), are dominating many sagebrush-steppe ecosystems. In these invaded areas, restoration is fundamental to recovering plant community structure and function of once productive and diverse systems. Seeding is a management practice that accelerates revegetation of perennial plants in annual grass invaded ecosystems. However, seeding generally produces poor establishment and patchy plant communities that are quickly replaced by invaders. Identifying and overcoming the processes limiting desirable plant recovery should increase restoration success in annual grass invaded ecosystems. Seed dispersal dynamics, including propagule pressure and priority effects, strongly influence plant establishment and community assembly, especially during invasion and restoration because they can control recruitment of newly arriving species by influencing safe site occupation. The overall objective of this research was to identify the role of propagule pressure and priority effects on seedling emergence, plant life history, and plant community assembly.

My study involved three experiments that were evaluated on seeded annual grass invaded sagebrush-steppe ecosystems in eastern Oregon. First, in order to identify the role of propagule pressure, or number of viable seeds in the seed bank, and annual grass dispersal timing, I conducted a factorially arranged experiment that tested the priority effects of seeding annual grasses in autumn or spring, adding water, and varying annual and perennial grass propagule pressure by seeding 150, 1,500, 2,500, or 3,500 seeds m^{-2}. My results suggested that providing perennial grasses a priority seeding effect by delaying annual grass seeding until spring initially facilitated perennial grass density; however, this effect did not persist into the second-year following seeding. In addition, when annual grass propagule pressure exceeded 150 seeds m^{-2}, an ecological threshold was crossed which limited perennial grass recruitment regardless of perennial grass seeding rate. When water availability was high, perennial grass establishment was high because safe site availability increased, but perennial grass establishment depended on annual grass propagule pressure. These results demonstrated that restoring perennial grasses to annual grass invaded ecosystems may be possible when perennial grass seeding rates and water availability are high. However, if annual grass propagule pressure exceeds 150 seeds m^{-2}, an ecological threshold occurs, where, perennial grass recruitment will be limited regardless of seeding strategy.

A second factorial experiment was designed to identify the priority effects of perennial grass seeding time and frequency, annual and perennial grass propagule pressure, and water availability on seedling emergence and annual and perennial grass density and biomass two-years following seeding. In this experiment, my results indicated that seeding perennial grasses seasonally split between the autumn and spring produced higher perennial grass density and biomass compared to seeding perennial grasses exclusively in either period. In addition, results supported my hypothesis that perennial grass density and biomass in seasonally split applications would be higher where perennial propagule pressure was high and annual grass propagule pressure was low. However, I found that there was a threshold between 150-1,500 annual grass seeds m^{-2}, where regardless of perennial grass seeding strategies, perennial grass density and biomass was low. When water was added, annual and perennial grass density was higher than in plots without additional water, suggesting that higher water availability facilitates the growth of all seeded species. Collectively, these results suggested that modifying perennial grass seeding times and frequency increased perennial grass recruitment to annual grass invaded ecosystems, but only if annual grass propagule pressure was below 1,500 annual grass seeds m^{-2}.

Third, a life history approach was used to identify and quantify the effect of ecological processes on plant population demography when annual grass seeding times varied (autumn or spring), annual and perennial grass propagule pressure was modified by 150, 1,500, 2,500, or 3,500 seeds m^{-2}, and watering occurred (ambient or water added treatments). In this study, we found that all species had low emergence rates, even though seedling germination was relatively high. Based on prior research, this suggests that freeze-thaw cycles, pathogen attack, and soil crusts may strongly inhibit plant growth from the germination to emergence growth stages. Alternatively, my finding that perennial grass germination rates were higher when they were seeded with annual grasses in autumn compared to delaying annual grass seeding until spring suggests that perennial grass germination is facilitated by neighboring annual grasses during this life history stage. Following seedling emergence, my data indicated that adding water enhances the establishment and growth of all species and that providing perennial grasses a priority seeding effect by delaying annual grass seeding until spring yields higher perennial grass density. However, delaying annual grass seeding until spring only provided perennial grasses a priority effect when annual grass propagule pressure was high. When annual grass propagule pressure was low, seeding perennial grasses in autumn yielded the highest perennial grass density through their life history suggesting low numbers of neighboring annual grasses facilitates the density of perennial grasses. By the second growing season, annual grass density was two-times higher than initial annual grass seeding rates and over four-times higher than perennial grass density, suggesting that annual grass interference may increase during the second growing season. Plant community assembly of restored shrub-steppe ecosystems degraded by annual grasses will likely be determined by the establishment of seeded species in the first growing season.

Because perennial grasses are facilitated by annual grasses in the germination stage, and by small numbers of neighboring annual grasses in later growth stages, if perennial grasses establish in areas with low annual grass propagule pressure in the first growing season, they will likely persist to become adults. Alternatively, high annual grass propagule pressure limits perennial grass recruitment regardless of seeding strategy because of their preemptive occupation of safe sites and soil resources and high density by the second growing season.

ROLE OF PROPAGULE PRESSURE AND PRIORITY EFFECTS ON PLANT ESTABLISHMENT DURING RESTORATION OF INVADED SHRUB-STEPPE

by
Merilynn C. Schantz

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APPROVED:

Co-Major Professor, representing Rangeland Ecology and Management

Co-Major Professor, representing Rangeland Ecology and Management

Head of the Department of Animal and Rangeland Sciences

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Merilynn C. Schantz, Author

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TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LIST OF TABLES

Table Page

1 General Introduction

1.1 Restoration of annual grass invaded ecosystems

Annual grass invasions and ecological disturbances associated with drought, wildfires, and energy development reduce ecosystem services throughout shrub-steppe rangelands (Eviner et al., 2012). Where annual grasses dominate, fire frequency and magnitude are higher, which leads to further annual grass invasion because annual grasses can easily germinate following fire and their litter provides substantial fuel for wildfires to be carried across the landscape (D'Antonio & Vitousek, 1992). Invasive annual grasses, like cheatgrass (*Bromus tectorum* L.) or medusahead (*Taeniatherum caput-medusae* L. Nevski), are highly problematic in arid ecosystems because their seeds can dominate seed banks and their regeneration success is high (Humphrey & Schupp, 2001; Smith et al., 2008). Consequently, many areas invaded by invasive annual grasses have degraded past an ecological threshold to a point where perennial grasses will not reestablish without substantial inputs (Bestelmeyer et al., 2013).

Restoration is fundamental to recovering the structure and function of healthy intact plant communities from annual grass invaded rangelands (Sheley et al., 2006). Seeding is a management procedure that can accelerate perennial grass recruitment into highly degraded and annual grass invaded areas. (Hull Jr. & Stewart, 1948; Seabloom et al., 2003). Perennial grass recruitment into annual grass dominated regions after seeding is highly variable and often stands fail to develop and/or mature to adults (Kulpa et al., 2012; Rinella et al., 2012). Perennial grass recruitment from seed is slow, whereas annual grasses populations reestablish quickly which greatly complicates restoration (James & Svejcar, 2010; Montoya et al., 2012). Furthermore, Kulpa et al. (2012) found that annual grasses produce up to 28 times more seed the first growing season compared to perennial grasses. Annual grasses also disperse, germinate, and emerge earlier than seeded perennial grasses (Orrock & Christopher, 2010). Coincidentally, dispersal traits, including the type and number of seeds in seed bank compared to seeded species, strongly affects plant community assembly following restoration of annual grass invaded shrub-steppe.

1.2 Dispersal

1.2.1 Dispersal dynamics

Seeds have evolved traits that promote their dispersal, such as attachment mechanisms, attractants, and aerodynamics properties to facilitate their movement onto new sites (Purschke et al., 2012). The relative success of dispersal depends on how these traits interact with potential safe sites (Davies & Sheley, 2007). Safe sites refer to patches in heterogeneous landscapes suitable for seedling germination and establishment (Titman, 1976; Drake, 1991). The number and suitability of safe sites varies through time and space depending on the relative growth stage of the plant community and resource availability (Duncan et al., 2009). Dovciak et al. (2003) found that when resource availability is high and/or during early growth stages, there are higher numbers of available safe sites for seedling recruitment. Moreover, higher numbers of seeds in the seed bank, or the propagule pressure, and low resource availability increases competition for available safe sites (Spiegel & Nathan, 2012). Because dispersal dynamics affect seedling emergence, growth, and ultimately plant community assembly, modifying propagule pressure and dispersal frequency may directly influence plant community structure and function, especially following restoration (Seabloom, 2011).

1.2.2 Propagule pressure and priority effects

Increasing the number of seeds increases the probability that a seed reaches a suitable safe site and can be modeled as a biased lottery (Lavorel & Lebreton, 1992; Lamont & Witkowski, 1995). Aicher et al. (2011) concluded that the propagule pressure of the dominant species allows these species to dominate safe sites and to affect community-level diversity. When annual grass seeding densities are high, perennial grass densities are typically low because annual grasses preemptively occupy safe sites and soil resources before perennial grasses begin growth (Abraham et al., 2009). Increasing the seeding rates of perennial grasses can increase perennial grass densities, but the relative rates of perennial to annual grasses is largely unknown.

Priority effects can greatly reduce competitive advantages because plants arriving and establishing earliest preempt resource use, which can have large effects on plant community assembly (Fukami et al., 2005). Wainwright et al. (2012) concluded that when perennial grasses were afforded a priority effect by initiating annual grass growth earlier than normal, perennial grass density was higher than when perennial grasses were not afforded a priority effect. Alternatively, DiVittorio et al. (2007) found that perennial grass density was low where annual grass dispersal was high, suggesting that perennial grasses are inhibited by the high densities of annual grass seeds regardless of seeding times. Consequently, there is no unified understanding of the magnitude and direction of propagule pressure and priority effects on plant-plant interactions, especially in resource-limited ecosystems, like the shrub-steppe.

1.2.3 Water availability

Seedling development in arid ecosystems, like the shrub-steppe, is primarily limited by water availability (Steers et al., 2011). When water availability is low, the number of safe sites and soil resource availability are also low (Shimono et al., 2006). Theoretically, increasing the availability of water should increase recruitment of desirable species by providing more resources for later developing species, like perennial grasses (Everard et al., 2010). The availability of water is also likely interacting with propagule pressure and priority effects, depending on the seeding timing and seed availability, because seedlings quickly respond to changes in matric potential (Evans & Etherington, 1991). The timing and amount of water strongly affects plant growth because species differentially respond to water availability (Soliveres et al., 2011). Consequently, plant community assembly is difficult to forecast because plants have differing species traits and life history strategies (Sheley & James, 2014). Understanding the interactions among propagule pressure, priority effects, and water availability on plant community assembly should increase the ability to forecast management outcomes.

1.3 Systems-based management approach

James et al. (2013) recently proposed using a system based management framework to restore annual grass invaded ecosystems (Fig. 1). Systems based management frameworks account for the underlying ecological processes affecting plant growth and can provide a quantitative assessment of plant community assembly (Evans et al., 2012). Unlike conceptual and theoretical models, systems models use a hierarchical modeling approach to identify underlying mechanisms and processes that drive model behavior through time, such as climate, by linking these processes to model components, like plant life history stage (Huxman et al., 2013; Adler et al., 2014). Accordingly, the effectiveness of restoration tools and strategies will differ depending on the outcome of various management inputs on plant growth through seedlings life history.

Plant community assembly is dynamic depending on the site and species life history strategies (Moles & Westoby, 2006). Rangeland ecological sites are heterogeneous and seeding generally produces patchy plant communities (Larios et al., 2013). Kulpa et al. (2012) suggest that species recovery following restoration is strongly determined by the interaction among climate, soils, aspect, propagule pressure, and species type. However, species have differing life history strategies, including dispersal times, leaf characteristics, and time to reproduction (Morales & Traveset, 2009). For example, Verdu and Traveset (2005) found that early seedling emergence increases plant fitness. Because of these various life history strategies among species, life history characteristics could be integrated into management models to increase our abilities to forecast seeding outcomes (James et al., 2013). Adler et al. (2014) suggest that plant functional traits are a predictable measure of plant community assembly. In addition, James et al. (2011) discovered that the limitation in seedling recruitment is between the germination and emergence growth stages in seeded sage-steppe when evaluating the demography of seeded perennial grasses in the Great Basin. Knowledge of the effects seeding time and seed numbers that influence propagule pressure and priority effects on plant community assembly should provide managers the ability to plan restoration of plant communities more successfully (James et al., 2013).

1.4 Dissertation outline

The goal of the studies presented in this dissertation was to conduct ecologically-based research that could provide information to improve restoration of degraded and annual grass invaded shrub-steppe. In Chapter 2 (first manuscript), we sought to identify the role of propagule pressure and priority effects on seedling emergence and survival during invasion and/or restoration. The objectives of this study were to evaluate effects of propagule pressure, priority effects, and water availability on perennial vs. annual seedling emergence and establishment. Our hypotheses were that the species which arrive earliest and have the highest seeding rate will produce the highest density. We also hypothesized that water additions would increase the density of perennial and annual grasses, and would ultimately favor the establishment of both functional groups. Based on the evidence that dispersal dynamics impact plant community assembly, a greater understanding of propagule pressure and priority effects should increase our ability to manage invasion, especially during restoration of invaded shrub-steppe ecosystems.

Chapter 3 (second manuscript) was focused on identifying how modifying perennial grass seeding times and frequency affects the density of annual and perennial grass seedling emergence, and shapes final plant community composition and biomass two years following seeding. In addition, we sought to quantify these dynamics with varying soil water availability and annual grass seed bank density. In this study, we hypothesized that perennial grass seed dispersal between autumn and spring would yield higher perennial grass density and biomass compared to seeding native grasses exclusively in either period. We also hypothesized that perennial grass density and biomass in seasonally split applications would be higher when perennial propagule pressure was high and annual grass propagule pressure was low. In addition, we hypothesized that adding water would increase perennial grass density and biomass, especially in plots with seasonally split seeding and high perennial grass propagule pressure. Identifying the relative effect of propagule pressure and dispersal timing and frequency on community assembly should allow ecologists to better plan successful restoration projects in annual grass invaded shrub-steppe ecosystems.

In Chapter 4 (third manuscript), we sought to quantify annual and perennial grass life history strategies when annual grass seeding times, annual and perennial grass seeding rates, and water availability varied. We hypothesized that species which arrived earliest and had the highest seeding rates would produce higher seedling density throughout their life history. We also hypothesized that seeding perennial grasses at high seeding rates and prior to annual grass seeding would increase perennial grass density by providing these species a priority effect for accessing safe sites and reducing invasive species interference in later life history stages. Lastly, we hypothesized that higher water availability would increase perennial grass density through their life history because higher resource availability can initially increase the number of available safe sites and reduce competition for resources in later life history stages (Rao & Allen, 2010).

Chapter 5 is a general conclusion chapter. In this chapter, I summarize the main findings from these studies and provide recommendations for future research. Collectively, these studies provide valuable information on the role of propagule pressure and priority effects in restoring annual-grass invaded shrublands.

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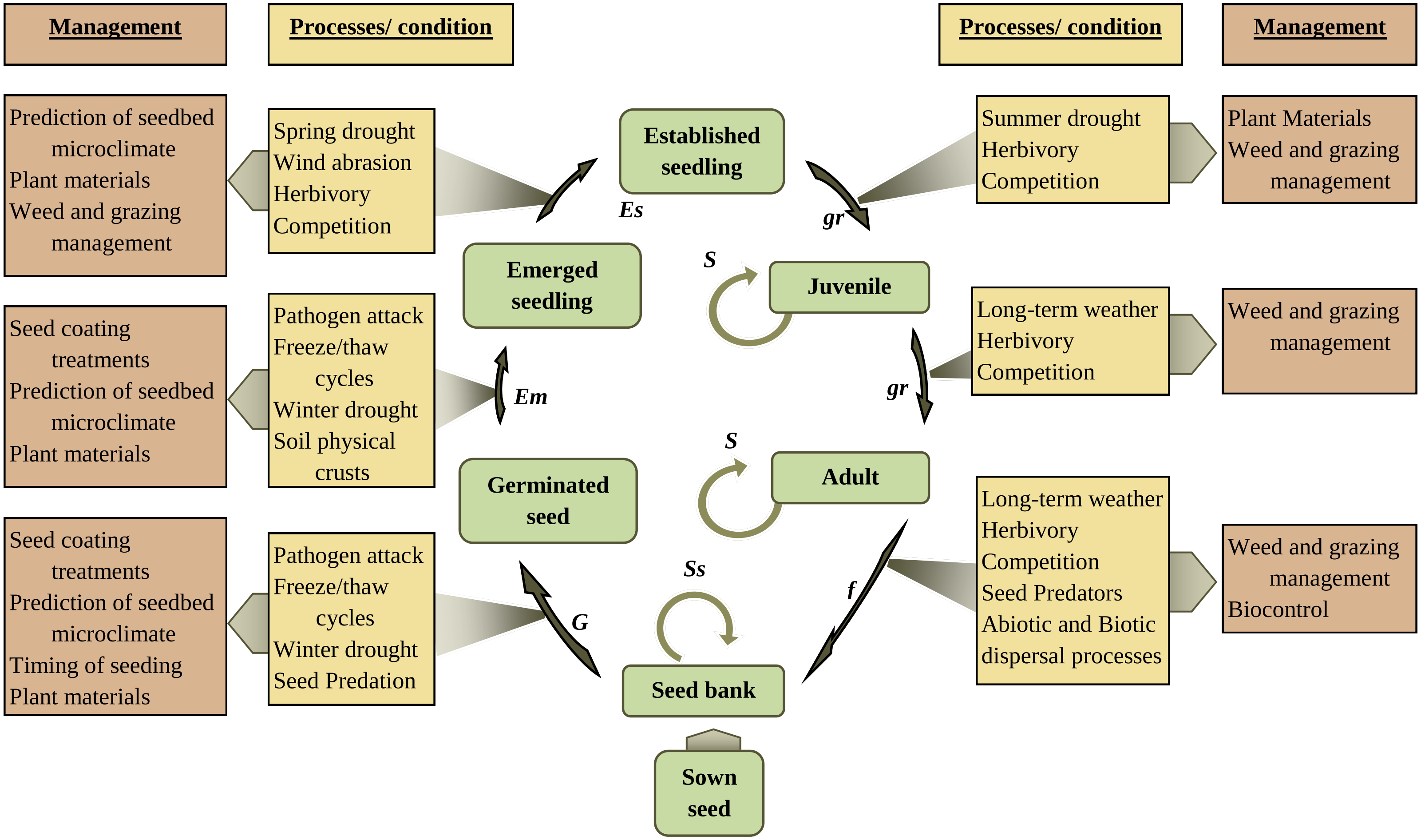
Fig. 1-1 Modifed from James et al. 2013. Systems framework for managing limitations to recruitment in rangeland systems (Modified from James et al. 2013). The **inner layer** of the framework is a life cycle population model that describes the demographic stages (boxes) and transitions (arrows) between stages a sown seed follows to recruit into the adult population. Symbols, *Ss* = seed survival, *G*= germination, *Em*=emergence, and *Es*=establishment, indicate transitions between distinct stages of seedling development. The text describes the developmental stages used to define each transition. Symbols *gr*, *f* and *S* are size dependent growth, fecundity and survival, respectively. The **middle layer** of the model identifies key ecological processes and conditions that the literature suggests can influence transitions among stages. The **outer layer** identifies representative management tools and strategies that could be used to modify processes and conditions that limit life stage transitions. (Continued on next page)


Management
Processes/ condition
Processes/ condition
Management
Prediction of seedbed microclimate
Plant materials
Weed and grazing management
Spring drought
Wind abrasion
Herbivory
Competition
Established seedling
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Summer drought
Herbivory
Competition
Plant Materials
Weed and grazing management
Emerged seedling
S
Juvenile
Seed coating treatments
Prediction of seedbed microclimate
Plant materials
Pathogen attack
Freeze/thaw cycles
Winter drought
Soil physical crusts
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Long-term weather
Herbivory
Competition
Weed and grazing management
S
Germinated seed
Adult
Seed coating treatments
Prediction of seedbed microclimate
Timing of seeding
Plant materials
Pathogen attack
Freeze/thaw cycles
Winter drought
Seed Predation
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Ss
f
Long-term weather
Herbivory
Competition
Seed Predators
Abiotic and Biotic dispersal processes
Weed and grazing management
Biocontrol
Seed bank
Sown seed

Role of propagule pressure and priority effects on seedlings during invasion and restoration of shrub-steppe

Merilynn C. Schantz, Roger L. Sheley, and Jeremy J. James

Biological Invasions

Springer Heidelberg

69126 Heidelberg

Germany

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2 First Manuscript

Role of propagule pressure and priority effects on seedlings during invasion and restoration of shrub-steppe

Merilynn C. Schantz [1], Roger L. Sheley [2], and Jeremy J. James [3]

[1] Department of Animal and Rangeland Sciences, Oregon State University, Corvallis, OR, 97331-6702, hirschm@onid.orst.edu, **Phone** 1(541)-737-3431, **Fax** 1(541)-737-4174 [2] United States Department of Agriculture-Agricultural Research Service, Burns, OR, 97720; [3] Sierra Foothills Research and Extension Center, University of California Division of Agriculture and Natural Resources, Browns Valley, CA 95918.

2.1 Abstract

Plant invasion and restoration outcomes are largely driven by the timing and magnitude of seed dispersal, and by the performance of dispersed species in an environment. Because seed dispersal controls recruitment of newly arriving species and facilitates safe site occupation, assembly will differ depending on seed dispersal processes and variable environmental conditions. The objective of this study was to identify how annual and perennial grasses assembled when dispersal times, propagule pressure, and water availability were modified. To assess these effects, we conducted a field experiment in an annual grass invaded shrub-steppe ecosystem in eastern Oregon. We tested the effects of seeding annual and perennial grasses in autumn or delaying annual grass seeding until spring, adding water, and varying annual and perennial grass seeding rate by 150, 1,500, 2,500, or 3,500 seeds m^{-2} on perennial and annual grass seedling emergence through time and final density and biomass. Providing perennial grasses a priority effect by delaying annual grass seeding until spring initially facilitated perennial grass establishment, but this effect did not persist into the second growing season. We found that if annual grass propagule pressure exceeded 150 seeds m^{-2}, perennial grass recruitment was limited. In addition, higher water availability increased perennial grass establishment, but was dependent upon annual grass propagule pressure. These findings suggest that seeding perennial grasses into annual grass dominated systems is more dependent upon the existing propagule pressure of annual grasses than the priority effects of perennial grasses, the propagule pressure of perennial grasses, or water availability.

Keywords: dispersal, propagule pressure, priority effects, invasion, assembly, water

2.2 Introduction

Biological plant invasions are diminishing the ecological integrity and function of ecosystems worldwide (Seastedt and Pyšek 2011). Limiting and mitigating invasion are dependent upon our ability to forecast the spread and dominance of invaders and restore invaded systems. A variety of models have been used to predict plant invasion into ecologically intact plant communities (Diaz et al. 2004) and to predict vegetation response to restoration procedures (Steers et al. 2011). These models incorporate a suite of abiotic and biotic factors to make estimates of future invasion and restoration (Borer et al. 2007; Bradford and Lauenroth 2006). It is becoming increasingly clear that mechanistic models that incorporate a range of ecological processes and their interactions to estimate community assembly have the highest likelihood of providing accurate forecasts of future vegetation trajectories.

Plant community assembly is complex and often driven by high order interactions among variable mechanisms, processes and conditions (Fargione et al. 2003; HilleRisLambers et al. 2010). Nutrient availability is patchy within a plant community and resource patches, termed safe sites, support diverse plant populations by providing conditions suitable for seedling germination and establishment (Grubb 1977; Tilman 1997; Titman 1976). Seed dispersal can be a major driving mechanism of plant assembly, especially during invasion and restoration because it may control recruitment of newly arriving species by influencing safe site occupation (Clark et al. 2007; Satterthwaite 2007). Propagule pressure and dispersal timing strongly influence seedling emergence, growth, and ultimately plant community assembly, depending on the number and timing of seeds reaching safe sites (Drake 1991). Increasing the number of seeds can increase the probability that a seed reaches a suitable safe site (Lavorel and Lebreton 1992b). However, priority effects can greatly reduce competitive advantages, because plants arriving and establishing earliest preempt resource use (Chambers and Wisdom. 2009 ; Grman and Suding 2010).

Propagule pressure and priority effects are known to drive plant-plant interactions, but the degree of impact will depend upon the magnitude of these effects. Aicher et al. (2011) concluded that dominant species dominate safe sites by high propagule supply in the seed bank and these effects will scale up to affect community-level diversity. Conversely, Lortie and Turkington (2002) found little evidence that initial seed density affected the interactions among species nor the vegetation structure in an desert annual community. The effect of propagule pressure on plant-plant interactions is compounded by the temporal patterns in which seeds of each species arrive (Stella et al. 2006). In a grassland community, temporal availability of seeds led to qualitative differences in the outcome of colonization between invasive and native plants (DiVittorio et al. 2007). Assembly of seeded communities seems to greatly differ depending upon the interactions between propagule pressure and priority effects.

There is no clear understanding of how propagule pressure and priority effects influence seedling emergence and survival during invasion and/or restoration. The objectives of this study were to evaluate effects of propagule pressure, priority effects, and water availability on perennial vs. annual seedling emergence and establishment. Our hypotheses are that the species which arrive earliest and have the highest seeding rate will produce the highest density. We also hypothesized that water additions would increase the density of perennial and annual grasses, and would ultimately favor both functional groups’ establishment. Understanding how the dispersal dynamics of propagule pressure and priority effects impact plant community assembly could increase our ability to manage invasion, especially during restoration, in shrub-steppe ecosystems.

2.3 Materials and Methods

2.3.1 Study site

This experiment was conducted on a low elevation (1,033 m), heavily infested shrub-steppe site located about 5 km south of Juntura in Malheur County, Oregon; Zone: 11, 410178 easting, 4840910 northing. Soils are within the Bogusrim series (fine, smectitic, mesic abruptic Xeric Argidurids), which receive an average 257 mm per year with a bimodal distribution peaking in the winter and spring. It has a very slight slope facing southwesterly. This site is devoid of sagebrush and has a monoculture of medusahead (*Taniatherum caput-medusae* (L.) Nevski) growing in association with species of cheatgrass (*Bromus tectorum* L.), Sandberg bluegrass (*Poa secunda* J. Presl), whitetop (*Cardaria draba* (L.) Desv.), squirreltail (*Elymus elymoides* (Raf.) Swezey), and morning glory (*Ipomoea eriocarpa* R. Br.).

2.3.2 Model system

To test the effects of propagule pressure and dispersal timing and frequency on plant establishment and growth, we used a model system consisting of annual grass functional groups represented by, cheatgrass and medusahead (50-50 mixture) as the invaders. The desired native system was represented by the perennial bunchgrass functional group, which included; bluebunch wheatgrass (Anatone *Pseudoroegneria spicata* (Pursh) A. Löve), squirreltail, sandberg bluegrass (Mountain Home), and Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth) seeded in equal proportions. Annual grass seeds were collected locally, by hand, from Harney Co. Oregon. Perennial bunchgrass seeds were purchased from Great Basin seed companies that have similar climate and soils to our ecological site. Sandberg bluegrass, squirreltail, and bluebunch wheatgrass were purchased from Granite Seed Co., Lehi, UT in 2011, and Thurber's needlegrass was purchased from Moses Lake, WA in 2010. Seeding rate was calculated on a per weight basis to ensure 100% pure-live seeds were added to each plot.

2.3.3 Study design

2.3.3.1 Propagule pressure and priority effects

Prior to initiating the study, the site was sprayed with 3.36 L ha^{-1} of glyphosate [N-(phosphonomethyl) glycine] and tilled to about 100 mm in order to remove existing vegetation. Densities and proportions of annual grasses and perennial grasses were arranged to provide four addition-series matrices (Radosevich 1987). Seeding densities of annual: perennial grasses in each matrix were 150:150, 1,500:1,500, 2,500:2,500, 3,500:3,500, 150:1,500, 1,500:150, 150:2,500, 2,500:150, 150:3,500, 3,500:150, 1,500:2,500, 2,500:1,500, 1,500:3,500, 3,500:1,500, 2,500:3,500, 3,500:2,500. Each matrix included one of the following treatments: simultaneously seeding annual and perennial grasses in autumn, delayed annual grass seeding until spring, simultaneous autumn seeding with added water, and delaying annual grass seeding until spring and adding water. Each matrix was replicated three-times in a completely randomized design. This study design yielded 192 1 m^2 plots.

For the simultaneously seeded matrices both annual and perennial grasses were randomly sown in November 2011 onto 1 m^2 plots by hand-broadcasting seeds onto the soil surface. In the remaining matrices, perennial grasses were seeded as describe above, but annual grasses were seeded in February 2012. After seeds were sown, they were covered with five cm of sifted weed-free topsoil collected from the site. For the water treatments, plots received twice the long-term monthly average precipitation during the growing season (March-May) and this was administered weekly. Plots were watered from watering cans with care to evenly distribute water on each plot.

2.3.3.1 Sampling and measurements

Precipitation (mm), and temperature (˚C) were monitored daily from November 2011 to June 2013 using HOBO data loggers (Onset Comp. Inc., USA), placed at the study site. Long-term (1963-1996) daily precipitation and temperature data for Juntura were collected from the Western Regional Climate Center (WRCC 2013) and summarized. Volumetric soil water content at five cm (%) and soil temperature at five cm (˚C) were collected using Decagon 5TM soil moisture sensors (Decagon Devices Inc., Pullman, WA, USA) from November 2011 to June 2013.

Plant density was counted within the center 0.5 m^2 of the plot for perennial species and the center 0.25 m^2 for annual species biweekly during the first growing season from March 13, to June 2, 2012. Plants were marked individually using toothpicks to assess total mortality during each sampling period. At the end of the second growing season in 2013, June 3-14, final density was counted and biomass was harvested.

2.3.4 Statistical analysis

All data were pooled by annual and perennial grasses and measured for the distribution and homogeneity of variance using with Shapiro-Wilk and Levene tests, respectively (SAS Institute Inc., Cary, NC, 2012). Annual plant density and biomass were normally distributed. Perennial plant density in 2012 and 2013 and perennial plant biomass had skewed distributions. Originally, we intended to predict plant biomass using plant density for each treatment using linear regression described by Spitters (1983); however the data did not fit a linear function. We tried various transformations in an attempt to linearize the data, but they did not improve the model fitness. Thus, all data were analyzed using analysis of variance (ANOVA) and all figures were created in SigmaPlot Version 10.0 (Systat Software, San Jose, CA).

Coleoptile emergence was evaluated using a repeated measures design and final density and biomass of annual and perennial grass seedlings was evaluated using a mixed-model ANOVA. All analyses were completed in SAS (SAS Institute Inc., Cary, NC, 2012) and modeled using SigmaPlot Version 12.2 (Systat Software, San Jose, CA). Coleoptile emergence was tested using the main effects and interactions among seeding time, watering, annual grass seeding rate, perennial grass seeding rate, and sampling time on the density of annual and perennial grass coleoptiles. Final plant density and biomass in 2013 were tested using the main effects and interactions among seeding time, watering, annual grass seeding rate, and perennial grass seeding rate. Coleoptile emergence and final density and biomass models both used replication as the random factor (1-3) and means were separated using the slice procedure (Schabenberger 2013). Significance was determined using a probability value which was set at $P \leq 0.05$.

2.4 Results

2.4.1 Environmental conditions

Average daily temperature was consistent with long-term averages, whereas average daily precipitation was lower than the 30 year mean in the summer months, and average throughout the rest of the year (Fig. 1). Both average daily volumetric water content and average daily soil temperature at 5 cm had higher variation in the water added treatments, but were not different than the no water treatments (Fig. 2). Average daily volumetric water content fluctuated from a high of 17% from November-April to a low of 7% from May-October (Fig. 2 A & B). Average daily soil temperature at 5 cm fluctuated similarly to air temperature but was about 5 ˚C higher than air temperature throughout the study period (Fig. 2 B & C).

2.4.2 Seedling emergence

Perennial grass seedling density increased within all treatments from mid- to late-April and generally to mid-May. Perennial grass seedling density appeared to increase with increasing seeding rate (Fig. 3). At low annual and high perennial grass seeding rates, delaying annual grass seeding until spring generally produced the highest final seedling density, especially when water was not added. Alternatively, at high annual and low perennial grass seeding rates, delaying annual grass seeding until spring in combination with water addition produced the highest perennial grass seedling density. The main effects or interactions of seeding time or watering did not affect perennial grass density in 2011.

At 150 annual grass seeds m^{-2}, all treatments produced similar annual grass density (Fig. 4). At the three higher seeding rates, delaying annual grass seeding until spring and adding water produced the highest annual grass seedling density after the first sampling time. Seeding annuals in autumn produced the second highest annual grass density where water was added. At the highest seeding rate, delaying annual grass seeding until spring produced higher annual grass density than seeding annual grasses in autumn where no water added. Increasing perennial grass seeding rate did not generally impact the density of annual grasses.

2.4.3 Final seedling density and biomass

Final perennial grass density in 2013 was not affected by any treatment interactions, but was significantly affected by the main effects of annual grass seeding rate and perennial grass seeding rate (Table 2; $P < 0.05$). These data show that higher perennial grass seeding rates produced higher perennial grass density since 0.71 plants m^{-2} were produced when the seeding rate was 150 perennial grass seeds m^{-2} and 3.38 plants m^{-2} were produced when the seeding rate was 3,500 perennial grass seeds m^{-2} (Fig. 5A; $P = 0.014$). Alternatively, when annual grass seeding rate was high, perennial grass density was low because perennial grass density was 5.21 plants m^{-2} when annual grass seeding rate was 150 annual grasses m^{-2} but was only 0.71 plants m^{-2} when 3,500 annual grass seeds m^{-2} were seeded (Fig. 5B; $P < 0.0001$).

Perennial grass biomass was higher when annual grasses were seeded in the spring and water was not added than when annual grass seeding occurred in spring and water was added (Fig. 6; $P = 0.052$). However, the biomass of perennial grasses was not affected by any main effects in this study. Perennial grass biomass also did not differ among watering treatments when annual were seeded in autumn or among seeding times when water was added.

Annual grass density was higher when water was added (Table 2; *P* = 0.020) and when annual grasses were seeded in autumn (Table 2; *P* <0.0001). When annual grass seeding rate increased, the density of annual grasses increased from about 378 plants m^{-2} at 150 annual grass seeds m^{-2} to about 762 plants m^{-2} at 3,500 annual grass seeds m^{-2} (Fig. 7A; *P* <0.0001). The combination of adding water and increasing perennial grass seeding rate also produced higher annual grass density (Fig. 7B; *P*=0.065). In this study, we were unable to detect any differences in seeding time at any annual grass seeding rate level. We did, however, find that the density of annual grasses at the three highest annual grass seeding rates was higher than when annual grass seeding rate was 150 annual grass seeds m^{-2}.

Annual grass biomass was 0.025 g plant^{-1} lower when water was added than when water was not added (Table 2; *P* = 0.0003). Delaying annual grass seeding until the spring produced higher biomass than when annual grasses were seeded in autumn (Table 2; *P* = 0.005). Biomass of annual grasses was highest at 150 annual grass seeds m^{-2} at 0.17 g plant^{-1} and lowest when 3,500 annual grass seeds m^{-2} were added at 0.05 g plant^{-1} (Table 2; *P* < 0.0001). When annual grass seeding was delayed until spring perennial grass seeding rate was 3,500 seeds m^{-2}, the biomass of an isolated individual was higher than when annual grasses were seeded in autumn (Fig. 8; *P* = 0.067). Alternatively, annual grasses had the highest biomass when water was not added, especially at the highest perennial and lowest annual grass seeding rates (Fig. 9; *P* = 0.048). When water was not added, perennial grass biomass did not differ until the seeding rate was 2,500 seeds m^{-2}, where annual grass biomass was higher when annual grass seeding rate was 150 seeds m^{-2} than any of the other annual grass seeding rates (Fig. 9A). When water was added, annual grass biomass was highest at the lowest annual grass seeding rate and the three lowest perennial grass seeding rates (Fig. 9B). Annual grass biomass was higher when annual grass seeding rates were 150 and 1,500 annual grass seeds m^{-2} than when annual grass seeding rates were 2,500 or 3,500 seeds m^{-2} when perennial grass seeding rate was 1,500 seeds m^{-2}. There were no effects of seeding time on annual grass biomass at any other perennial grass seeding rate.

2.5 Discussion

2.5.1 Seedling emergence

Over the past few decades, seed sowing experiments have indicated that increasing the number of seeds can increase establishment, especially because seedling emergence has been identified as the bottleneck in seedling establishment within arid land restorations (Clark et al. 2007; James et al. 2011). Our hypothesis that high seeding rates would be necessary for high seedling densities was accepted for coleoptile emergence, regardless of functional group. To emerge, seeds must find suitable safe sites for germination, radical elongation, and penetration through soil surfaces (Fowler 1988). In arid systems, such as the sagebrush steppe, these safe sites may be limited when seeds are broadcast during autumn or spring (Duncan et al. 2009). In this study, we found that the number of available seeds interacts with the number of available microsites to determine the level of plant emergence in grassland ecosystems, suggesting that increasing the seeding rate likely increased the probability that any particular seed would reach safe sites (Crowley et al. 2005).

Our finding that annual grasses emerged earlier and at higher rates than perennial grasses support the conclusions that the traits of annual grasses provide them assembly advantages in arid environments (Leffler et al. 2013; Steers et al. 2011). Annual grass functional traits include, high relative growth rate (Arredondo et al. 1998), high specific leaf area (Svejcar 1990), and high specific root length (Svejcar 1990).   In addition, annual grasses resource preemption can begin as early as the seedling stage (Ray-Mukherjee et al. 2011). Species that have the earliest order of emergence are argued to preemptively acquire soil resources before their neighbors (Leffler et al. 2011), increase the occupancy of safe sites (Satterthwaite 2007), and produce higher numbers and more viable seeds (Abraham et al. 2009). Our study supports these findings because annual grasses emerged earlier and at higher rates than perennial grasses regardless of seeding rates.

Annual grasses are seemingly well suited to the harsh environment of the sagebrush steppe because they do not need to store resources for later growth and development (Adair and Burke. 2010). Our data support this general conclusion because annual grasses had a strong positive response to adding water, especially when annual grass seeding was delayed until spring. Our hypothesis that adding water would increase seedling density was accepted for annual grass coleoptiles, but only at the three highest annual grass seeding rates. It is likely that when propagule pressure is low, safe sites are not limiting; thus the total coleoptile density was too low to detect a difference in response to watering. On the other hand, our finding that annual grass seedling density was highest when annual grass seeding was delayed until spring contradicts our hypothesis that species that arrived the earliest would produce the highest density. Freezing conditions throughout the winter months can significantly decrease annual seed and/or seedling survival (Carey and Watkinson 1993; Watkinson 1978). Because air and soil temperature in December 2011 and January 2012 were below freezing, it is likely seedling mortality increased when annual grasses were seeded in autumn and that delaying annual grass seeding until spring removed much of the winter mortality associated with seeding in autumn (Thomsen et al. 2006).

Perennial grass seedling density was highest when annual grass seeding was delayed until spring, suggesting that providing perennial grasses a priority effect gives perennial grasses a performance advantage over annual grasses (Grman and Suding 2010). Alternatively, when water was added, perennial grass emergence density was generally lower than in no water added treatments. Because annual grasses are readily adapted to usurp available water (Gordon and Rice 1993), when water was added, perennial grass priority effects at the emergence stage were likely nullified by the high density and preemptive resource use of annual grasses (Wainwright et al. 2012). Surprisingly, perennial grass density was higher when annual grass seeding was delayed until spring and water was added at low perennial grass and high annual grass seeding rates. It may be possible that the higher resource availability in watered sites is high enough for all seeded species to coexist, but perennial grasses are only able to capitalize on higher resource availability when they receive a priority effect by delaying annual grass seeding until spring.

2.5.2 Seedling density and biomass after two growing seasons

Seeding perennial grasses into annual grass invaded rangelands is very difficult and often results in very low densities because of the high existing annual grass propagule pressure available to occupy safe sites (Thomsen et al. 2006). DiVittorio et al. (2007) found that when annual grass propagule pressure is high, perennial grass density will be low. Similarly, we found that increasing annual grass seeding rate decreased perennial grass density. Because annual grasses germinate and emerge earlier than perennial grasses, annual grasses can preemptively occupy safe sites when seeded in autumn, (Hardegree et al. 2003). Thus, it is likely that safe sites for perennial grass establishment were limited by preemptive annual grass growth (Grubb 1977; Mangla et al. 2011).

In general, seeds are subject to ‘the law of diminishing returns’, or the theory that as more safe sites are filled it becomes less likely that the next seed will find an available safe site (Clark et al. 2007) (Aicher et al. 2011). Our results support this law since increasing seeding rates beyond 150 seeds m^{-2} increased the chance that a seed found a safe site, but there were no differences in the three highest seeding rates for annual or perennial grasses. Consequently, we accepted our hypothesis that increasing the propagule pressure of annual or perennial grasses increased their respective final seedling density. These findings suggest that the interactions between propagule pressure and safe site availability may be reasonable predictors of plant assembly (Aicher et al. 2011; Grubb 1977) because high propagule pressure can increase safe site occupation (Davies and Sheley 2011). However, because perennial grasses only had higher final plant density when 2,500 seeds m^{-2} or more seeds were sown, adding at least 2,500 perennial grass seeds m^{-2} is likely necessary to produce adequate perennial grass densities acceptable for restoration. Alternatively, because annual grass density was only limiting at the lowest annual grass seeding rate, annual grass propagule pressure of at least 1,500 annual grass seeds m^{-2} likely yields high numbers of annual grasses that may interfere with perennial grass growth.

Grman and Suding (2010) suggest that seeding perennial grasses before annual grasses will provide perennial grasses a priority effect of occupying safe sites before annual grasses. Similarly, our data support this conclusion because we accepted our hypothesis that delaying annual grass seeding until the spring would produce lower annual grass density than seeding annual grasses in autumn and when annual grass seeding was delayed until spring, perennial grass biomass was higher than when annual grasses were seeded in autumn. However, perennial grass biomass was only higher when annual grass seeding was delayed until the spring and water was not added. High total plant density reduces available resources for individual plant growth and will usually reduce the final plant density (White 2001). In addition, annual grasses interference on seeded perennial grasses can be high at the early perennial grass growth stages (Hardegree et al. 2010). In our study, adding water to plots in 2012 produced extremely high annual grass density and high interference from annual grasses on perennial grasses likely decreased final perennial grass biomass when water was added. Our data also indicate that the density of annual grasses was higher at higher perennial grass seeding rates when annual grasses were seeded in autumn. It is possible that neighboring perennial grasses facilitate annual grass density, especially when the numbers of neighboring perennial grasses are high (Tielborger and Prasse 2009). Coincidently, seeding annual grasses in autumn, even with higher water availability, will still likely favor annual grass dominance since seeded perennial grasses only had the higher density when they were provided a priority effect by delaying annual grass seeding until spring.

We were unable to accept our hypothesis that the density of annual and perennial grasses would be higher when water was added. In general, plant populations follow the law of constant final yield, or the notion that at high density populations maintain a constant final biomass, even as density continues to increase (Kira et al. 1953). Our data on annual grasses somewhat support this law because when annual grass density increased, total biomass remained fairly constant. Increasing perennial grass seeding rate increased annual grass biomass when water was not added suggesting that annual grasses do not have a constant biomass and instead are facilitated by the increasing presence of perennial grass seeds (Lortie and Turkington 2008). Because annual grasses have specific functional traits, such as high relative growth rate (Svejcar 1990), high resource acquisition (Svejcar and Sheley 2001), and high root growth (Monaco et al. 2003), the ability of annual grasses to acquire resources may not be as constrained by the available resources when annual grasses have high neighboring seed density. In addition, it is possible that when water was applied in 2012, annual grass density was so high in these areas that resource availability and seed production in water added plots of 2013 was limited. Consequently, our data contradict the theory that higher resource availability at early plant growth stages increases perennial grass establishment in annual grass invaded shrub steppe because of the high resource preemption from annual grasses in these systems.

2.5.3 Conclusions and management implications

Native perennial grass recruitment into invasive annual grass dominated sites depended on the interaction among dispersal timing, propagule pressure and water availability in this study. Providing perennial grasses a priority effect by delaying annual grass seeding until spring initially facilitated perennial grass density but this effect did not persist into the second-year following seeding. When annual grass propagule pressure exceeded 150 seeds m^{-2}, an ecological threshold was crossed which limited perennial grass recruitment regardless of perennial grass seeding rate. We also found that higher soil water availability increased perennial grass establishment by increasing safe site availability but was dependent on annual grass propagule pressure. Based upon the results, success of seeding perennial grasses into annual grass dominated systems is more dependent upon the existing propagule pressure of annual grasses than the priority effects of perennial grasses, the propagule pressure of perennial grasses, or the water availability. Several management strategies could be helpful in mitigating propagule pressure effects in these degraded rangelands. First, ensuring that the existing seed bank does not exceed 150 annual grass seeds m^{-2} before seeding is likely necessary to ensure perennial grass recruitment following seeding. In addition, increasing perennial grass propagule pressure to at least 2,500 seeds m^{-2} will likely yield increased perennial grass density. Using these management strategies should increase perennial grass recruitment in annual grass dominated shrub-steppe.

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Table 2-1 Seeding factors and factor levels (n = 192)

Dispersal Timing	*Water*	*Annual grass seeding rate (seeds m^{-2})*	*Perennial grass seeding rate (seeds m^{-2})*
November	No-Water	150	150
February	Water	1,500	1,500
		2,500	2,500
		3,500	3,500

Table 2-2 ANOVA table of main effects and interactions of treatment effects in 2013 ($P < 0.05$; n = 192). Table includes density degrees of freedom (*df*), final annual grass density and biomass, and final perennial grass density and biomass. Bold numbers are significant.

		***p* Value**			
		Perennial Grass		Annual Grass	
Effects and Interactions	***df***	Density	Biomass	Density	Biomass
Seeding Time (Timing)	2	0.2011	0.3259	**0.0196**	**0.0003**
Water	1	0.3878	0.3363	**<.0001**	**0.0052**
Timing + Water	2	0.9762	**0.0521**	0.1608	0.4974
Annual seeding rate (Annual)	3	**<0.0001**	0.2226	**<.0001**	**<.0001**
Timing + Annual	6	0.3632	0.7793	0.7595	0.6445
Water + Annual	3	0.6822	0.7212	0.065	0.4512
Timing + Water + Annual	6	0.398	0.6424	0.6611	0.9884
Perennial Seeding Rate (Perennial)	3	**0.0138**	0.7729	0.9798	0.3420
Timing + Perennial	6	0.6790	0.4166	0.1182	0.7548
Water + Perennial	3	0.8074	0.6745	0.2857	0.0670
Timing + Water + Perennial	6	0.8091	0.3244	0.6918	0.6925
Annual + Perennial	9	0.3202	0.6348	0.3748	0.9273
Timing + Annual + Perennial	18	0.4931	0.7024	0.4232	**0.0481**
Water + Annual + Perennial	9	0.7019	0.4542	0.2149	0.3323
Timing + Water + Annual + Perennial	18	0.8590	0.6105	0.7004	0.1513

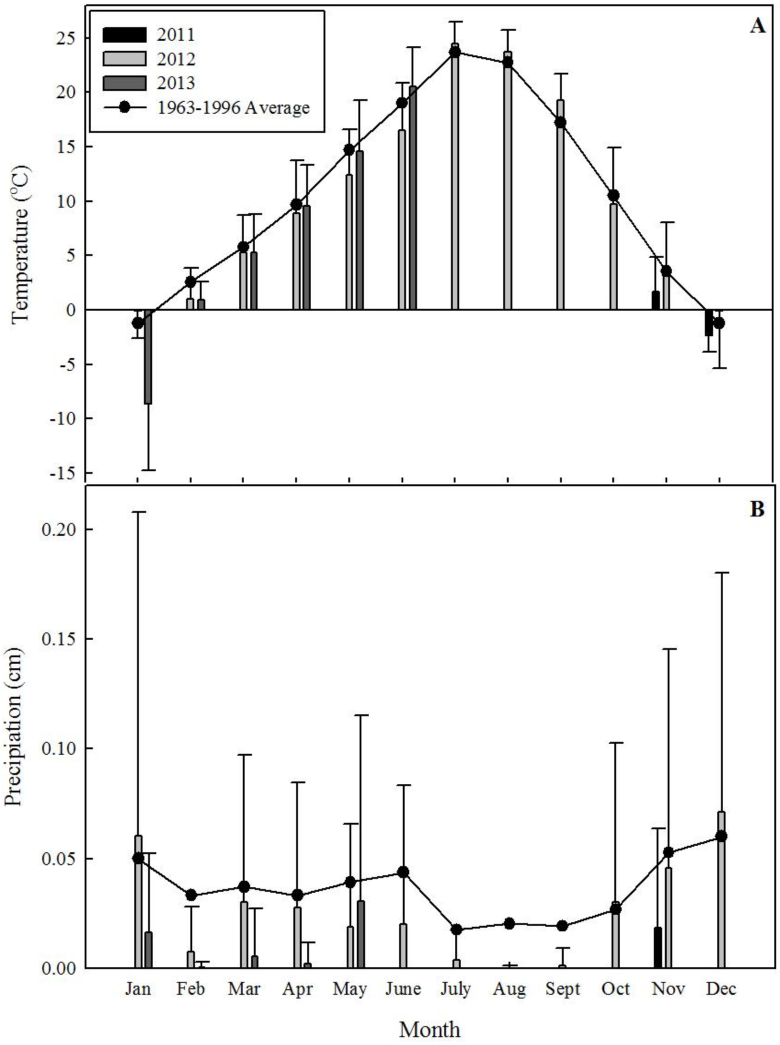


Figure 2-1 Mean and standard deviation of climate data during the study period (November, 2011- June, 2013) and the 30 year average (1963-1996) for precipitation and temperature. Figure A represents daily precipitation (cm); Figure B represents daily temperature (˚C).

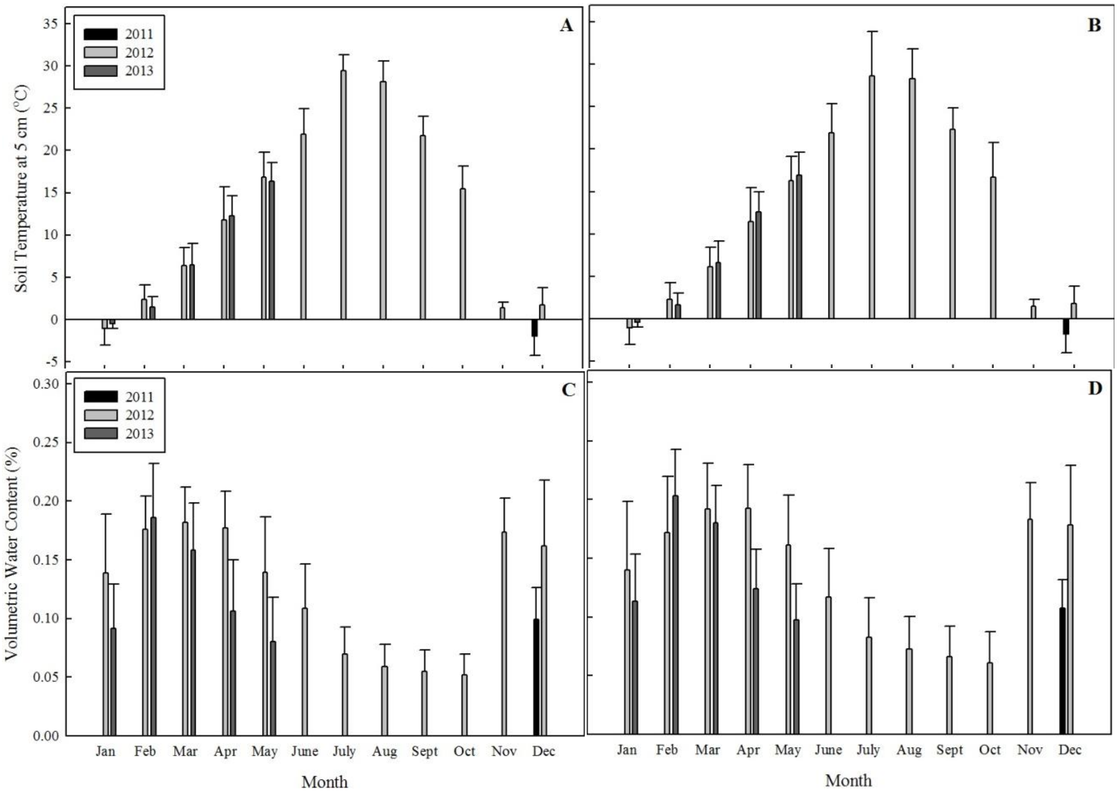


Figure 2-2 Means and standard deviation of soil temperature at 5 cm (˚C) and volumetric water content at 5 cm (%) during the study period (December, 2012-May 2013). Figure A represents soil temperature in the no water treatments, Figure B represents soil temperature in the water added treatments, Figure C represents volumetric water content in the no water treatments, and Figure D volumetric water content in the water added treatments.

Figure 2-3 Least squared means and standard error of perennial grass seedling density (density m^{-2}) at 6 sampling times in 2012 by seeding time and watering interaction for each annual and perennial grass propagule pressure ($P < 0.05$). The panel of figures represents the difference in propagule pressure where perennial grass propagule pressure increases along the y-axis and annual grass propagule pressure increases along the x-axis. Within each figure, perennial grass density (plants m^{-2}) increases along the y-axis and sampling time (March 13- June 2) increases along the x-axis. Points in each figure represent the perennial grass density by the seeding time by watering interaction. Bars indicate standard error. (Continued on next page)

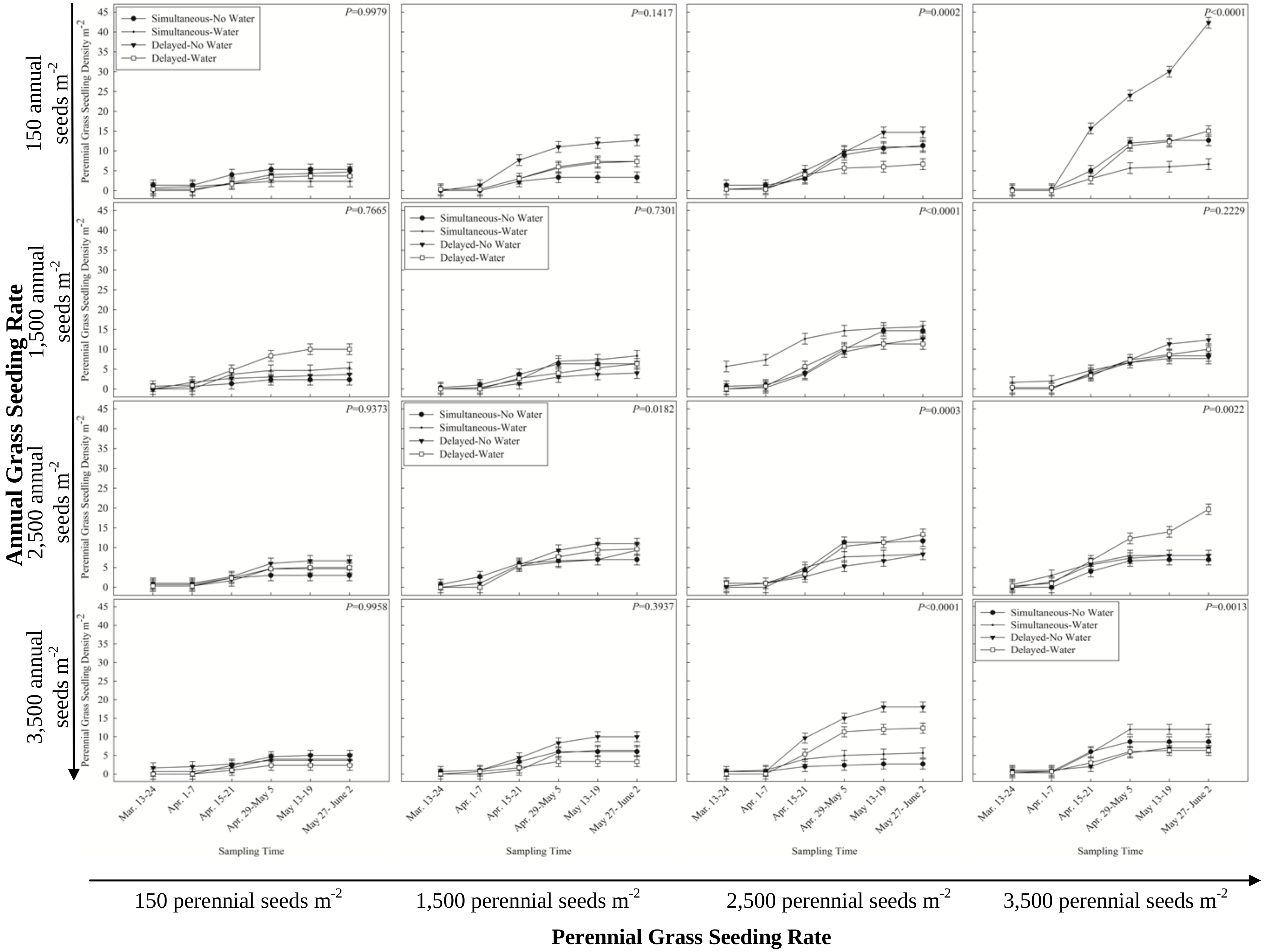
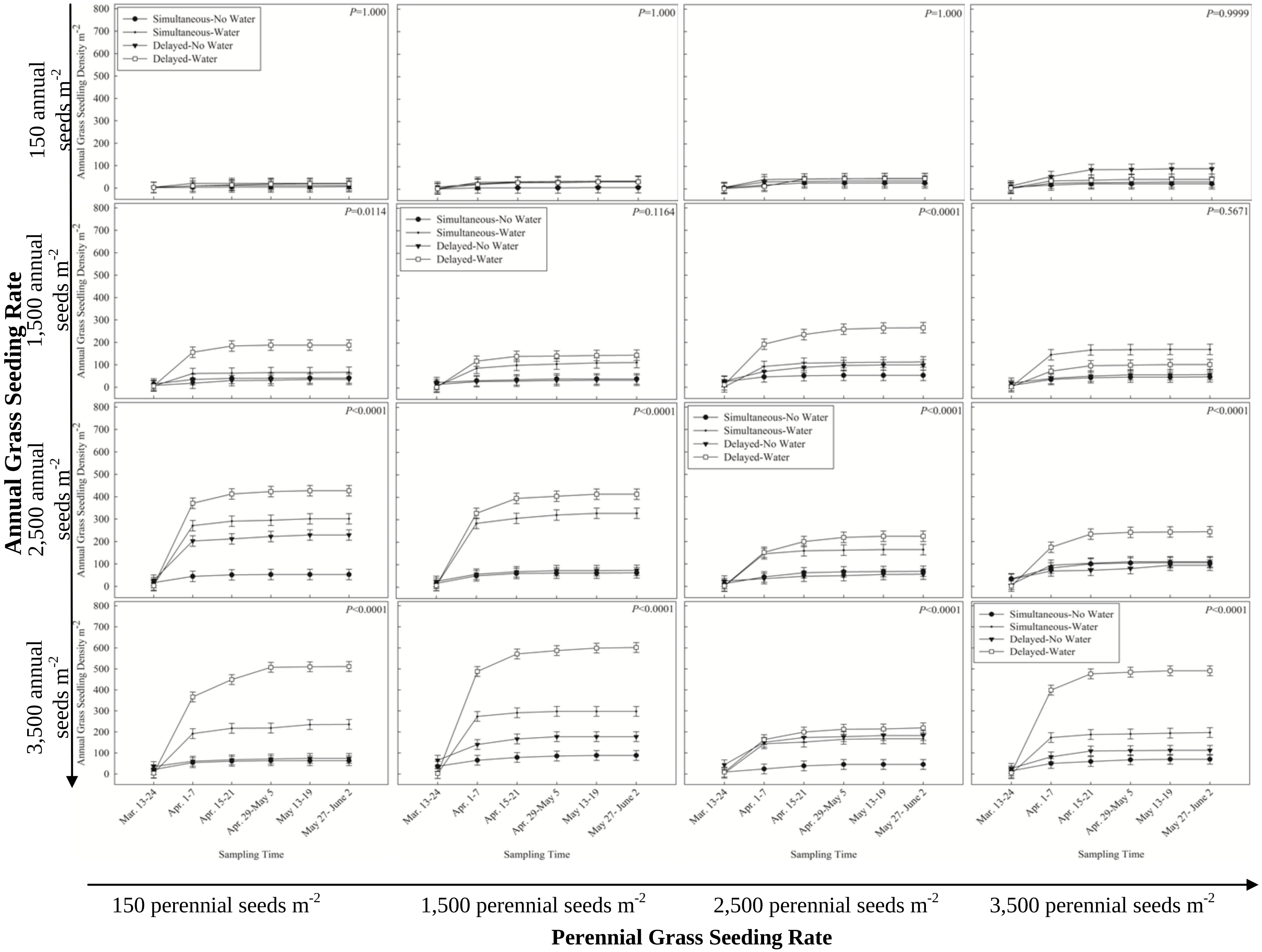

Annual Grass Seeding Rate
150 annual seeds m^{-2}
1,500 annual seeds m^{-2}
2,500 annual seeds m^{-2}
3,500 annual seeds m^{-2}
Perennial Grass Seedling Density m^{-2}
0
5
10
15
20
25
30
35
40
45
Simultaneous-No Water
Simultaneous-Water
Delayed-No Water
Delayed-Water
P=0.9979
P=0.1417
P=0.0002
P<0.0001
P=0.7665
P=0.7301
P<0.0001
P=0.2229
P=0.9373
P=0.0182
P=0.0003
P=0.0022
P=0.9958
P=0.3937
P<0.0001
P=0.0013
Mar. 13-24
Apr. 1-7
Apr. 15-21
Apr. 29-May 5
May 13-19
May 27- June 2
Sampling Time
150 perennial seeds m^{-2}
1,500 perennial seeds m^{-2}
2,500 perennial seeds m^{-2}
3,500 perennial seeds m^{-2}
Perennial Grass Seeding Rate

Figure 2-4 Least squared means and standard error of annual grass seedling density (density m^{-2}) at 6 sampling times in 2012 by seeding time and watering interaction for each annual and perennial grass propagule pressure ($P < 0.05$). The panel of figures represents the difference in propagule pressure where perennial grass propagule pressure increases along the y-axis and annual grass propagule pressure increases along the x-axis. Within each figure, annual grass density (plants m^{-2}) increases along the y-axis and sampling time (March 13- June 2) increases along the x-axis. Points in each figure represent the annual grass density by the seeding time by watering interaction. Bars indicate standard error. (Continued on next page)


Annual Grass Seeding Rate
150 annual seeds m^{-2}
1,500 annual seeds m^{-2}
2,500 annual seeds m^{-2}
3,500 annual seeds m^{-2}
Annual Grass Seeding Density m^{-2}
0
100
200
300
400
500
600
700
800
Simultaneous-No Water
Simultaneous-Water
Delayed-No Water
Delayed-Water
P=1.000
P=1.000
P=1.000
P=0.9999
P=0.0114
P=0.1164
P<0.0001
P=0.5671
P<0.0001
P<0.0001
P<0.0001
P<0.0001
P<0.0001
P<0.0001
P<0.0001
P<0.0001
Mar. 13-24
Apr. 1-7
Apr. 15-21
Apr. 29-May 5
May 13-19
May 27- June 2
Sampling Time
150 perennial seeds m^{-2}
1,500 perennial seeds m^{-2}
2,500 perennial seeds m^{-2}
3,500 perennial seeds m^{-2}
Perennial Grass Seeding Rate

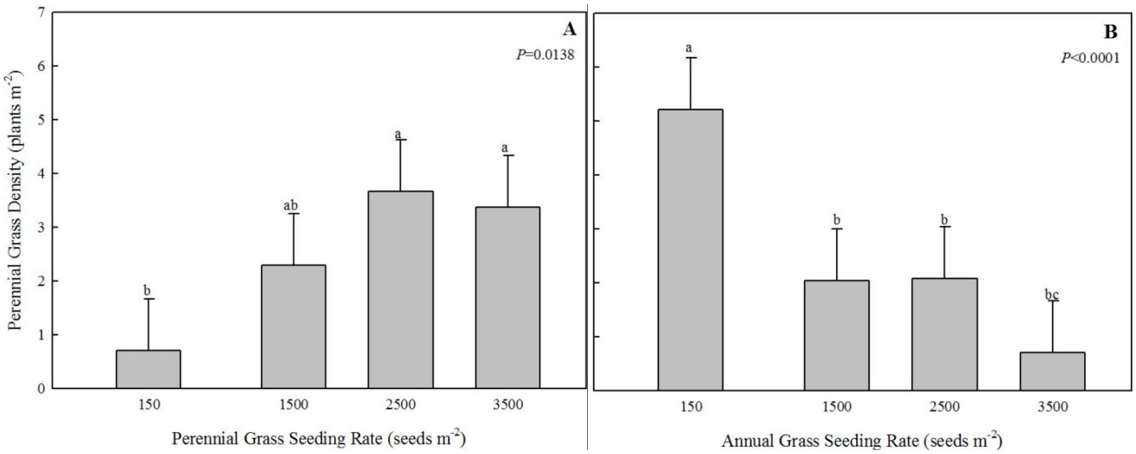


Figure 2-5 Least squared means and standard error of perennial plant density (density m^{-2}) in 2013. Figure A represents perennial grass seeding rate (*P*=0.0138). Figure B represents annual grass seeding rate (*P* <0.0001). Letters indicate significant differences.

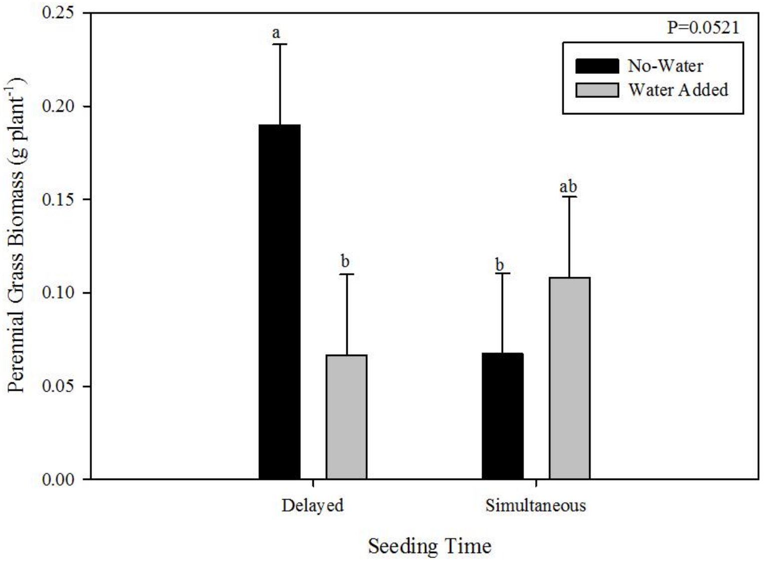


Figure 2-6 Least squared means and standard error of individual perennial plant biomass (g plant^{-1}) in 2013 by watering and seeding time (*P* = 0.0521). Letters indicate significant differences.

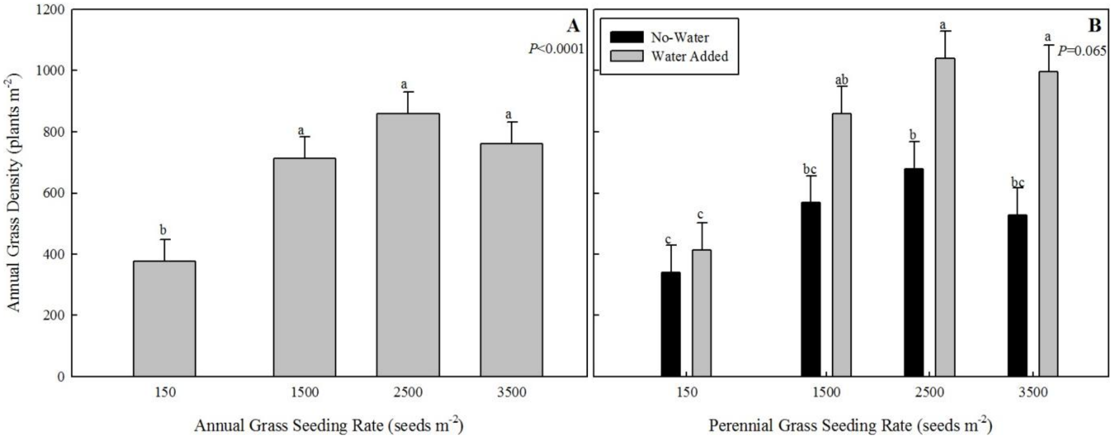


Figure 2-7 Least squared means and standard error of annual plant density (density m^{-2}) in 2013. Figure A represents annual grass seeding rate (*P* <0.0001). Figure B represents seeding time and perennial seeding rate interaction (*P* = 0.065). Letters indicate significant differences.

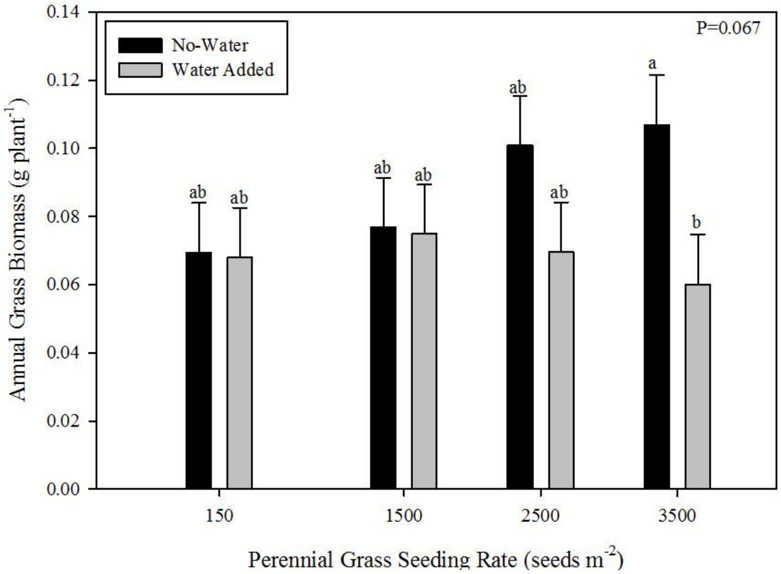


Figure 2-8 Least squared means and standard error of individual annual plant biomass (g plant^{-1}) 2013 based upon the timing and perennial seeding rate treatment interactions (P = 0.067). Letters indicate significant differences.

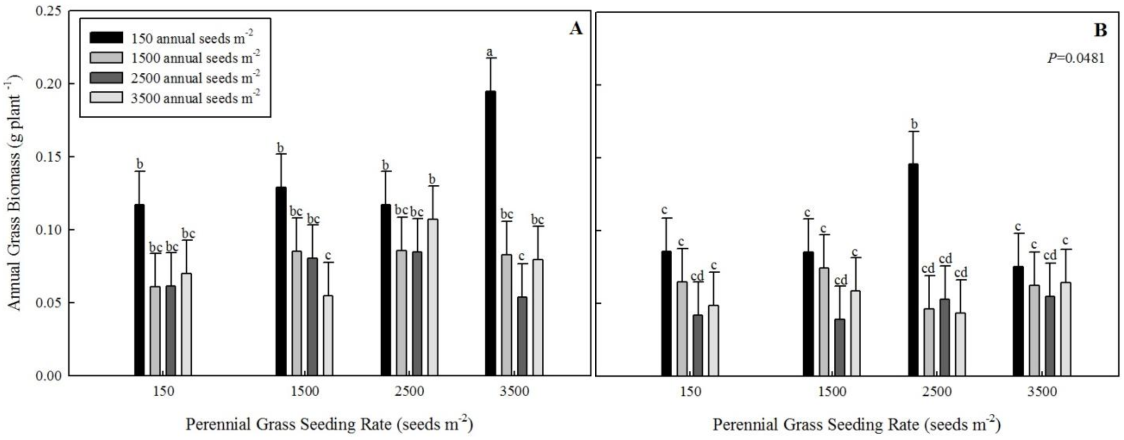


Figure 2-9 Least squared means and standard error of individual annual plant biomass (g plant^{-1}) in 2013 by water availability, annual grass propagule pressure, and perennial grass propagule pressure interaction (*P* = 0.0481). Figure A represents the no-watering treatment. Figure B represents the watering treatment. Letters indicate significant differences.

Annual grass propagule pressure limits perennial grass recruitment regardless of seeding strategy or water availability

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3 Second Manuscript

Annual grass propagule pressure limits perennial grass recruitment regardless of seeding strategy or water availability

Merilynn C. Schantz [1], Roger L. Sheley [2], Jeremy J. James [3], Erik P. Hamerlynck [2]

[1] Department of Animal and Rangeland Sciences, Oregon State University, Corvallis, OR 97332; [2] United States Department of Agriculture-Agricultural Research Service, Burns, OR, 97720; [3] Sierra Foothills Research and Extension Center, University of California Division of Agriculture and Natural Resources, Browns Valley, CA 95918.

3.1 Abstract

Perennial grass dispersal dynamics can strongly affect plant community assembly in restored annual grass infested ecosystems, yet the impacts of dispersal timing and magnitude on plant community assembly is poorly understood. To assess these effects, we established a field experiment consisting of 288-1 m^{-2} plots in an annual grass dominated shrub-steppe ecosystem in eastern Oregon. We manipulated the amount, timing, and frequency of perennial grass seeding events while simultaneously manipulating soil moisture availability and annual grass seed bank density. We found that more frequent perennial grass seeding events combined with high perennial grass seeding rates produced the highest density and biomass of perennial grasses two years following seeding. However, if annual grass seed density exceeded 1,500 seeds m^{-2}, perennial grass density and biomass decreased, regardless of perennial seeding strategy. It appears that a threshold is crossed between 150-1,500 annual grass seeds m^{-2}, where perennial grass recruitment was low regardless perennial grass seeding strategies. Increasing water availability in the first growing season initially facilitated perennial grass establishment, but only produced higher perennial grass density following the second growing season when annual grass density was lowest. We conclude that assessing the existing annual grass seed bank prior to seeding can forecast restoration outcomes because if annual grass seed densities are higher than 1,500 seeds m^{-2}, annual grasses will likely interfere with, and reduce perennial grass recruitment. In addition, if annual grass seeding density is 1,500 seeds m^{-2} or lower, modifying the temporal patterns of perennial grass seed arrival will increase the likelihood that a perennial grass seed finds a safe site.

Keywords: Dispersal, Propagule Pressure, Water Availability, Assembly, Restoration

3.2 Introduction

Invasive annual grasses threaten a number of perennial dominated dryland systems across the globe (Hobbs et al. 2006; Seastedt and Pyšek 2011). Limiting annual grass dominance is dependent on our understanding of the processes promoting annual grass invasion and spread to non-invaded areas (Krueger-Mangold et al. 2006). Annual grasses rapidly spread and establish into recently disturbed regions because of their short life-cycle and key functional traits (Epanchin-Niell et al. 2009). Functional traits that promote annual grass establishment and persistence include relatively thin leaf and root tissue, which facilitates rapid seedling growth, and greater proportional allocation to seed production in established plants (Dyer et al. 2012). In addition, Leffler et al. (2013) found that annual grasses initiate growth earlier than perennial grasses, allowing these species to preemptively occupy space and exploit soil resources. Coupled with these functional traits; if annual grasses dominate an ecosystem, disturbance cycles from wildfire increase (Brooks et al. 2004; D'Antonio and Vitousek 1992) and biogeochemical cycles are modified (Ehrenfeld 2010), inducing negative feedbacks that perpetuate further annual grass invasion and dominance (Yelenik and D'Antonio 2013).

Restoring structure and function to annual-grass degraded drylands requires intense management inputs like seeding (Sheley et al. 2006). Seeding can accelerate native plant recovery and stabilize native populations in highly degraded and annual grass invaded areas (Seabloom et al. 2003). If a seeded plant community is stable, seeded species are capable of developing into reproductive adults that leave, on average, one offspring that will survive to reproductive maturity (Moles and Leishman 2008).

However, restoring stable native plant communities into invaded plant communities typically has low success rates (Rinella et al. 2012). A good example of this is found in seeding native perennial grasses into annual grass invaded shrub-steppe ecosystems (Allen and Cox 2008). Degraded shrub-steppe ecosystems have low perennial grass seedling recruitment because exotic annual grasses establish from extensive seed banks and preemptively occupy space and soil resources before native perennials initiate growth (Orrock and Christopher 2010). Further complicating these restoration efforts, perennial grass develop slowly from seed compared to invasive annuals (Montoya et al. 2012), and annual grasses can produce up to 28 times more seeds compared to native perennial grasses in their first growing season (Kulpa et al. 2012). Because of such temporal limitations to perennial grass seedling recruitment, modifying the timing and seeding patterns of perennial grasses could increase the likelihood that a perennial grass seed finds a viable safe site (Stella et al. 2006).

Seed dispersal can be a major driving mechanism of plant community assembly, especially during invasion and restoration, because dispersal controls recruitment of newly arriving species by influencing safe site occupation (Satterthwaite 2007). Safe sites, or resource patches that support diverse plant populations, provide conditions suitable for seedling germination and establishment (Grubb 1977; Titman 1976). Plant community assembly is largely determined by the interaction between seed and safe site availability for successful plant growth (Doll et al. 2011). Safe site availability varies through time and space depending on the resource availabilities and safe site occupation (Duncan et al. 2009). Modifying dispersal dynamics of desired species to better match the availability of safe sites may increase their recruitment into annual grass dominated systems. However, DiVittorio et al. (2007) found that perennial grasses did not establish in areas with high annual grass propagule pressure, as these likely preemptively occupied available safe sites. Alternatively, Orloff et al.(2013) showed that bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) could co-exist with annual grasses if it was able to establish to two- to four-leaf stages before annual grasses were seeded. Thus, there is no unified understanding of how plant community assembly is affected by seeding dispersal time and frequency under varying annual grass propagule pressure and resource availability.

Here, we present the results of a multi-year study where we sought to quantify how the amount, timing, and frequency of perennial grass seeding affects the temporal trajectories of annual and perennial grass seedling emergence, and shapes final plant community composition and biomass two years following seeding. In addition, we sought to quantify how these dynamics are modified by soil water availability and annual grass seed bank density. We experimentally varied seeding rates of desired native species across three distinct seed timing regimes: (1) seeding exclusively in the autumn, (2) exclusively in the spring, or (3) evenly splitting seeding between spring and autumn. These perennial grass seeding regimes were applied into plots with varying invasive annual autumn seeding rates and water availability. Based on the fact that under drier conditions invasive annual grasses are better able to recruit from their extensive seed banks than native perennial grasses (Walck et al. 2011), and frequently initiate seedling germination and emergence earlier in the spring (Abraham et al. 2009; Wainwright and Cleland 2013), we specifically hypothesized that:

1) Perennial grass seed dispersal split between the autumn and spring would result in higher perennial grass density and biomass compared to seeding native grasses exclusively in either period.
2) Perennial grass density and biomass in seasonally split applications would be higher when perennial propagule pressure was high and annual grass propagule pressure was low.
3) Adding water would increase perennial grass density and biomass, especially in plots with seasonally split seeding and high perennial grass propagule pressure.

Identifying the relative effect of propagule pressure and dispersal timing and frequency on community assembly should allow ecologists to better plan successful restoration projects in annual grass invaded shrub-steppe ecosystems.

3.3 Materials and Methods

The study site was located in low elevation (1,033 m) shrub-steppe dominated by annual grasses located ca. 5 km south of Juntura, Malheur County, Oregon (Zone: 11, 410178 easting, 4840910 northing). This site has a very slight slope facing southwesterly and is devoid of sagebrush. Current vegetation structure is a near monoculture of medusahead (*Taniatherum caput-medusae* (L.) Nevski) growing in association with species of cheatgrass (*Bromus tectorum* L.), with scattered individuals of Sandberg bluegrass (*Poa secunda* J. Presl), whitetop (*Cardaria draba* (L.) Desv.), squirreltail (*Elymus elymoides* (Raf.) Swezey), and morning glory (*Ipomoea eriocarpa* R. Br.). Soils at the site are sandy- loams within the Bogusrim series (fine, smectitic, mesic abruptic Xeric Argidurids). Soil in the Bogusrim series receives an average 457 mm precipitation per year with a bimodal distribution peaking in the winter and spring.

Average daily precipitation (cm), and temperature (˚C) were recorded daily from November 2011 to June 2013 using a HOBO rain gauge smart sensor that was connected to a HOBO weather station and was mounted approximately 3 meters from the soil surface, inside of a HOBO solar shield (Onset Comp. Inc., Cape Cod, MA, USA). Long-term (1963-1996) daily average precipitation and temperature data from Juntura, OR were obtained from the Western Regional Climate Center (WRCC 2013). Volumetric soil water content (%) and soil temperature (˚C) at five cm were monitored using Decagon 5TM soil moisture sensors (Decagon Devices Inc., Pullman, WA, USA) from November 2011 to June 2013.

3.3.1 Model system

To test how seeding strategies affect species density through their life history, we used a model system consisting of the invasive annual grasses, cheatgrass, and medusahead (50-50 mixture) as the invaders. The desired native system was represented by the perennial grasses Anatone bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), bottlebrush squirreltail, Mountain Home Sandberg bluegrass, and Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth) seeded in equal proportions. Annual grass seeds were collected locally, by hand, from Harney Co. Oregon, bottlebrush squirreltail, Sandberg bluegrass, and bluebunch wheatgrass were purchased from Granite Seed Co., Lehi, UT in 2011, and Thurber’s needlegrass was purchased from BFI Native Seeds Co., Moses Lake, WA in 2010. Seeding rate was applied on a per weight basis so that each plot received 100% pure-live seeds per plot.

3.3.2 Propagule pressure and dispersal timing and frequency

Prior to initiating the study, the site was sprayed with 3.36 L ha^{-1} of glyphosate [N-(phosphonomethyl) glycine] and tilled to about 100 mm to remove any existing vegetation. Densities and proportions of annual grasses and perennial grasses were arranged to provide four addition-series matrices (Radosevich 1987). Seeding densities of annual: perennial grasses in each matrix were 150:150, 150:1,500, 150:2,500, 150:3,500, 1,500:150, 1,500:1,500, 1,500:2,500, 1,500:3,500, 2,500:150, 2,500:1,500, 2,500:2,500, 2,500:3,500, 3,500:150, 3,500:1,500, 3,500:2,500, and 3,500:3,500 seeds m^{-2}. Annual grass seeds were exclusively sown in the autumn (November 2011), while perennial grasses were sown in three experimental periods: autumn only, spring only (February 2012), and seasonally split (even seeding in autumn and spring). Half of the plots of each seeding regime were randomly selected for a watering treatment (see below) to complete the treatment matrix. Each matrix was replicated three times in a completely randomized design yielding 288 1-m^2 plots (Table 1).

Seeding was achieved by hand broadcasting seeds onto the soil surface of 1 m^2 plots and covering seeds with two cm of sifted weed-free topsoil collected from the site. Watering was administered weekly during the growing season in year one (March 1,-May 30, 2012) using watering cans to evenly distribute water on each water added treatment plot. Water was added at twice the long-term monthly precipitation average of water (March-May), which varied from 2.05-2.61 L added per month. Watering only occurred during the first year of the study to identify how water availability during the first growing season affected plant performance in subsequent years.

3.3.3 Sampling and measurements

Plant density was counted within the center 0.5 m^2 of the plot for perennial species and the center 0.25 m^2 for annual species biweekly during the first growing season (March 25, - June 9, 2012). Because of the high density of annual grasses and the difficulty of counting all annual and perennial grasses within each plot, the measurement area for annual grass density was lower than that for perennial grasses. Plants were individually marked, bi-weekly, with toothpicks as they emerged. Total mortality was measured by counting the number of free standing toothpicks from each emergence period. At the end of the second growing season (June 3-14, 2013), final density was counted and all plants were clipped to ground level, sorted by species, dried at 60 ºC, and weighed to determine individual plant biomass (g plant $^{-1}$).

3.3.4 Statistical analysis

All data were pooled by annual and perennial grasses and analyzed for the distribution and homogeneity of variance using with Shapiro-Wilk and Levene tests, respectively (SAS Institute Inc., Cary, NC, 2012). Annual grass emergent coleoptile density, established final grass density, and biomass were normally distributed. However, these variables from perennial grasses showed distinct right-skewing. Log, square root, and log+1 transformations were used, but did not improve data distribution or helped the model fit. Thus, all models were generated from non-transformed data for perennial species.

To test for differences the seasonal emergence of perennial and annual grasses, emergent coleoptile seedling density was analyzed using a repeated-measures analysis of variance (RM-ANOVA; SAS 9.2; SAS Institute, Cary, NC, 2012). In this model, main effects tested for were perennial grass dispersal time (autumn, spring, and split seeding), watering (control vs. water added), annual grass seeding rate (150, 1,500, 2,500, or 3,500 seeds m^{-2}), perennial grass seeding rate (150, 1,500, 2,500, or 3,500 seeds m^{-2}), and sampling time (bi-weekly yielding 1728 total samples) and all interaction effects were tested on the density of annual and perennial grass coleoptiles. A mixed-model ANOVA was used to test for differences in final plant density and biomass using the 2013 data using SAS (SAS 9.2; SAS Institute, Cary, NC, 2012). Main effects in this model were (autumn, spring, and split seeding), watering (control vs. water added), annual grass seeding rate (150, 1,500, 2,500, or 3,500 seeds m^{-2}), and perennial grass seeding rate (150, 1,500, 2,500, or 3,500 seeds m^{-2}) were made using the 2013 data. In both the coleoptile emergence and final density and biomass models, the random factor was replication, means were separated using the slice procedure (Schabenberger, 2013), and F-test results with an associated *P* value of ≤ 0.05 considered significant.

Data of specific interest to this study were the seeding period-by-sampling time interaction, as this would show treatment-specific differences in annual and perennial grass emergence to seasonal environmental variability. In addition, the main perennial seeding time effect was used to test our hypothesis split seeding will do better than spring or fall exclusive seeding. The two-way seeding time-by-seeding rate effect was used to test our hypothesis that split seeding at high perennial seeding and low annual seeding will result in higher plant density and biomass. Finally, the two-way seeding time-by-watering interaction was used to test our hypothesis that perennial biomass in split seeding will respond better to watering than the other perennial seeding times.

3.4 Results

3.4.1 Environmental conditions

Temperature was consistent with long-term averages, while precipitation was lower than the 30 year mean in the summer months and average throughout the rest of the year (Fig. 1). Volumetric water content was somewhat higher in the water added sites, although volumetric water content and soil temperature at 5 cm were not different between the ambient water and water added plots (Fig. 2). Volumetric water content fluctuated from a high of about 25% from November-April to a low of about 10% from May-October (Fig. 2 A, B). Soil temperature at 5 cm fluctuated similarly to air temperature, but was generally 5˚C higher than air temperature throughout the study period (Fig. 2 C, D).

3.4.2 Seedling density

When perennial grass seeding rates were 150 seeds m^{-2}, all treatments produced low perennial grass density. Higher perennial grass seeding rates produced greater perennial grass seedling density (Fig. 3; $F_{3,144} = 33.16$; $P<0.0001$). Pooled across watering and seeding rates, timing of perennial grass seeding resulted in significant differences in perennial grass density ($F_{2, 48} = 4.12$; $P=0.0223$), with grass seeding in spring, split between autumn and spring yielding higher perennial grass density than sowing in autumn (Fig. 3). When water was added, perennial grass seeding density was higher across all seeding treatments (Fig. 3; $F_{1, 12} = 41.17$; $P<0.0001$). However, the lack of a significant seeding rate-by-watering treatment interaction showed that adding water did not increase perennial grass density when annual grass seeding rates were high and perennial grass seeding rates were low (Fig. 3; $F_{9, 44} = 0.91$; $P=0.5212$). Across all seeding treatments, perennial grass seedling density increased from about mid- to late-April to mid-May (Fig. 3; $F_{5, 12} = 43.39$; $P < 0.0001$).

Annual grass density varied significantly with annual grass (Fig.4; $F_{3,144} = 21.9$; $P<0.0001$) and perennial grass seeding rates ($F_{3,144} = 5.93$; $P=0.0008$). At 150 annual grass seeds m^{-2}, all treatments produced similar annual grass density. Seeding perennial grasses in autumn produced higher annual grass density than spring or seasonally-split perennial grass seeding (Fig. 4; $F_{2, 48} = 16.46$; $P<0.0001$). When water was added, annual grass density was higher (Fig. 4; $F_{1, 12} = 10.11$; $P=0.0079$). Across all seeding treatments, annual grasses had the greatest increase in seedling density from late-March to early-April, after which, seedling density remained fairly constant (Fig. 4; $F_{5, 12} = 38.33$; $P<0.0001$).

3.4.3 Final seedling density and biomass

Final perennial grass density in 2013 was 2 plants m^{-2} higher in water added plots (3.44 plants m^{-2} ± 0.26) than those receiving ambient precipitation (1.47 plants m^{-2} ± 0.26; Table 2). Split seasonal seeding of perennial grasses produced the highest final perennial grass density (3.60 plants m^{-2} ± 0.31), followed by exclusive spring seeding (2.11 plants m^{-2} ± 0.31) and autumn seeding (1.66 plants m^{-2} ± 0.31; Table 2). Perennial grass seedling densities were highest when annual grass seeding rates were low and perennial grass seeding rate were high (Table 2; $P<0.0001$). Similarly, higher perennial grass seeding rates produced higher perennial seedling density; when perennial grass seeding rate was 150 seeds m^{-2} perennial grass density was only about 1 plant m^{-2}, but adding 3,500 seeds m^{-2} produced about 4 plants m^{-2} (Fig. 5A; $P<0.0001$). Perennial grass density was higher in watered plots, especially at low annual grass seeding rates (Fig. 5B; *P*=0.0312). In addition, when water was added, perennial grass density was about 6 plant m^{-2} when annual grass seeding rate was 150 seeds m^{-2}, but perennial grass density was 2-3 plant m^{-2} at all other annual grass seeding rates (Fig. 5B). Adding water produced the highest perennial grass density when perennial grass seeding occurred in autumn and spring, followed by seeding in spring (Fig. 5C; *P*=0.0403). However, when water was not added, perennial grass density did not differ between perennial grass seeding treatments (Fig. 4C).

Pooled across seeding rates and watering treatments, splitting seeding perennial grasses between autumn and spring produced the highest perennial grass biomass (0.170 g plant $^{-1}$ ± 0.033), followed by seeding in spring (0.063 g plant $^{-1}$ ± 0.033), and autumn (0.040 g plant $^{-1}$ ± 0.033; Table 2; *P*=0.0054). When annual grass seeding rates were low, perennial grass biomass was higher than at higher annual grass seeding rates pooled across all other treatments (Table 2). Consequently, when annual grass seeding rates were low, splitting seeding perennial grasses between autumn and spring produced marginally higher perennial grass (Fig. 6; *P*=0.0601).

Higher annual grass seeding rates yielded higher final annual grass density pooled across all treatment combinations (Table 2). However, the relative density of annual grasses decreased when annual grass seeding rates increased. For example, when 150 annual grass seeds m^{-2} were seeded, final annual grass density was about 200 plant m^{-2} (± 38.67), but seeding 3,500 annual grass seeds m^{-2} only produced about 600 plants m^{-2} (± 38.67). Annual grass density was about 200-400 plants m^{-2} higher at the three highest annual grass seeding rates within a seeding time as compared to when 150 annual grass seeds m^{-2} were added (Fig. 7; *P*=0.0654). When annual grass seeding rates were 1,500 or 3,500 seeds m^{-2}, annual grass density was highest when perennial grasses were seeded in autumn, than seeding perennial grasses in autumn and spring. In addition, annual grass density was higher when 3,500 annual grass seeds m^{-2} were added and perennial grasses were seeded in autumn as compared to delaying perennial grass seeding until spring. Seeding perennial grasses in spring produced higher annual grass density than evenly splitting seeding perennial grasses between autumn and spring when annual grass seeding rate were 2,500 or 3,500 seeds m^{-2}.

Annual grass biomass was highest when perennial grasses were split seeding (0.104 g plant $^{-1}$ ± 0.0132), followed by seeding perennial grasses in exclusively in spring (0.085 g plant $^{-1}$ ± 0.0132) or autumn (0.065 g plant $^{-1}$ ± 0.0132; Table 2). Adding water produced higher annual grass biomass (Table 2). However, when water was added, annual grass biomass did not depend on annual grass seeding rate (Table 2). When water was not added, seeding 150 annual grass seeds m^{-2} produced the highest annual grass biomass, especially when perennial grass seeding was distributed over autumn and spring (Fig. 8; *P*=0.0134). High annual grass seeding rates resulted in lower individual plant biomass in annual plants; at 150 annual seeds m^{-2} seeding rates, plant biomass was 0.135 g plant^{-1} (± 0.014), and only 0.07 g plant^{-1} (± 0.014) at a 3,500 seeding rate (*P*<0.0001; post-hoc slice). In addition, we detected a marginally significant effect of higher annual grass biomass when annual grass seeding rates were low and perennial grass seeding occurred in autumn, or autumn and spring, across all perennial grass seeding rates and water treatments (Fig. 9; *P*=0.084). Alternatively, perennial grasses were seeded in spring, annual grass biomass was higher when perennial grass seeding rates were higher and annual grass seeding rates were lower (Fig. 9).

3.5 Discussion

3.5.1 Seedling density

Seedlings are prone to high mortality, especially between the germination and emergence growth stages (James et al. 2011). However, mortality depends on inter-annual and seasonal climate and resource variability (Thomsen et al. 2006; Adair et al. 2008) and seedling functional traits (Steers et al. 2011). Annual grasses avoid many of the harsh environmental conditions of the shrub-steppe by growing early and quickly (Abraham et al. 2009). In our study, annual grasses emerged about two weeks earlier and had 2.5 times higher emergence rates than perennial grasses. Because annual grasses initiate and complete their life cycle early, they preempt resources from seeded perennial grasses (Orloff et al. 2013). In addition, arid regions like the shrub-steppe are limited by the total number of safe sites available for plant growth (Graae et al. 2011; Gross et al. 2005). It appears that perennial grasses in our study were limited by safe site availability because the total numbers of safe sites were low and those safe sites that were available were likely occupied by earlier growing annual grasses.

Our hypothesis that perennial grass seedling density would be highest when perennial grass seeding was evenly split between autumn and spring was supported by the results of this study (Table 2). Modifying perennial grass seeding timing and frequency seems to have increased the chance that a desirable seed reached a safe site (Yelenik and Levine 2010). When seeding is delayed until spring, the likelihood that a seed reached a safe site likely increased because autumn seeded -plants can have high winter mortality, which may increase safe sites for spring seeds (James et al. 2012). James et al. (2011) identified that winter mortality in shrub-steppe can affect about 90%

of graminoid seedlings between the germination and emergence life history stages. In a previous study, we also found that when annual grasses were seeded in the spring, annual grass density and biomass was higher than when annual grasses were seeded in autumn (Schantz et al. *in press*). However, the effect of seeding time on plant community assembly likely depends upon the seeding rate of desirable species and invader propagule pressure.

Annual grass preemption of safe sites can reduce perennial grass density, especially when annual grass propagule pressure is high (DiVittorio et al. 2007). In this study, our results supported our hypothesis that the density of emerging perennial grass coleoptiles would be highest when annual grass propagule pressure was low, perennial grass propagule pressure was high, and when perennial grass seeding occurred in autumn and spring (Fig. 3) (Aicher et al. 2011; Bergelson and Perry 1989). Perennial grass density was also high when perennial grasses were seeded in spring, but only when annual grass propagule pressure was low. Because annual grasses begin growth earlier than perennial grasses, it seems that annual grasses preemptively occupy safe sites and diminish soil resources, thereby reducing perennial grass density (Chambers et al. 2011). However, our finding that delaying perennial grass seeding until spring increased the probability of a seed reaching a safe site when annual grass propagule pressure was low, suggests that modifying seeding times increases perennial grass seedling density because of the high over-winter mortality of autumn seeded species, but only if annual grass propagule pressure is low (James et al. 2012). Consequently, when annual grass propagule pressure is low, seeding perennial grasses in spring, or autumn and spring, will likely provide the highest perennial grass seedling density.

Higher water availability during seedling emergence should increase seedling growth because higher water availability increases soil resource availability and reduces stress (Blumenthal 2006; Everard et al. 2010). Despite the fact our watering treatment did not appreciably increase monitored volumetric soil moisture contents (Fig. 2), it did increase perennial grass seedling density, especially when seeding was distributed across spring and autumn periods, as we hypothesized. Seeding Great Basin ecosystems in the spring can be risky because site access can be limited by wet soils from winter snow melt and wet spring conditions that commonly occur across this region (Fischer and Turner 1978). In addition, spring moisture for seedling growth in the Great Basin varies and models forecasting moisture availability are unreliable (Blank et al. 2007). The first year following seeding, our study site received lower than average precipitation. Increasing water availability likely increased perennial grass seedling emergence rates, especially when these species were seeded in the spring. In addition, even small differences in volumetric soil moisture can result in dramatic differences in soil matric potential, which can strongly affect seed germination and establishment (Evans and Etherington 1991). Also, the coarse soils at our site may have led to rapid surface evaporation and infiltration to rooting depths below the monitoring soil depths (Roundy et al. 1997). Thus, while our volumetric soil water content measurements may have missed the enhancement of added water, the plants did not. Also, we should point out that annual grasses seedling density also increased when water was added and perennial grass seedling density was low when annual grass propagule pressure reached 3,500 seeds m^{-2}. Thus, seeding perennial grasses in spring, or autumn and spring, will likely produce higher perennial grass seedling density when water availability is high.

3.5.2 Seedling density and biomass after two growing seasons

Species performance at the end of two growing seasons can indicate the trend of community assembly (HilleRisLambers et al. 2010). Because annual grass density tends to be high two years following perennial grass seeding in an arid system, perennial seedlings are prone to mortality from competitive annual grasses (Hirsch-Schantz et al. *in press*). Consequently, if perennial grasses are able to persist two years following seeding, it is likely they will continue to survive because perennial grasses are better competitors for soil resources when annual grasses reach their later growth stages (Corbin and D'Antonio 2004).

Attaining successful establishment by seeding perennial grasses into degraded, annual grass dominated rangelands is difficult and often results in low desired plant densities (Hardegree et al. 2010). In our study, seeding annual and perennial grasses in the autumn (November) produced low perennial grass densities and high annual grass densities. Providing perennial grasses a priority seeding can increase perennial grasses competiveness against annuals in annual grass invaded regions (Orloff et al. 2013). In addition, since asymmetric competition occurs in this system, or where one species (annual grasses) remove resources from another species (perennial grasses); natives that establish early are more competitive against annual grasses (Grman and Suding 2010). Our data support our hypothesis that perennial grass density and biomass would be highest when enough perennial grasses were seeded in autumn and spring. Because perennial grasses are better competitors for resources than annual grasses once they are established (Steers et al. 2011), it is possible when perennial grasses emerge prior to annual grasses, they will either co-exist or out-compete annual grasses, and may eventually suppress annual grass density and biomass.

Our results supported our hypothesis that increasing perennial grass propagule pressure and seeding frequency by splitting seasonal dispersal between autumn and spring would yield higher perennial grass density. These findings suggest that the interactions between propagule pressure and safe site availability may be reasonable predictors of community assembly (Aicher et al. 2011; Grubb 1977). However, adding more than 2,500 perennial grass seeds m^{-2} did not increase perennial grass density. It appears that this site had few safe sites and increasing the perennial grass seeding rate, in combination with increasing the seeding frequency, increased the probability that a seed found a safe site, but only up to the point of safe site saturation, which was about 2,500 perennial grass seeds m^{-2} in our system (Clark et al. 2007). When species propagule pressure is high, the likelihood of a seed reaching a safe site increases (Davies and Sheley 2011), but only if safe sites are available (Grubb et al. 1996). DiVittorio et al. (2007) found that where annual grass density is high, perennial grass density was low. Similarly in this study, we found that perennial grass density was low in areas that had high annual grass propagule pressure. Our finding that seeding perennial grasses in autumn and spring produced low perennial grass biomass when annual grass seeding rates were 1,500 seeds m^{-2} or higher suggests that annual grass interference is high when annual grass propagule pressure exceeds 1,500 seeds m^{-2}. Annual grasses are known for having aggressive traits, such as extensive root systems (Monaco et al. 2003), high nutrient acquisition rates (Leffler et al. 2011), and low space requirements (Cleland et al. 2004), which allow annual grasses to inhibit neighboring species growth (Corbin and D'Antonio 2004). In a previous study, we found that in areas where high annual grass propagule pressure was high, safe site availability was low (Schantz et al. *in press*). Consequently, there appears to be a threshold between 150-1,500 annual grass seeds m^{-2}, where annual grass interference will reduce perennial grass density, regardless of seeding time.

Water availability increases soil nitrate availability (Norton et al. 2012), as well as directly affects root structure and function and safe site availability (Knochel et al. 2010; Parsons et al. 2011). Consistent with our hypotheses, increasing water availability in the first year increased final perennial grass density and biomass. Herman et al. (2012) found that when annual grasses were grown under drought stress in the first growing season, the resilience of their offspring to drought in later growing seasons was higher. Similarly, in our study, it appears that the growing conditions of perennial grasses in the first growing season increased their fitness in the second growing season. However, because adding water only increased perennial grass density when annual grass density was lowest and adding water increased the biomass of annual grasses; annual grass interference for soil resources limits perennial grass density if annual grass seeding rates exceed 150 seeds m^{-2} (Fig. 6). Where annual grasses dominate, density-dependence, or the theory that population growth rates are regulated by the density of the population, is common (Goldberg et al. 2001; Turkington et al. 2005). Our finding that annual and perennial grass density and biomass was lower in the second growing season when initial annual grass propagule pressure was high, suggests that intra- and interspecific competition for resources during the initial growing season affects plant community structure in the second growing season. Lortie and Turkington (2002) concluded that initial seed density can affect density dependent relationships in established plant communities, but plant community assembly was more dependent on soil resource availability. However, in this study, higher perennial grass seeding rates had a neutral effect on both annual and perennial grass biomass, suggesting that higher initial annual grass seed density increases density-dependence in these seeded shrublands, while perennial grass seeds have no effect on density dependent relationships. Annual grasses require yearly development from seed and have specific functional traits, such as high relative growth rate (Svejcar 1990), high resource acquisition rates (Svejcar and Sheley 2001), and high root growth (Ray-Mukherjee et al. 2011). Alternatively, perennial bunchgrasses over the long-term have developed associations among a variety of species in the plant community, which reduce competition among species within the plant community (Booth et al. 2003). Thus, the competitive relationships among these seedlings favor annual grass production, especially at early growth stages (Blank 2010; Corbin and D'Antonio 2010). In cases, such as these, it seems reasonable that changing the timing of planting facilitates the establishment of the “loser” plant species, i.e. perennial grasses, as it minimizes the temporal overlap, and thereby opens a gap in the spatial relationship. Contrary to Lortie and Turkington (2002), our data suggest that water availability is not as important in structuring plant communities as seedling arrival and frequency and propagule pressure in annual grass dominated shrub-steppe.

3.5.3 Conclusions and management implications

Increasing perennial grass recruitment into annual grass dominated ecosystems may be possible when seeding dispersal and propagule pressure are modified and seeding occurs in water abundant years. In this study, we found increasing the frequency of perennial grass seeding to autumn and spring or delaying perennial grass seeding until spring produced higher perennial grass density and biomass than seeding in autumn. Increasing perennial grass seeding rates also increased perennial grass density and biomass, especially when seeding frequency and water availability was higher. However, there was a threshold between 150-1,500 annual grass seeds m^{-2}, where regardless of perennial grass seeding strategies, perennial grass density and biomass was low. Higher water availability increased perennial grass establishment, but only when annual grass propagule pressure was low. This study confirms that modifying dispersal dynamics can increase the probability of a perennial grass seed reaching a safe site. However, because high annual grass propagule pressure limits perennial grass density and biomass, perennial grass recruitment will depend upon existing annual grass propagule pressure. Based on our results, we suggest a few tools and strategies for increasing perennial grass recruitment to these degraded rangelands. First, increasing perennial grass propagule pressure to at least 2,500 seeds m^{-2} will likely yield higher perennial grass density following seeding. Reducing the annual grass seed bank prior to seeding using preemergent herbicides, like imazapic or rimsulfuron, should reduce the interference from annual grasses. Increasing perennial grass seeding frequency or delaying perennial grass seeding until spring should also increase the likelihood that a seed reaches a safe site. Caution should be applied, in that, herbicides can have residual effects on perennial grass establishment, so care should be taken if attempting to seed following herbicide application. In addition, if annual grass propagule pressure is higher than 1,500 annual grass seeds m^{-2}, an ecological threshold has likely been crossed such that seeding perennial grasses into these degraded rangelands will be unsuccessful, regardless of perennial grass seeding strategy.

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Table 3-1 Seeding factors and factor levels (n = 288)

Dispersal Timing	*Water*	*Annual grass seeding rate (seeds m^{-2})*	*Perennial grass seeding rate (seeds m^{-2})*
November	No-Water	150	150
February	Water added	1,500	1,500
Split (Nov + Feb)		2,500	2,500
		3,500	3,500

Table 3-2 ANOVA F-test results for perennial seeding timing (spring, autumn, and split), watering (control and water added), and annual and perennial seeding rate on the final density and biomass of annual and perennial grasses obtained in 2013 (n = 288; Den-DF=190). Bold numbers are significant. Bold F-test results are significant at * $p \leq 0.05$ and ** at $p \leq 0.01$, respectively.

		F-Value			
		Perennial Grass		Annual Grass	
Effects and Interactions	***Num-df***	Density	Biomass	Density	Biomass
Seeding Time (Timing)	2	**10.51****	**5.36****	**10.26****	**7.53****
Water	1	**29.56****	0.14	0.14	**13.96****
Timing + Water	2	**3.27***	0.13	1.14	1.34
Annual seeding rate (Annual)	3	**13.68****	**5.23****	**29.44****	**19.22****
Timing + Annual	6	0.84	2.06	2.02	1.77
Water + Annual	3	**3.02***	0.32	0.87	**5.32****
Timing + Water + Annual	6	0.66	0.33	1.8	**2.77***
Perennial Seeding Rate (Perennial)	3	**17.30****	1.19	1.11	0.56
Timing + Perennial	6	0.84	0.81	1.38	1.43
Water + Perennial	3	1.00	1.32	1.41	0.30
Timing + Water + Perennial	6	1.35	1.44	0.46	0.79
Annual + Perennial	9	1.01	0.87	0.68	0.75
Timing + Annual + Perennial	18	1.37	1.13	0.87	1.53
Water + Annual + Perennial	9	0.42	1.28	1.3	0.82
Timing + Water + Annual + Perennial	18	1.35	1.20	0.59	1.35

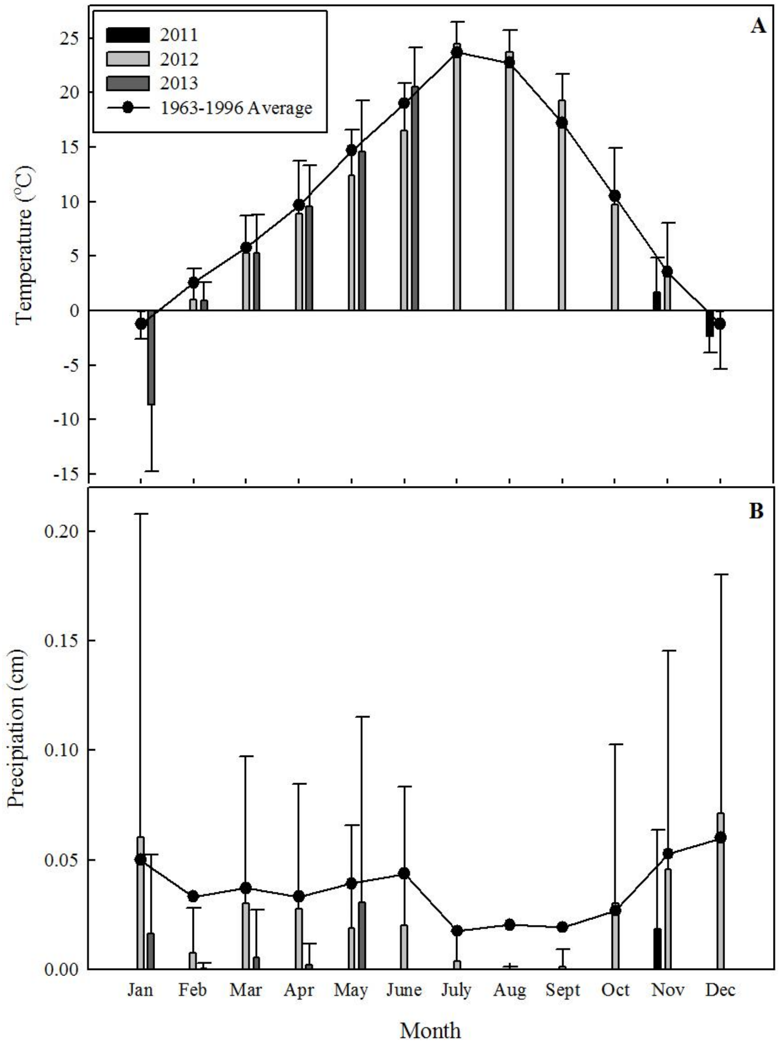


Fig. 3-1 Mean and standard deviation of climate during the sampling period (November 2011- June 2013) and the 30 year average daily precipitation and temperature. Figure A represents average daily temperature (˚C); Figure B represents the average daily precipitation (cm).

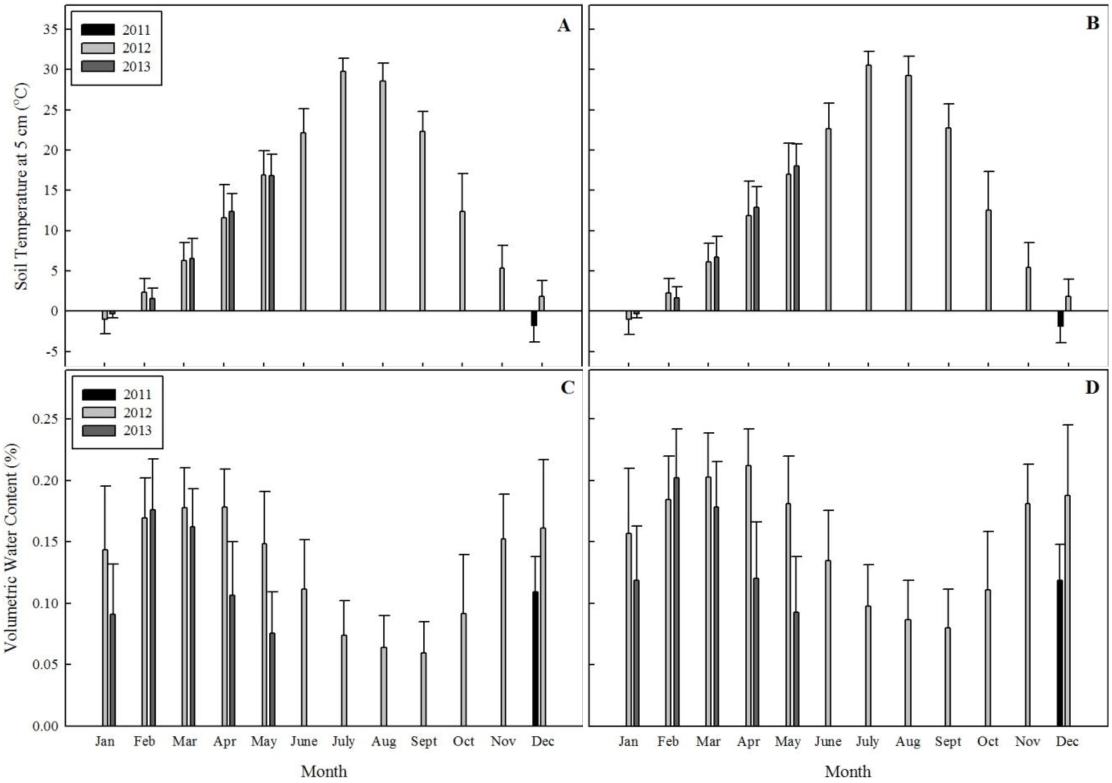


Fig. 3-2 Means and standard deviation of soil temperature at 5 cm (˚C) and volumetric water content at 5 cm (%) measured from December 2012-May 2013. Figure A represents soil temperature in the control (no water) treatment. Figure B represents soil temperature in the water added treatment. Figure C represents volumetric water content in the control treatment. Figure D represents volumetric water content in the water added treatment.

Fig. 3-3 Least squared means and standard error of perennial grass seedling density (density m^{-2}) at 6 sampling times in 2012 by seeding time (autumn (Nov.), spring (Feb), or autumn and spring (Nov+Feb)) and watering treatments (water added (water) or no water added (control)) interactions for each annual and perennial grass propagule pressure (150, 1,500, 2,500, or 3,500 seeds m^{-2}) ($P<0.05$). The panel of figures represents the difference in propagule pressure, where perennial grass propagule pressure increases along the y-axis and annual grass propagule pressure increases along the x-axis. Within each figure, perennial grass density (plants m^{-2}) increases along the y-axis and sampling time (March 25- June 9) increases along the x-axis. Sampling points indicate the treatment effects and associated bars represent the error. (Continued on next page)

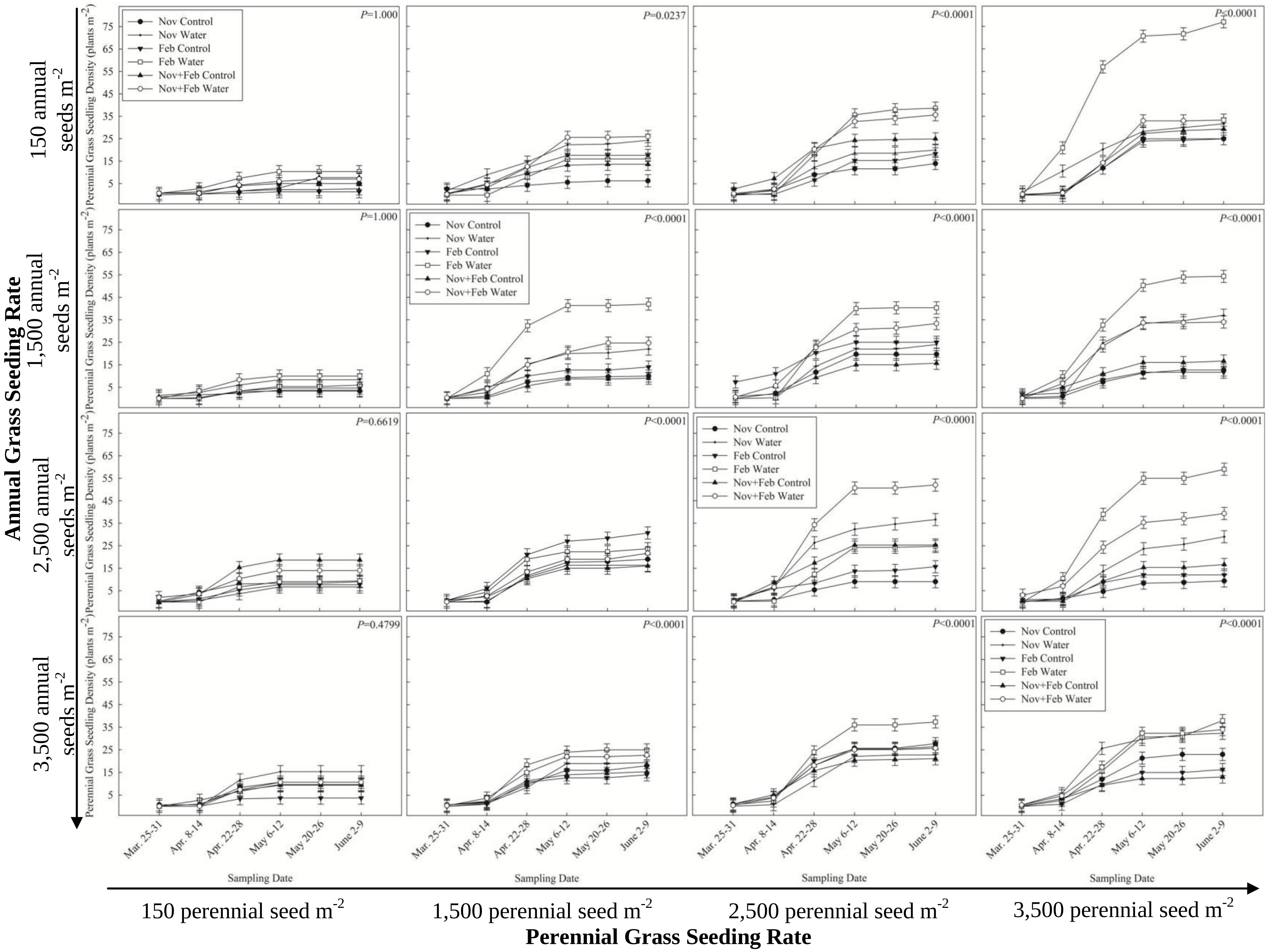
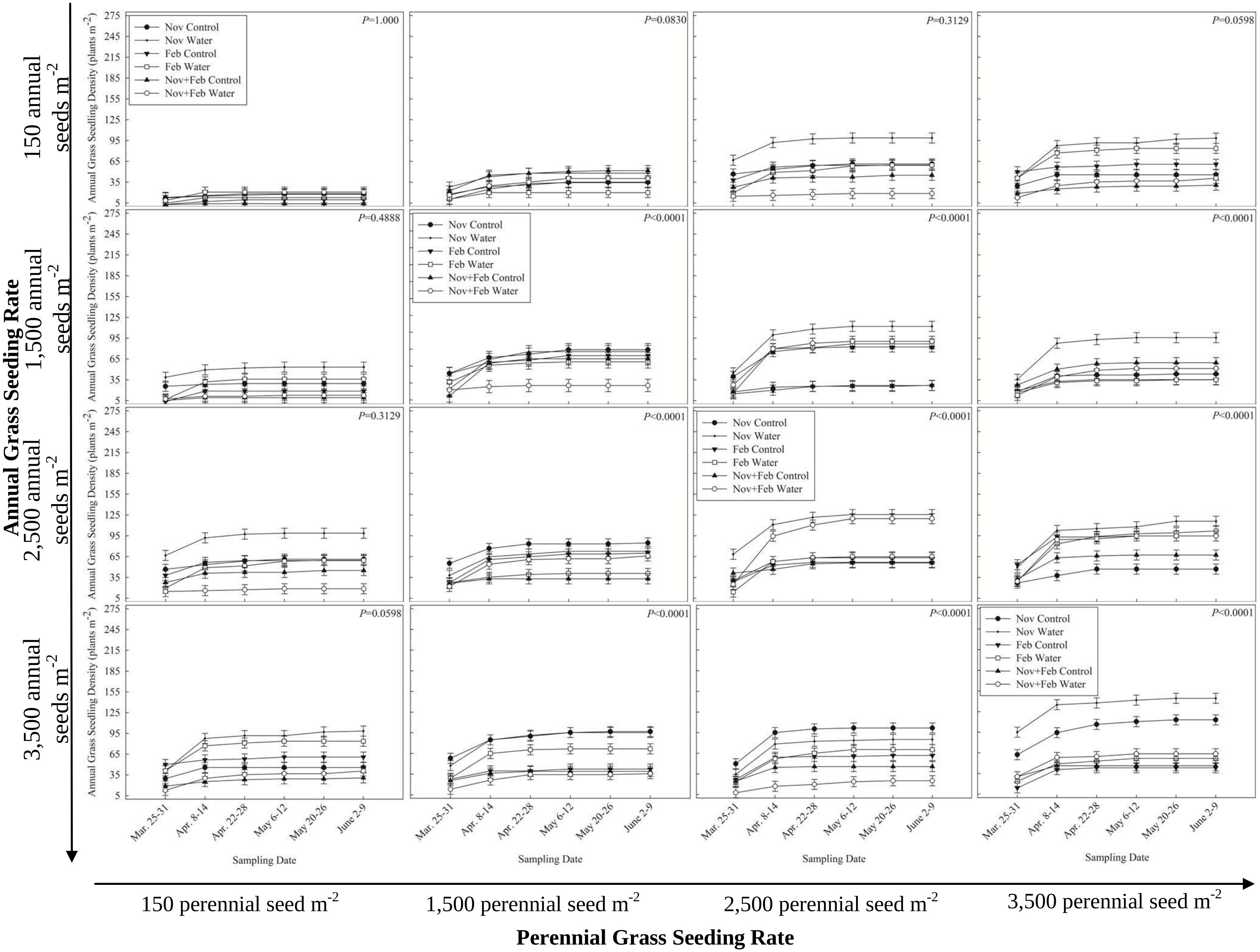

Annual Grass Seeding Rate
150 annual seeds m^{-2}
1,500 annual seeds m^{-2}
2,500 annual seeds m^{-2}
3,500 annual seeds m^{-2}
Perennial Grass Seedling Density (plants m^{-2})
Nov Control
Nov Water
Feb Control
Feb Water
Nov+Feb Control
Nov+Feb Water
P=1.000
P=0.0237
P<0.0001
P≤0.0001
P=1.000
P<0.0001
P<0.0001
P<0.0001
P=0.6619
P<0.0001
P<0.0001
P<0.0001
P=0.4799
P<0.0001
P<0.0001
P<0.0001
75
65
55
45
35
25
15
5
Mar. 25-31
Apr. 8-14
Apr. 22-28
May 6-12
May 20-26
June 2-9
Sampling Date
150 perennial seed m^{-2}
1,500 perennial seed m^{-2}
2,500 perennial seed m^{-2}
3,500 perennial seed m^{-2}
Perennial Grass Seeding Rate

Fig. 3-4 Least squared means and standard error of annual grass seedling density (density m^{-2}) at 6 sampling times in 2012 by seeding time (autumn (Nov.), spring (Feb), or autumn and spring (Nov+Feb)) and watering treatments (water added (water) or no water added (control)) interactions for each annual and perennial grass propagule pressure (150, 1,500, 2,500, or 3,500 seeds m^{-2}) ($P<0.05$). The panel of figures represents the difference in propagule pressure, where perennial grass propagule pressure increases along the y-axis and annual grass propagule pressure increases along the x-axis. Within each figure, annual grass density (plants m^{-2}) increases along the y-axis and sampling time (March 25- June 9) increases along the x-axis. Sampling points indicate the treatment effects and associated bars represent the error. (Continued on next page)


Annual Grass Seeding Rate
150 annual seeds m^{-2}
1,500 annual seeds m^{-2}
2,500 annual seeds m^{-2}
3,500 annual seeds m^{-2}
Annual Grass Seedling Density (plants m^{-2})
275
245
215
185
155
125
95
65
35
5
Nov Control
Nov Water
Feb Control
Feb Water
Nov+Feb Control
Nov+Feb Water
P=1.000
P=0.0830
P=0.3129
P=0.0598
P=0.4888
P<0.0001
P<0.0001
P<0.0001
P=0.3129
P<0.0001
P<0.0001
P<0.0001
P=0.0598
P<0.0001
P<0.0001
P<0.0001
Mar. 25-31
Apr. 8-14
Apr. 22-28
May 6-12
May 20-26
June 2-9
Sampling Date
150 perennial seed m^{-2}
1,500 perennial seed m^{-2}
2,500 perennial seed m^{-2}
3,500 perennial seed m^{-2}
Perennial Grass Seeding Rate

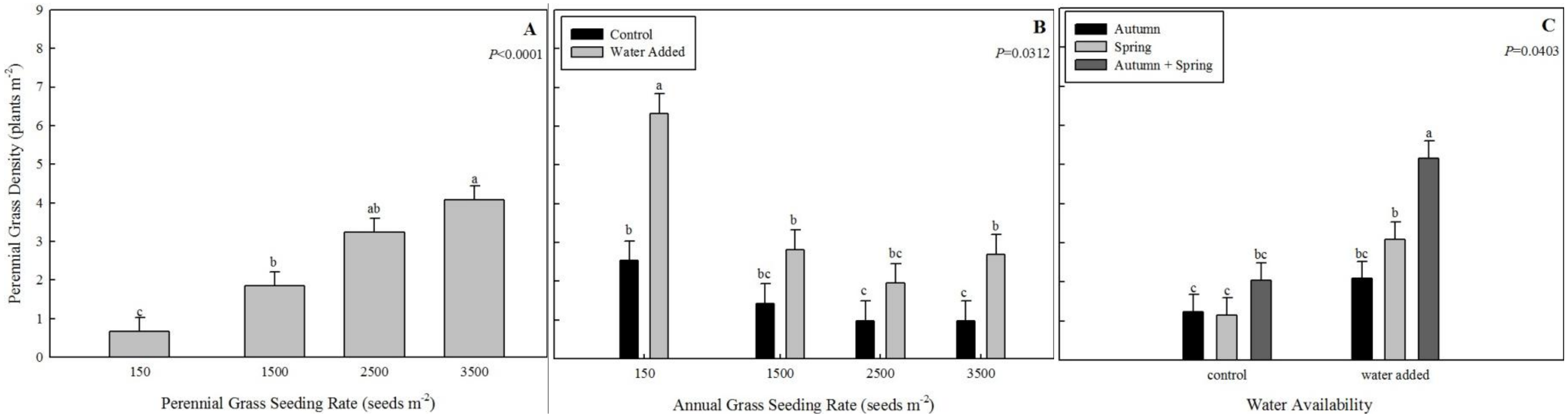


Fig. 3-5 Least squared means and standard error of perennial plant density (density m^{-2}) in 2013. Figure A represents perennial grass seeding rate (*P*<0.0001; n=288). Figure B represents water availability by annual grass seeding rate interaction (*P*=0.0312; n=288). Figure C represents seeding time and water availability interaction (*P*=0.0403; n=288).

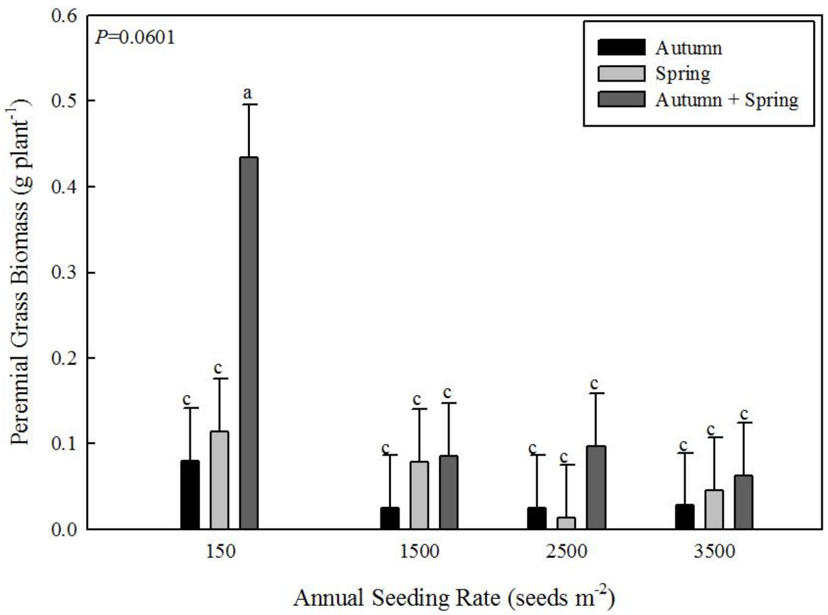


Fig. 3-6 Least squared means and standard error of individual perennial plant biomass (g plant^{-1}) in 2013 by seeding time and annual grass propagule pressure interaction (*P*=0.0601; n=288).

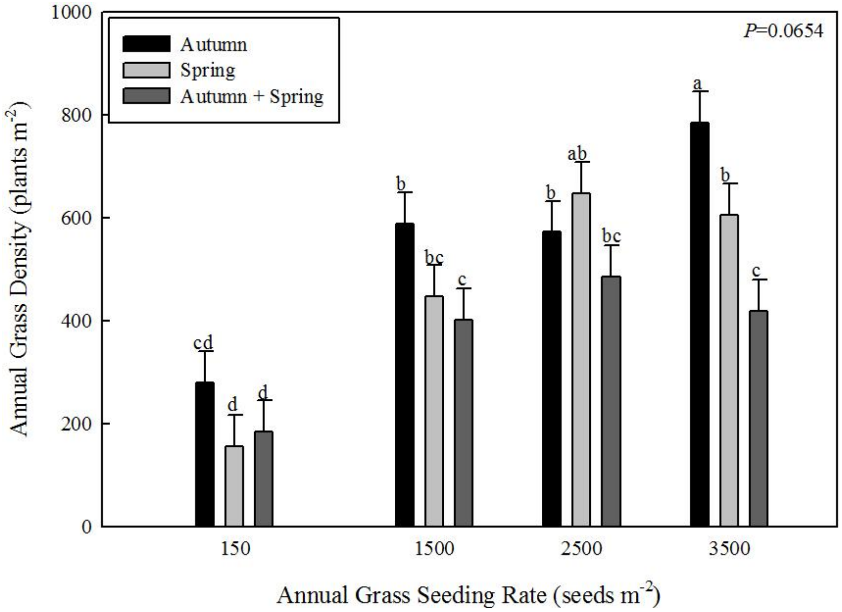


Fig. 3-7 Least squared means and standard error of annual plant density (density m^{-2}) in 2013 by seeding time by annual grass propagule pressure interaction (*P*=0.0654; n=288).

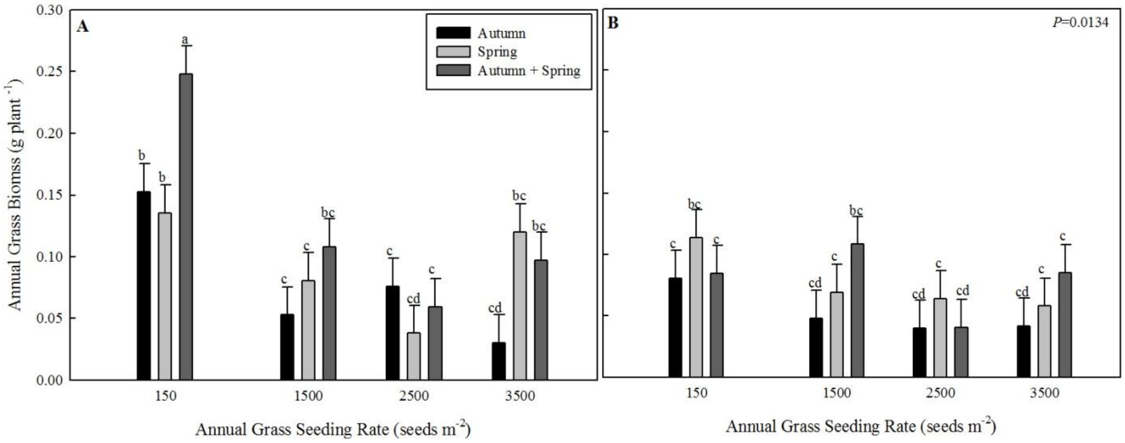


Fig. 3-8 Least squared means and standard error of individual annual plant biomass (g plant^{-1}) in 2013 by water availability by seeding time by annual grass propagule pressure interaction (*P*=0.134; n=288). Figure A represents the control (no-water) treatment. Figure B represents the water added treatment.

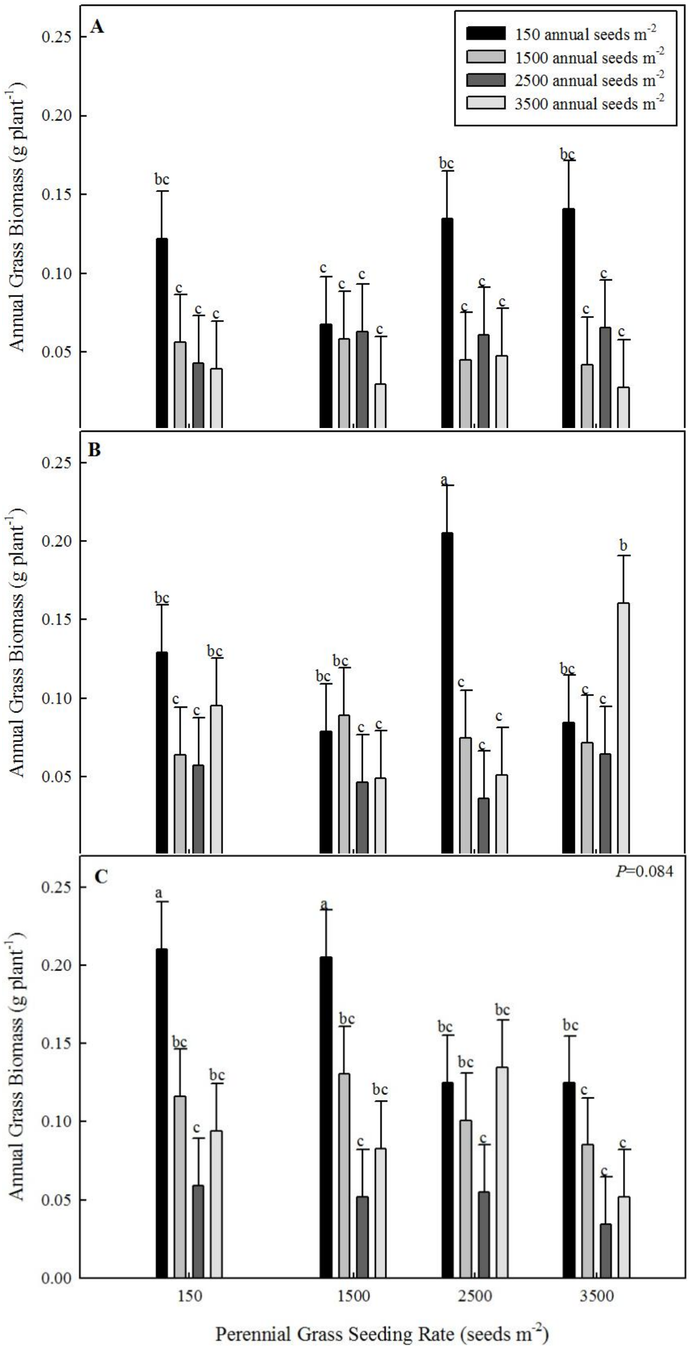


Fig. 3-9 Least squared means and standard error of individual annual plant biomass (g plant^{-1}) in 2013 by the seeding time by annual grass propagule pressure by perennial grass propagule pressure interaction (*P*=0.84; n=288). In all figures annual grasses were seeded in autumn. Figure A represents perennial grass seeding in autumn. Figure B represents perennial grass seeding in spring. Figure C represents perennial grass seeding in autumn and spring.

4 Third Manuscript

Ecological processes limiting shrub-steppe restoration: Role of propagule pressure and priority effects on seedling life history

4.1 Abstract

Restoring annual grass invaded ecosystems may be possible if managers can quantify the effects of management treatments on species transitions, and associate those transitions with specific ecological processes occurring at that time. The objective of this study was to identify how annual and perennial grass demography transitioned from germination to second-growing season adult life history stages when seeding times, propagule pressure, and water availability varied. To assess these effects, we conducted a field experiment in an annual grass invaded shrub-steppe ecosystem in eastern Oregon. We tested the effects of seeding annual grasses in autumn or delaying annual grass seeding until spring, adding water, and varying annual and perennial grass seeding rate by 150, 1,500, 2,500, or 3,500 seeds m^{-2} on perennial and annual grass life stage development. In all species, survival rates were lowest from germination to emergence stages. However, perennial grass germination rates were higher when they were seeded with annual grasses in autumn. Perennial grass density was similar from the juvenile to second-season adult stage, suggesting that there are few ecological processes limiting perennial grass growth following the juvenile life history stage. Watering facilitated all species' growth, except when annual and perennial grass seeding rates were highest, because earlier emerging annual grasses preemptively occupied space and soil resources before perennial grasses emerged. Our results indicate that modifying seeding conditions may facilitate perennial grass recruitment through their life history, but will depend on the interactions among dispersal timing, propagule pressure and water availability.

Keywords: life history, seeding time, propagule pressure, priority effects, invasion, assembly, water

4.2 Introduction

Biological plant invasions are diminishing the ecological integrity and function of ecosystems worldwide (Seastedt and Pyšek 2011). Limiting and mitigating invasion are dependent upon our understanding of key ecological processes driving the spread and dominance of invaders and restored ecosystems. A variety of models have been used to predict plant invasion into intact plant communities (Diaz et al. 2004) and to predict vegetation response to restoration procedures (Steers et al. 2011). Conceptual models suggest that restoring desirable species into invaded regions is possible when using a variety of management tools and strategies (Bagchi et al. 2013). However, these models do not provide quantitative assessments and advances in our ability to restore degraded arid ecosystems are not proportional to the knowledge of restoration ecology, especially when areas invaded by exotic annual grasses (Sheley et al. 2010). To help overcome this limitation, James et al. (2013) proposed using a systems approach to restoration of invaded ecosystems (Fig. 1).

Systems-based management frameworks account for the ecological processes driving plant populations and can provide a quantitative assessment of plant community assembly (Evans et al. 2012). Unlike conceptual and phenomenological models, systems models account for the underlying mechanisms and processes that drive model behavior through time, such as climate, life history stage, or invasive species presence (Adler et al. 2014; Huxman et al. 2013). In addition, systems models may also provide realistic mathematical relationships based on management inputs (Evans 2012). These approaches can systematically identify and solve site-specific restoration problems (James et al.

2013), especially when a systems approach uses plant life histories to quantify and forecast vegetation patterns after management.

Plant community dynamics are driven by the independent effects and interactions among climatic regimes, major ecological processes dominating each ecosystem, and species life history strategies (Fargione et al. 2003; HilleRisLambers et al. 2010). Species have differing life history strategies, including the dispersal time, leaf characteristics, and time to reproduction (Adler et al. 2014) and the ecological processes that affect plant life history vary through time (Benton et al. 2006). For a seed to become a reproductive adult, seedlings must possess the ability to withstand and capitalize from a variety of processes affecting plant production through time (Moles and Leishman 2008). Germinated seedlings are vulnerable to soil pathogens that infect seeds and reduce seed viability and gramnivores that consume and destroy newly germinating seeds (Moles and Westoby 2006). Freeze-thaw cycles are also common in many seeded rangelands and increase winter mortality on germinated seedlings that were seeded in autumn (James et al. 2012). Ecological processes strongly limit seedlings transition between growth stages. James et al. (2011) discovered that a primary limitation in seedling recruitment occurs between the germination and emergence growth stages in newly seeded sage-steppe ecosystems. If a seedling is able to emerge, seedlings risk mortality from herbivory, weather and moisture extremes, competition, and climate effects to survive to be a reproductive adult (Benton et al. 2006). Because of the processes that seedlings must endure to become reproductive adults, using management strategies that directly affect these limiting processes should increase seedling recruitment in seeded regions (James et al. 2013). Understanding the effect of key ecological processes on life histories of important functional groups may help identify new management strategies that could lead to improved plant establishment during restoration.

Seed dispersal can be a major driving mechanism of plant assembly, especially during invasion and restoration because it may control recruitment of newly arriving species by influencing safe site occupation (Satterthwaite 2007). Safe sites refer to resource patches within a plant community that support diverse plant populations by providing conditions suitable for seedling germination and establishment (Grubb 1977; Titman 1976). Propagule pressure and dispersal timing strongly influence seedling emergence, growth, and ultimately plant community assembly, depending on the number and timing of seeds reaching safe sites (Drake 1991). Aicher et al. (2011) concluded that areas invaded by annual grasses have low numbers of available safe sites because annual grasses produce high numbers of propagules that dominate the seed bank these species grow earlier than neighboring native grasses, thus preempting available safe sites. The effect of propagule pressure on plant-plant interactions is compounded by the temporal patterns in which seeds of each species arrive because plants arriving and establishing earliest preempt soil resource use (Chambers and Wisdom. 2009). In addition, most annual grass invaded regions are resource limited and when water availability is low, native grass seedling recruitment is low (James and Svejcar 2010). Managers may be able to overcome these limitations by modifying species arrival times and seeding rates or by seeding in a wet year; however, the effects of these management inputs on desired species life histories have not been quantified.

Plant populations’ life histories and, thus, plant community assembly, can be directed by management influence on various ecological processes at each growth stage

(Fridley et al. 2007; Goldberg et al. 2001). To determine whether plant life history strategies varied by management input, we quantified annual and perennial grass life history strategies when annual grass seeding times, annual and perennial grass seeding rates, and water availability varied. We hypothesized that the species which arrived earliest and had the highest seeding rates would produce higher seedling density throughout their life history. In addition, because James et al. (2011) found that seedlings are vulnerable to ecological processes early in their life history, we hypothesized that seeding perennial grasses at high seeding rates and prior to annual grass seeding would increase perennial grass density by providing these species a priority effect for accessing safe sites and reducing invasive species interference in later life history stages. Lastly, we hypothesized that higher water availability would increase perennial grass density through their life history because higher resource availability can initially increase the number of available safe sites and reduce competition for resources in later life history stages (Rao and Allen 2010).

4.3 Materials and Methods

4.3.1 Study site

The study was conducted about 5 km south of Juntura, Malheur County, Oregon (Zone: 11, 410178 easting, 4840910 northing) in low elevation (1,033 m) shrub-steppe dominated by annual grasses. Soils at the site are sandy-loams within the Bogusrim series (fine, smectitic, mesic abruptic Xeric Argidurids). Soil in the Bogusrim series receives an average 457 mm precipitation per year with a bimodal distribution peaking in the winter and spring. This site has a very slight slope facing southwesterly and is devoid of sagebrush. Current vegetation structure is a near monoculture of medusahead (*Taniatherum caput-medusae* (L.) Nevski) growing in association with species of cheatgrass (*Bromus tectorum* L.), with scattered individuals of Sandberg bluegrass (*Poa secunda* J. Presl), whitetop (*Cardaria draba* (L.) Desv.), squirreltail (*Elymus elymoides* (Raf.) Swezey), and morning glory (*Ipomoea eriocarpa* R. Br.).

Climate variables, including average daily precipitation (cm), and temperature (˚C), were recorded daily from November 2011 to June 2013 using a HOBO rain gauge smart sensor that was connected to a HOBO weather station and was mounted approximately 3 meters from the soil surface, inside of a HOBO solar shield (Onset Comp. Inc., Cape Cod, MA, USA). Long-term (1963-1996) daily precipitation and temperature data from Juntura, OR were obtained from the Western Regional Climate Center (WRCC 2013). Volumetric soil water content (%) and soil temperature (˚C) at five cm were monitored using Decagon 5TM soil moisture sensors (Decagon Devices Inc., Pullman, WA, USA) from November 2011 to June 2013.

4.3.2 Model system

To test how seeding strategies affect species density through their life history, we used a model system consisting of the invasive annual grasses, cheatgrass and medusahead (50-50 mixture) as the invaders. The desired native system was represented by the perennial grasses Anatone bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), bottlebrush squirreltail, Mountain Home Sandberg bluegrass, and Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth) seeded in equal proportions. Annual grass seeds were collected locally, by hand, from Harney Co. Oregon, bottlebrush squirreltail, Sandberg bluegrass, and bluebunch wheatgrass were purchased from Granite Seed Co., Lehi, UT in 2011, and Thurber's needlegrass was purchased from BFI Native Seeds Co., Moses Lake, WA in 2010. Seeding rate was applied on a per weight basis so that each plot received 100% pure-live seeds per plot.

4.3.3 Propagule pressure and priority effects

Prior to initiating the study, the site was sprayed with 3.36 L ha^{-1} of glyphosate [N-(phosphonomethyl) glycine] and tilled to about100 mm in order to remove existing vegetation. Densities and proportions of annual grasses and perennial grasses were arranged to provide four addition-series matrices (Radosevich 1987). Seeding densities of annual:perennial grasses in each matrix were 150:150, 150:1,500, 150:2,500, 150:3,500, 1,500:150, 1,500:1,500, 1,500:2,500, 1,500:3,500, 2,500:150, 2,500:1,500, 2,500:2,500, 2,500:3,500, 3,500:150, 3,500:1,500, 3,500:2,500, and 3,500:3,500. In each matrix, all perennial grasses were seeded in autumn (November 2011), while annual grasses were either simultaneously seeded with perennial grasses in autumn (November 2011), or annual grass seeding was delayed until spring (February 2011). In addition, half of the plots were allocated to a watering treatment, where water was either ambient, or water was added at two times the historical average, which varied from 2.05-2.61 L added per month. Each matrix was then replicated three-times in a completely randomized design (Table 4-1).

Seeding occurred by hand-broadcasting seeds onto the soil surface of the 1 m^2 plots and covering seeds with two cm of sifted weed free topsoil collected from the site. Watering was administered weekly during the growing season in year one (March-May) using watering cans to evenly distribute water on each water added treatment plot.

4.3.4 Germination Bags

Field germination assessments were conducted in 2013 and measured using the buried bag technique (Abbott and Roundy 2003). The buried bag technique involves filling 10 cm^2 nylon bags with seeds and 200 mL sifted on-site soil before planting these bags in the 0-2 cm soil layer. Germination bags were created to mimic field study conditions so that seeding densities of annual:perennial grasses in each matrix were 6:6, 6:60, 6:120, 6:160, 60:6, 60:60, 120:60, 160:60, 120:6, 60:120, 120:120, 120:160, 160:6, 60:160, 160:120, and 160:160 seeds per germination bag (10 cm^{-2}). Each matrix included simultaneous seeding all species in autumn or delaying annual grass seeding until spring. For the simultaneously seeded germination bags, all seeds were seeded into one germination bag and planted in autumn (November 2012). Delayed germination bags included one perennial grass germination bag that was filled with only perennial grasses and seeded in autumn (November 2012) and an annual grass germination bag that only included annual grasses and was seeded in spring (February 2013). All germination bags were harvested on March 15, 2013. Germination bag sampling involved washing the contents of the bag through a 710 µm screen, collecting seeds, and scoring seeds as germinated or dead.

4.3.5 Life history analysis

Annual and perennial grass density of was counted within the center 0.5 m^2 of the plot for perennial species and the center 0.25 m^2 for annual species biweekly during the first growing season, from March 13, to June 2, 2012. Because of the high density of annual grasses and the difficulty of counting all annual and perennial grasses within each plot, the measurement area for annual grasses was lower than that for perennial grasses. Plants were individually marked as they emerged with colored toothpicks to indicate the emergence time. Density was counted bi-weekly and total mortality was measured by the amount free standing toothpicks from each emergence period. Emerged seedlings from previous sampling periods were re-assessed during the bi-weekly sampling times for average leaf number to indicate the growth stage of seedlings through time. Growth stage was estimated by counting the number of leaves on 5 randomly chosen plants by the week they emerged and averaging these leaf numbers. We categorized growth stages as emerged seedlings (coleoptile or single leaf), established species (1-5 leaves), juveniles (5-10 leaves), adults (10 or more leaves), and surviving second season adults (plants surviving in 2013).

4.3.6 Statistical analysis

All data were pooled by annual and perennial grasses and tested for distribution and homogeneity of variance using Shapiro-Wilk and Levene tests, respectively **(**SAS

Institute Inc., Cary, NC, 2012). Germinated annual and perennial grasses, annual grasses from emergence to adult life history stages, and annual and perennial grasses in the second growing season were all normally distributed. However, perennial grasses from the emergence to adult life history stage was not normally distributed. A number of transformations, including log, log base 10, square root, and log+1, were used to normalize these skewed data, however, no transformations improved the distribution or helped the model fit. Because perennial grasses had low density in the adult life history stage, repeated measures were only used for perennial grasses from the emergence to juvenile life history stages and perennial grasses in the adult stage was tested using a mixed-model ANOVA.

Density of annual and perennial grass life history stages were evaluated using SAS (SAS Institute Inc., Cary, NC, 2012). Annual grass density from emergence to adult life history stages and perennial grass density from emergence to juvenile life history stages were analyzed using a repeated-measures analysis of variance (RM-ANOVA) because of their biological importance across these life history stages, while germination and second season adult life history stages were analyzed using a mixed-model ANOVA. A mixed-model ANOVA was used to test differences in the main effects and interactions among seeding time, annual grass seeding rate, and perennial grass seeding rate on number of annual and perennial grass germinates and annual and perennial grass density of adults in the second growing. Alternatively, a RM-ANOVA was used to test differences among the main effects and interactions of seeding time, watering, annual grass seeding rate, perennial grass seeding rate, and growth stage from the emergence to adult life history stages on the density of annual and perennial grasses from the emergence to adult life history stages. In all models means were separated using the slice procedure (Schabenberger, 2013), and F-test results with an associated *P* value of ≤ 0.05 were considered significant.

4.4 Results

4.4.1 Environmental Conditions

Temperature was consistent with long-term averages, while precipitation was lower than the 30 year mean in the summer months and average throughout the rest of the year (Fig. 4-2). Volumetric water content was slightly higher in the water added plots compared to ambient water plots, although soil temperature at 5 cm were not different between the ambient water and water added plots (Fig. 4-3). Volumetric water content fluctuated from a high of about 25% from November-April to a low of about 10% from May-October (Fig. 2 A, B). Soil temperature at 5 cm fluctuated similarly to air temperature, but was generally 5˚C higher than air temperature throughout the study period (Fig. 4-3 C, D).

4.4.2 Germination

Perennial grass germination rates were similar among all seeding treatments when 150 perennial grass seeds m^{-2} were sown (Fig. 4-4; $F_{3, 48} = 0.62$; $P=1.000$). Seeding annual grasses simultaneously with perennial grasses in autumn produced 1,004.6 ± 41.9 perennial grass seedlings m^{-2}, yet delaying annual grass seeding until spring only produced 488.7 ± 41.9 perennial grass seedlings m^{-2} ($F = 75.8$; $P<0.001$). Perennial grass germination rates were higher when perennial grass seeding rates were high since adding 150 perennial grass seeds m^{-2} only produced 67.2 ± 59.2 perennial grass seedlings m^{-2}, yet when perennial grass seeding rates were 3,500 seeds m^{-2}, perennial grass density was 1,339.6 ± 59.2 ($F_{3, 48} = 82.5$; $P<0.001$). However, annual grasses seeding rates did not affect perennial grass germination rates ($F_{3, 12} = 0.5$; $P=0.709$). When annual grasses were seeded in autumn, perennial grass density was only 96.9 ± 83. 8 perennial grass seedlings m^{-2}, but adding 3,500 perennial grass seeds m^{-2} produced 1,695.7 ± 83.8 perennial grass seedlings m^{-2}. Alternatively, when annual grasses were seeded in spring, perennial grass density was only 37.5 ± 83.8 perennial grass seedlings m^{-2}, but adding 3,500 perennial grass seeds m^{-2} produced 983.6 ± 83.8 perennial grass seedlings m^{-2} ($F_{3, 48}$ = 7.81; P=0.0002). When annual grasses were delayed seeding until spring, perennial grass germination rates ranged from 22-28% compared to when annual grasses were seeded in autumn, where perennial grass germination rates ranged from 48-64%.

Annual grass germination rates were similar among all seeding treatments when 150 perennial grass seeds m^{-2} were sown (Fig. 4-5; $F_{3, 48}$ = 0.1; P=1.000). High annual grass seeding rates produced high annual germination rates since adding 150 annual grass seeds m^{-2} only produced 118.8 ± 31.5 perennial grass seedlings m^{-2}, yet when perennial grass seeding rates were 3,500 seeds m^{-2}, perennial grass density was 2,587.3 ± 31.5 ($F_{3, 12}$ = 1,591.8; P<0.001). Annual grasses were not affected by the interaction between annual grass seeding rates and seeding time, ($F_{1, 12}$ = 0.8; P=0.157), although there were two cases where similar seeding rates yielded different numbers of germinated annual grasses depending on the season that annual grasses were seeded. Seeding 1,500 annual grass seeds m^{-2} and 3,500 perennial grass seeds m^{-2} in autumn produced only 900 ± 79.8 annual grass seedlings m^{-2}, compared to 1,187.5 annual grass seedlings m^{-2} when annual grass seeding was delayed until spring ($F_{1, 48}$ = 6.5; P=0.014). Similarly, when 3,500 annual grass seeds m^{-2} and 2,500 perennial grass seeds m^{-2} were seeded in autumn, annual grass germination rates were 2,676.9 ± 79.8 annual grass seedlings m^{-2} compared to only 2,433.8 ± 79.8 annual grass seedlings m^{-2} when annual grass seeding was delayed seeding until spring ($F_{1, 48} = 4.6$; $P=0.004$). Collectively, annual grass germination rates varied from 73-81% across all seeding treatments.

4.4.3 Life History

Perennial grass density was similar across all seeding treatments when perennial grass seeding rates were lowest (Fig. 4-6; $F_{3, 288} = 0.6$; $P=1.00$). Adding water increased perennial grass seedling density from an average of 12.8 ± 1.4 plants m^{-2} to an average of 16.56 ± 1.4 plants m^{-2} (Table 4-2; $P=0.056$). When annual grass seeding was delayed until spring and annual grass seeding rates were 1,500 seeds m^{-2} or higher, perennial grass density was about 4 plants m^{-2} higher than when annual grasses were seeded in spring at 150 annual grass seeds m^{-2} ($P=0.034$). Alternatively, when annual grasses were seeded in autumn perennial grass density was 19.61 ± 2.4 plants m^{-2} when annual grasses were seeded at 150 seeds m^{-2}, but seeding more than 1,500 annual grass seeds m^{-2} produced perennial grass densities between 9.60-11.3 ± 2.4 plants m^{-2} ($P=0.0343$). The density of annual grasses was highest in the emergence growth stage (18.7 ±1.7 plants m^{-2}), followed by the establishment stage (15.84 ±1.66 plants m^{-2}), and was lowest in the juvenile life history stage (9.5 ±1.7 plants m^{-2}) ($P=0.013$). The difference in perennial grass density among growth stages was high when annual grasses were seeded in autumn ($P=0.005$) and when annual grass seeding rates were high ($P=0.075$). Perennial grass density was not affected by the independent effect of annual grass seeding rates ($P=0.279$), yet high perennial grass seeding rates yielded high perennial grass density since perennial grass density was only 6.8 plant m^{-2} when 150 perennial grass seeds m^{-2} were added, but seeding 3,500 perennial grass seeds m^{-2} yielded 20.5 plants m^{-2} ($P<0.001$). When annual grasses were seeded at 150 seeds m^{-2} and perennial grasses were seeded at 3,500 seeds m^{-2}, perennial grass density was 1.5 times higher than when perennial grass seeding rates were 2,500 seeds m^{-2} (P=0.024). Alternatively, when annual grass seeding rates were 3,500 seeds m^{-2}, perennial grass density in the emergence stage was 19.7 ± 2.4 plants m^{-2}, but by the adult life history stage perennial grass density was only 4.1 ± 2.4 plants m^{-2} (P<0.001). The greatest reduction in perennial grass density was between the germination and emergence life history stages ($F_{3, 38} = 2.3$; P=0.002). Perennial grasses did not transition from the emergence growth stage to later growth stages until late-April, early-May (Table 3). In addition, perennial grasses did not begin developing into juveniles until about mid-May. By the end of the first growing season, only 1% of seeded perennial grasses developed into adults.

The number of adult perennial grass seedlings from the first growing season did not differ from the number of surviving adults in the second growing season (Fig. 4-6; $F_{3, 5} = 0.28$; P=0.925). However, perennial grass density in the adult life history stage was 8 ± 1.8 plants m^{-2} when annual grass seeding rates were 150 seeds m^{-2}, yet when annual grass density was 3,500 seeds m^{-2}, perennial grass density was only 0.5 ± 1.8 plants m^{-2} ($F_{3, 24} = 3.45$; P=0.033). When perennial grass seeding rates were high, perennial grass density was high because seeding 3,500 perennial grass seeds m^{-2} produced 6.2 ± 1.4 perennial grass seedlings m^{-2} ($F_{3, 96} = 3.0$; P=0.033). Similarly, in the second growing season, adult perennial grass density was high when perennial grass seeding rates were higher because adding 3,500 perennial grass seeds m^{-2} produced 3.4 ± 0.7 perennial grass seedlings m^{-2}, yet only seeding 150 perennial grass seeds m^{-2} produced 0.7 ± 0.7 plants m^{-2} ($F_{3, 96} = 3.6$; P=0.017). Conversely, when annual grass seeding rates were 150 seeds m^{-2}, perennial grass density in the adult life history stage was 5.2 ± 0.7 plants m^{-2}, yet when annual grass density was 3,500 seeds m^{-2}, perennial grass density was only 0.7 ± 0.7 plants m^{-2} ($F_{3, 24}$ = 7.3; *P*=0.001). The annual grass seeding time did not interact with perennial grass seeding rates to affect perennial grass density ($F_{3, 24}$ = 0.49; *P*=0.695). However, when 1,500 annual and 2,500 perennial grass seeds m^{-2} were seeded in autumn, the density of perennial grasses in the second growing season was only 1.3 ± 2.0 plants m^{-2}, yet was 5.7 ± 2.0 plants m^{-2} when annual grass seeding was delayed until spring ($F_{1, 96}$ = 4.6; *P*=0.035). Alternatively, seeding 150 annual and 3,500 perennial grass seeds m^{-2} in autumn produced 9 ± 2.03 plants m^{-2} compared to only 5.3 ± 2.0 plants m^{-2} when annual grass seeding was delayed until spring ($F_{1, 96}$ = 6.1; *P*=0.015).

Annual grass density was not affected by any treatments when annual grass seeding rates were lowest (Fig. 4-7; $F_{3, 288}$ = 0.1; *P*=1.000). Adding water (166.5 ± 10.5 plants m^{-2}) (Table 4-2; *P*<0.001), delaying annual grass seeding until spring (194.5 ± 9.7 plants m^{-2}) (*P*<0.001), and higher seeding rates of annual grasses (204.0 ± 13.6 plants m^{-2} at 3,500 annual grass seeds m^{-2} added) (*P*<0.001) all produced high annual grass density compared to ambient water (96.5 ± 9.7 plants m^{-2}), seeding annual grasses in autumn (68.4 ± 9.7 plants m^{-2}), or when annual grass seeding rates were low (31.4 ± 13.6 plants m^{-2} at 150 annual grass seeds m^{-2} added). Annual grass density was about 70 plants m^{-2} (± 13.6) higher when annual grass seeding was delayed until spring and water was added compared to seeding annual grasses in autumn in ambient water conditions (*P*=0.047). When annual grasses were seeded in spring and annual grass seeding rates were high, annual grass density was 306.6 ± 19.2 plants m^{-2} compared to only 28.7 ± 19.2 plants m^{-2} when annual grasses were seeded in autumn at low annual grass seeding rates (*P*<0.001). Furthermore, annual grass density was highest at when annual grasses were seeded in spring, water was added, and annual grass seeding rates were highest at 395.9 ± 27.0 (*P*<0.001). Perennial grass seeding rates did not affect annual grass density (*P*=0.604). However, high annual and perennial grass seeding rates produced high annual grass density that averaged 190.8 ± 26.9 plants m^{-2} (*P*<0.001) and this effect was especially apparent when annual grass seeding was delayed until spring because annual grass density averaged 277.3 ± 38.0 (*P*=0.028). Annual grasses had the greatest reduction in density from the germination to emergence stage ($F_{3, 86} = 3.3$; *P*=0.027) and their density was fairly constant from the emergence to juvenile life history stages, where annual grass density averaged about 135 ± 8.2 plants m^{-2}. However, annual grass density was lower in the adult life history stage than the juvenile life history stage because annual grass density in the juvenile stage was 135.3 ± 8.2 plants m^{-2}, but was only 116.8 ± 8.2 plants m^{-2} in the adult life history stage (*P*=0.060). By the adult life history stage, when annual grasses were seeded in spring, annual grass density was low since annual grass density in the emergence to juvenile stage ranged from 205.3-202.1 ± 11.1 plants m^{-2}, but was only 165.5 ± 11.1 plants m^{-2} in the adult life history stage (*P*=0.003). When annual grass seeding rates were high, the difference in annual grass density between growth stages was high (*P*<0.001). For example, when 150 annual grass seeds m^{-2} were added, the difference in annual grass density from the emergence to adult life history stages was only 0.7 ± 15.8 plants m^{-2}, yet when 3,500 annual grass seeds m^{-2} were added, the difference in annual grass density from the emergence to adult life history stages was 61 ± 15.8 plants m^{-2}, and when water was added, the magnitude difference between the emergence and adult life history stages was amplified to 107.3 ± 21.3 plants m^{-2} when 3,500 annual grass seeds m^{-2} were seeded (*P*=0.002). When annual grasses were seeded in spring and annual grass seeding rates were 3,500 seeds m^{-2}, the difference in annual grass density from the emergence to adult life history stage was 121.6 ± 21.3 plants m^{-2}. Alternatively, when annual grasses were seeded in autumn at 3,500 annual grass seeds m^{-2}, the difference in annual grass density from the emergence to adult life history stage was only 0.4 ± 21.3 plants m^{-2} ($P<0.001$) and this effect was even greater when water was added. When water was added, annual grasses were seeded in spring, and annual grass seeding rates were highest, the difference in annual grass density from the emergence to adult life history stage was 214.5 ± 29.9 plants m^{-2} ($P=0.002$). Annual grasses transitioned quickly among growth stages (Table 4). By mid-April, 82% of emerged annual grasses transitioned to established species. By late-April, early-May, annual grass seedlings were generally evenly distributed between the establishment and juvenile stages. However, only about 25% of annual grasses reached the 10-leaf adult stage by the first year of this study.

The density of annual grasses in the second growing season was higher than the adult life history stage from the previous year (Fig. 4-7; $F_{3,16} = 1.7$; $P=0.078$). In the second growing season, seeding annual grasses in autumn produced 827.2 (± 43.3) annual grasses m^{-2} compared to only 529.4 (±43.3) annual grasses m^{-2} when annual grass seeding was delayed until spring ($F=23.7$; $P<0.001$). Annual grass density in the second growing season was also higher when annual grass seeding rates were higher because adding 150 annual grass seeds m^{-2} only produced 378 (± 55.6) annual grass seedlings m^{-2} in the second growing season compared to 762.2 (± 55.6) annual grass seedlings m^{-2} when annual grass seeding rates were 3,500 seeds m^{-2} ($F_{3,24} = 15.2$; $P<0.001$). The interactions between annual and perennial grass seeding rates did not affect annual grass density ($F_{9, 96} = 1.1$; $P=0.401$). However, there were a number of cases where annual grass density was higher when annual grasses were seeded in autumn at high annual and perennial grass seeding rates compared to these same seeding rates when annual grasses were seeded in spring. For example, 1,500 annual and 2,500 perennial grasses m^{-2} were seeded in autumn, annual grass density was 1,005.3 ± 155.1 plants m^{-2} compared to only 742.7 ± 155.1 plants m^{-2} when annual grasses were seeded in spring ($F_{3, 96} = 3.5$; $P=0.019$) and when 3,500 annual and 2,500 perennial grasses m^{-2} were seeded in autumn, annual grass density was 954.7 ± 155.1 plants m^{-2} compared to only 356.0 ± 155.1 plants m^{-2} when annual grasses were seeded in spring ($F_{3, 96} = 3.1$; $P=0.03$).

4.5 Discussion

4.5.1 Systems approach

Quantifying plant community assembly when management inputs vary is possible when using a systems management approach (Ramo and St. Clair 1998). Systems management approaches are built to identify the effects of various processes that occur within model components, such as the effects of dispersal processes on plant growth (Evans 2012); thus, these models are well fit to pinpoint the relationships among ecological processes and plant densities following management inputs (Cornwell and Ackerly 2010). However, there are a suite of processes limiting plant growth throughout species life history (Yelenik and D'Antonio 2013). In addition, quantifying the effect of ecological processes is challenging because species are differentially affected by ecological processes occurring from the germination to reproductive adult life history stages (James et al. 2012). Modifying propagule pressure and priority effects can strongly influence plant community assembly because these dispersal dynamics may determine safe site occupation (Satterthwaite 2007). In this study, we sought to evaluate the effects of differing propagule pressure and priority effects on plant community assembly and life history dynamics in a multi-year study using a systems management approach (James et al. 2013) (Fig. 4-1).

4.5.2 Germination

Germination has historically been thought to be the limiting growth stage for plant recruitment (Haferkamp et al. 1995; Young and Evans 1977). However, our finding that germination rates ranged from 70-90% of initial seeding rates, regardless of seeding time, suggests that seedling growth is not limited during the germination stage. Similarly, James et al.(2011) also found that germination rates were high in a nearby sage-steppe system. Low resource availability in arid regions, like in the sage-steppe, has been suggested as the primary mechanism limiting plant growth (Huxman et al. 2004). However, resource availability during early growth stages, like the germination stage, is high in the sage-steppe regions because the majority of the moisture occurs in late winter or early spring (Hardegree et al. 1999). Although competition for water may reduce species richness through time (Adler and Levine 2007), it appears that low resource availability does not limit seed germination for annual or perennial grasses.

Contrary to our hypothesis, annual grass germination rates were similar when annual grasses were seeded in autumn or spring. Alternatively, when perennial grasses were seeded with annual grasses in autumn, perennial grass germination rates were two-times higher than when annual grasses were delayed seeding until spring. These findings suggest that neighboring annual grasses facilitate perennial grasses in early growth stages (Leger and Espeland 2010). The higher density of perennial grasses when seeded with annual grasses in autumn may be because perennial grasses prefer to be seeded with high numbers of neighboring seeds . However, in this study, we found that the relative germination rates of annual and perennial grasses did differ by seeding rate (i.e. annual grass germination rates ranged from 74-81% across all annual grass seeding rates, while perennial grass germination rates ranged from 38-45% across all perennial grass seeding rates). Perennial grasses may be facilitated by neighboring annual grasses because the onset of germination by one seed can spread to all neighboring seeds in a process called accelerated germination (Tielborger and Prasse 2009). Orrock and Christopher (2010) suggest that when competing seeds are seeded together, the time to initiate germination is shorter. Annual grasses germinate earlier than perennial grasses and annual grasses rely on subtle cues to initiate germination (Wainwright et al. 2012). Because perennial grasses had higher germination rates when seeded with annual grasses, it seems likely that when perennial grasses are seeded with annual grasses in autumn, the early germination of neighboring annual grasses accelerates perennial grass germination in the germination life history stage.

4.5.3 Life History (emergence through second growing season)

Our data support our hypotheses that providing perennial grasses a priority effect by seeding perennial grasses prior to annual grasses yields higher perennial grass density through their life history. Earlier seeded species can have higher individual plant production because they have unrestricted access to soil resources (Turkington et al. 2005). In addition, if perennial grasses are able to emerge before annual grasses, they can be strong competitors of soil resources against annual grasses (Orloff et al. 2013). Our data suggest that when annual grass seeding is delayed until spring, perennial grasses had almost 4-times higher emergence rates than when annual and perennial grasses were simultaneously seeded in autumn and this effect continues through the first growing season. However, in this study we found that providing perennial grasses a priority seeding effect only produced higher perennial grass density when annual grass propagule pressure was high (Fig. 4-6). If annual grass propagule pressure was low, perennial grasses had higher density when annual grasses were seeded in autumn, suggesting that perennial grasses are likely facilitated by low numbers of neighboring grasses, even though they are annuals (Lortie and Turkington 2008). Facilitation tends to be high among native species in shrub-steppe ecosystems (Diaz et al. 2004; HilleRisLambers et al. 2010) and HuberSannwald et al. (1996) found that native grasses have high morphological flexibility, which allows them to survive in diverse and low-competitive plant communities by their plastic responses to available resources, especially in later growth stages. Consequently, delaying annual grass seeding until spring can increase perennial grass density by providing perennial grasses a priority seeding effect when annual grass propagule pressure is high, yet seeding perennial grasses in autumn will likely yield higher perennial grass density when annual grass propagule pressure is low (Grman and Suding 2010).

Contrary to our hypotheses, when annual grass seeding was delayed until spring, annual grass density was two-times higher than when annual grass seeding occurred in autumn. When annual grasses are seeded in autumn, the extended time spent underground before emerging can increase seedling mortality (Boyd and Lemos 2013). Seedling mortality can be high in the winter because freeze-thaw cycles in arid environments are common (Eviner and Chapin 2003). Pathogen attack during winter can be also high, especially when water availability is high (Seabloom et al. 2009). Although, our finding that if annual grasses were able to emerge, they were likely to develop into adults, suggests that there are few ecological processes that limit annual grass growth following annual grass emergence. Annual grasses have a short life cycle and high relative growth rates (Arredondo et al. 1998). Wainwright and Cleland (2013) found that annual grasses germinate quickly under a variety of germination cues and before neighboring plants. By initiating growth early, annual grasses can capitalize on available resources before neighboring plants (Corbin and D'Antonio 2010). In addition, because annual grasses produce copious amounts of seed that has high regeneration success (Humphrey and Schupp 2001; Smith et al. 2008), it seems that managing annual grasses following emergence may not be as useful as controlling these species prior to emergence.

Theoretically, higher propagule pressure should yield higher plant densities (Lortie and Turkington 2002), but is dependent on competitor seed densities and safe site availability (Thomsen et al. 2006). Lortie et al. (2005) found that higher seed density within plant patches decreased seedling emergence but strongly increased species survival. In this study, we found that life history stage was not as important as competitor densities because higher perennial grass seeding rates only produced higher seedling densities from emergence to adult life history stages when annual grass seeding rates were low. Annual grass preemption of safe sites and soil resources from perennial grasses can be high in annual grass dominated systems (Abraham et al. 2009). In a previous study, we found that if the annual grass seeding rate exceeded 150 seeds m^{-2}, the likelihood of perennial grass survival would be low because of annual grass preemption of resources (Schantz et al. *in press*). Similarly, in this study, perennial grass density throughout their life history was low when annual grass seeding rates were higher than 150 seeds m^{-2}. Additionally, increasing annual grass seeding rates past 1,500 seeds m^{-2} did not affect annual grass density. Thus, annual grass propagule pressure likely limits both annual and perennial grass growth, first by occupying safe sites in early life history stages, then by acquiring a majority of soil resources in later life history stages (Fridley et al. 2007; Goldberg et al. 2001).

Our finding that annual grass density in the second growing season was two-or more times higher than initial annual grass seeding rates and over five-times higher than perennial grass density in the second growing season, suggests that annual grass interference with themselves and with seeded perennial grasses will be high by the second growing season. Because annual grasses grow in the late winter and spring, a resource abundant time in the shrub-steppe, and annual grasses have a short life cycle, there appear to be few ecological processes limiting annual grass production through their life history (Sheley and James 2014). Alternatively, our finding that annual grasses can be density-dependent, such that they are self-limited when initial seeding rates were higher than 1,500 seeds m^{-2}, suggests that annual grass density is self-limiting when space and/or soil resources become scarce (Turkington et al. 2005). Because annual grasses appear to only be limited by their own occupation of safe sites and soil resources, they will likely persist in plant communities, through their life history, if there are available seeds, safe sites, and soil resources for their growth (Yelenik and Levine 2011).

4.5.3.1 Second growing season

It has been well documented that the annual grasses preemptively acquire safe sites and soil resources from developing perennial grasses in early life history stages (Craine et al. 2005; Wedin and Tilman 1993). However, in this study, we found that annual grasses had higher densities from emergence through the second growing life history stages when seeded with perennial grasses. Annual grasses likely benefit from being seeded with perennial grasses because perennial grasses provide structure and protection from harsh environmental conditions (Arredondo et al. 1998). Alternatively, because perennial grasses only had higher density in the second growing season when annual grasses were delayed seeding until spring suggests that perennial grasses are unlikely to establish in areas that have high annual grass propagule pressure (Larios et al. 2013). DiVittorio et al. (2007) also found that in areas that had high annual grass propagule pressure, perennial grass establishment was low. Because annual grasses have high relative growth rates (Svejcar 1990), seed production (Smith et al. 2008), and resource acquisition (Ray-Mukherjee et al. 2011), annual grass interference with seeded perennial grasses is high. In addition, our finding that annual grass density in the second-growing season was two-times higher than the adult annual grass density in the first growing season suggests that annual grass interference with its neighbors will increase through their life history (Hirsch-Schantz et al. *in press*). Consequently, establishing perennial grasses in the first growing season is important, because annual grass interference with perennial grasses in the second growing season will likely be high.

4.5.4 Water availability

Higher water availability during the first growing season was important at increasing plant fitness throughout all species life history. Soil nutrient availability and safe site abundance are usually higher when water availability is high (Abbott and Roundy 2003). When water availability is high, competition for resources is lower and plant community composition is higher (Burke et al. 1998). However, in this study, adding water only increased perennial grass density when annual and perennial grass seeding rates were lower than 2,500 seeds m^{-2}. Our finding that when seeding rates exceed 2,500 seeds m^{-2} for both annual and perennial grasses, suggests that safe site availability becomes limited when seeding rates exceed 2,500 seeds m^{-2} for both annual and perennial grasses (Clark et al. 2007). Similarly, Goldberg et al. (2001) suggests that density-dependence, or the theory that population growth rates are regulated by species density, strongly affects plant growth at all life history stages. When water availability is high, safe site abundance will increase, but safe sites for plant growth will still be limiting in this ecosystem when both annual and perennial grass seeding rates are higher than 2,500 seeds m^{-2}.

4.5.5 Conclusions and management implications

A systems based management approach can be advantageous to forecasting the effect of ecological processes on plant growth. In this study, we found that when management inputs were modified, plant community assembly varied, and generally benefited the desirable perennial grass density through their life history. Facilitation dominated species interactions in early life history stages because when perennial grasses were seeded with annual grasses, they had higher germination rates than when annual grass seeding was delayed until spring. Competition for space and soil resources did not affect plant interactions until the emergence life history stage. We found that when seeding rates were high, competition for space and soil resources was also high, which resulted in low annual and perennial grass densities from the emergence to the second-season adult growth stages. Regardless of management input, all species were limited between the germination and seedling emergence growth stages, suggesting that freeze-thaw cycles, pathogen attack, and soil crusts strongly inhibit plant growth from the germination to emergence growth stages. When annual grass seeding was delayed until spring, perennial grasses were provided a priority seeding effect, which resulted in higher perennial grass densities through the first growing season, but only when annual grass propagule pressure 1,500 seeds m^{-2} or higher. If annual grass propagule pressure was low, perennial grasses had higher density through their life history when annual and perennial grasses were seeded in autumn. Consequently, perennial grasses are likely facilitated from small numbers of neighboring annual grasses, but if annual grass density is higher than 150 seeds m^{-2}, modifying management strategies, by providing these species a priority seeding effect will increase their density. Higher water availability benefited the growth of all species, likely because when water availability is high, soil resource and safe site availability are high. By the second-growing season, perennial grass densities were generally lower than 5 plants m^{-2} and these species had especially low densities where their first year plant densities were low. Alternatively, the densities of annual grasses in the second growing season were almost 2-times higher than the adult densities from the first growing season. Consequently, establishing perennial grasses in the first growing season is essential to restoring these species to annual grass dominated ecosystems because annual grass interference on perennial grasses in the second growing will likely be high. Based on our findings, managers will likely have the greatest perennial grass recruitment to annual grass dominated areas when attempting to limit annual grass propagule pressure prior to seeding perennial grasses. In addition, if perennial grasses establish poorly in the first year, imploring adaptive management strategies, such as targeted grazing or prescribed fire, before the second growing season should help increase perennial grass recruitment to these annual grass invaded regions.

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Table 4-1 Seeding factors and factor levels (n=192)

Annual Grass Dispersal Timing	**Water**	**Annual grass seeding rate (seeds m^{-2})**	**Perennial grass seeding rate (seeds m^{-2})**
November (Simultaneous)	No-Water	150	150
February (Delayed)	Water	1,500	1,500
		2,500	2,500
		3,500	3,500

Table 4-2 ANOVA table of main effects and interactions among growth stages and treatments ($P \leq 0.05$; n = 288 annuals; n=192 perennials). Table includes density degrees of freedom (*df*), annual grass density and perennial grass density. Bold numbers are significant. (Continued on next page)

		Annual Density		**Perennial Density**	
Effects and Interactions	***df***	**F-Value**	***p*-Value**	**F-Value**	***p*-Value**
water	8	26.91	**0.0008**	5.56	0.0564
timing	16	87.46	**<.0001**	5.69	**0.0345**
water + timing	16	5.78	**0.0287**	3.66	0.0800
annuals (ann)	96	33.79	**<.0001**	1.31	0.2789
water + ann	96	2.76	**0.0465**	2.07	0.1119
timing + ann	96	10.91	**<.0001**	4.38	**0.0069**
water + timing + ann	96	1.39	0.2519	0.48	0.7000
perennials (per)	96	0.62	0.6043	14.65	**<.0001**
water + per	96	0.13	0.9429	1.64	0.1842
timing + per	96	1.21	0.3114	0.89	0.4477
water + timing + per	96	0.04	0.9903	0.41	0.7462
ann + per	96	3.65	**0.0006**	2.27	**0.0236**
water + ann + per	96	1.48	0.1669	1.28	0.2561
timing + ann + per	96	2.21	**0.0276**	0.96	0.4747
water + timing + ann + per	96	1.19	0.3128	0.76	0.6574
growth stage (stage)	8	3.77	0.0593	9.72	**0.0131**
water + stage	8	0.84	0.5080	0.71	0.5290
timing + stage	16	7.28	**0.0027**	8.63	**0.0048**
water + timing + stage	16	0.93	0.4479	0.49	0.6254
ann + stage	96	3.49	**0.0009**	4.82	**0.0003**
water + ann + stage	96	3.24	**0.0018**	1.02	0.4216
timing + ann + stage	96	3.50	**0.0009**	2.01	0.0749
water + timing + ann + stage	96	3.27	**0.0016**	1.69	0.1348
per + stage	288	26.91	**0.0008**	1.75	**0.0112**
water + per + stage	288	87.46	**<.0001**	0.96	0.4544
timing + per + stage	288	5.78	**0.0287**	1.03	0.4084
water + timing + per + stage	288	33.79	**<.0001**	1.02	0.4116
ann + per + stage	288	2.76	**0.0465**	1.52	0.0860
water + ann + per + stage	288	10.91	**<.0001**	0.95	0.5151
timing + ann + per + stage	288	1.39	0.2519	1.06	0.3950
water + timing + ann + per + stage	288	0.62	0.6043	1.12	0.3313

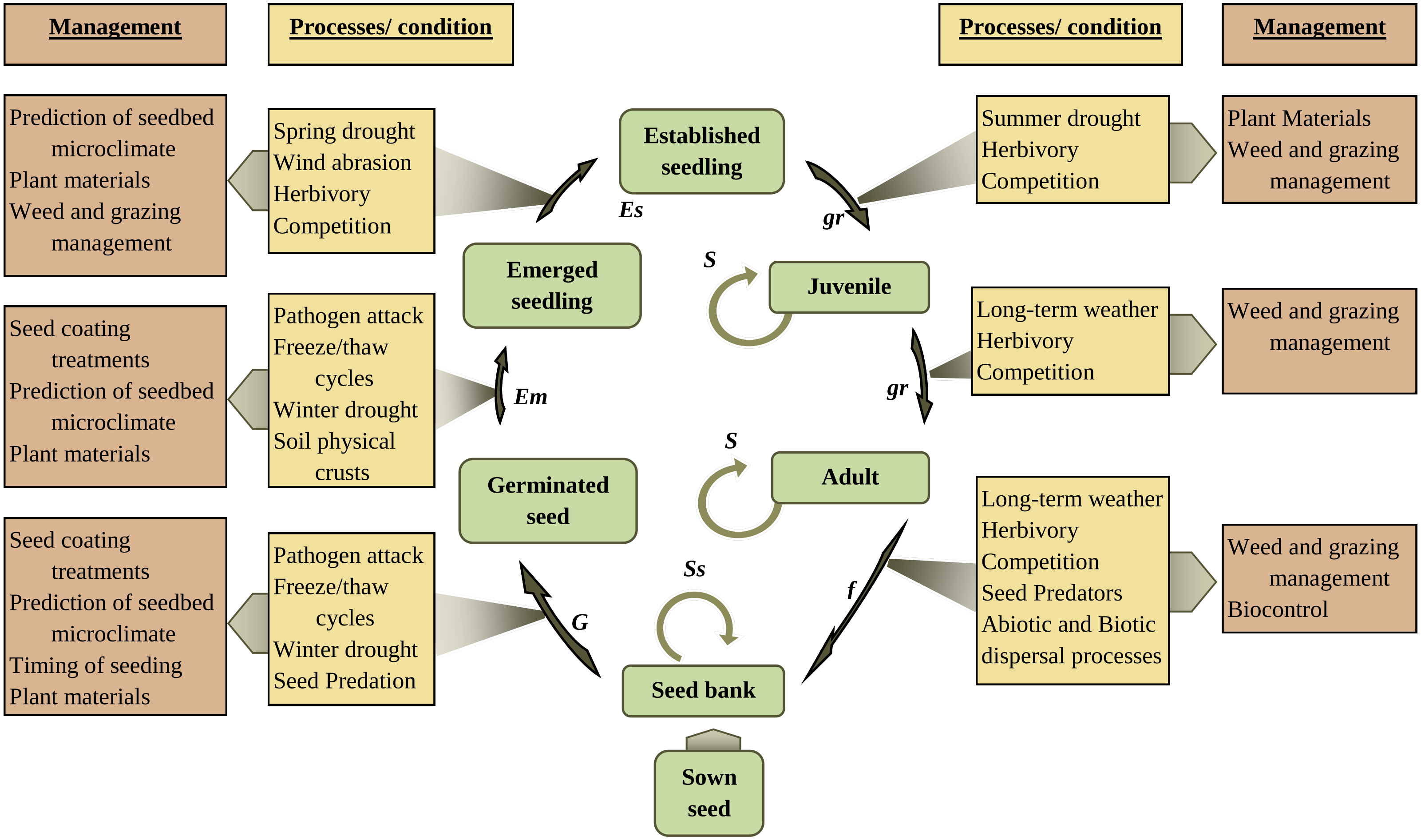
Table 4-3 Percentage of perennial grass seedlings at each life history stage in 2012.

Sampling Date	**emergence**	**establishment**	**juvenile**	**adult**
March 13-24	100%	0%	0%	0%
Apr. 1-7	100%	0%	0%	0%
Apr. 15-21	100%	0%	0%	0%
Apr. 29-May 5	87.5%	12.5%	0%	0%
May 13-19	47%	50%	3%	0%
May 27-June 2	46%	41%	11%	1%

Table 4-4 Percentage of annual grass seedlings at each life history stage in 2012.

Sampling Date	**emergence**	**establishment**	**juvenile**	**adult**
March 13-24	100%	0%	0%	0%
Apr. 1-7	100%	0%	0%	0%
Apr. 15-21	17%	82%	1%	0%
Apr. 29-May 5	4%	52%	38%	6%
May 13-19	2%	23%	47%	27%
May 27-June 2	4%	17%	56%	23%

Fig. 4-1 Modifed from James et al. 2013. Systems framework for managing limitations to recruitment on rangeland Modified from James et al. 2013. The **inner layer** of the framework is a life cycle population model that describes the demographic stages (boxes) and transitions (arrows) between stages a sown seed follows to recruit into the adult population. Symbols, *Ss* = seed survival, *G*= germination, *Em*=emergence, and *Es*=establishment, indicate transitions between distinct stages of seedling development. The text describes the developmental stages used to define each transition. Symbols *gr*, *f* and *S* are size dependent growth, fecundity and survival, respectively. The **middle layer** of the model identifies key ecological processes and conditions that the literature suggests can influence transitions among stages. The **outer layer** identifies representative management tools and strategies that could be used to modify processes and conditions that limit life stage transitions. (Continued on next page).


Management
Processes/ condition
Processes/ condition
Management
Prediction of seedbed microclimate
Plant materials
Weed and grazing management
Spring drought
Wind abrasion
Herbivory
Competition
Established seedling
Es
gr
Summer drought
Herbivory
Competition
Plant Materials
Weed and grazing management
Emerged seedling
S
Juvenile
Seed coating treatments
Prediction of seedbed microclimate
Plant materials
Pathogen attack
Freeze/thaw cycles
Winter drought
Soil physical crusts
Em
gr
Long-term weather
Herbivory
Competition
Weed and grazing management
S
Germinated seed
Adult
Seed coating treatments
Prediction of seedbed microclimate
Timing of seeding
Plant materials
Pathogen attack
Freeze/thaw cycles
Winter drought
Seed Predation
G
Ss
f
Long-term weather
Herbivory
Competition
Seed Predators
Abiotic and Biotic dispersal processes
Weed and grazing management
Biocontrol
Seed bank
Sown seed

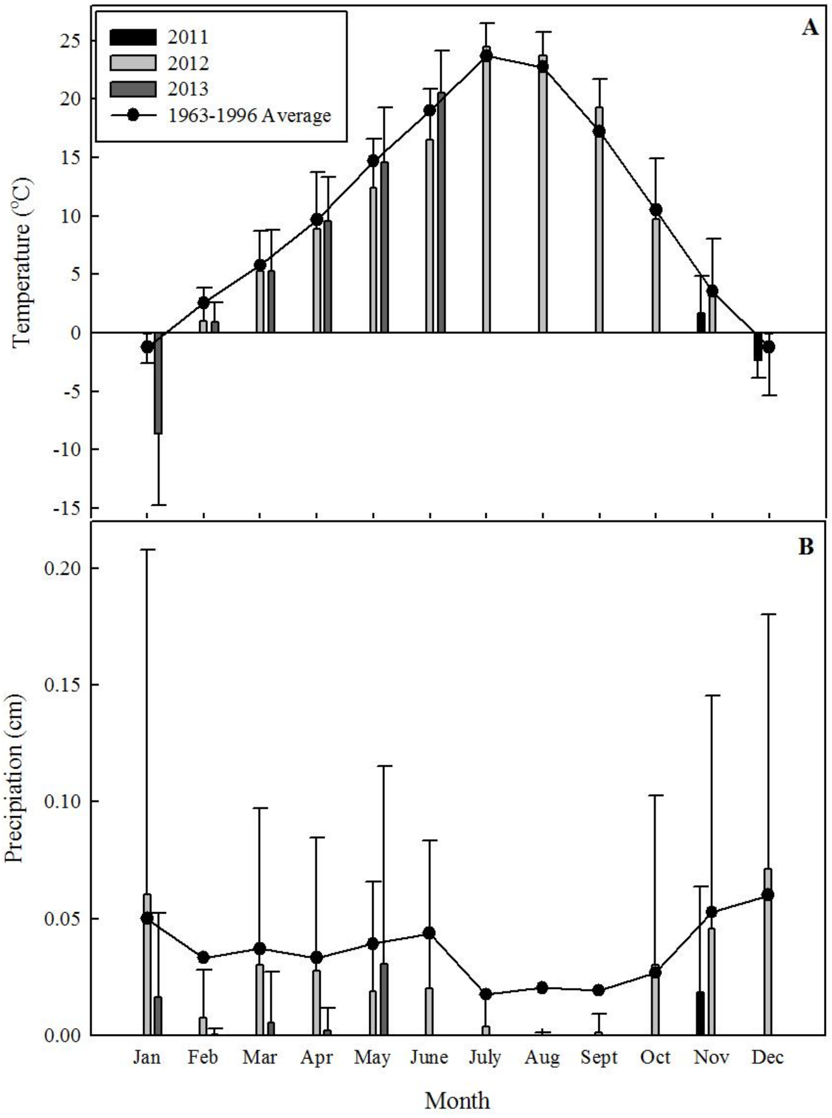


Fig. 4-2 Climate data over the sampling period (November, 2011- June, 2013) and the 30 year average for precipitation and temperature. Figure A represents the mean daily precipitation and its standard deviation (mm); Figure B represents the mean and standard deviation of daily temperature (˚C).

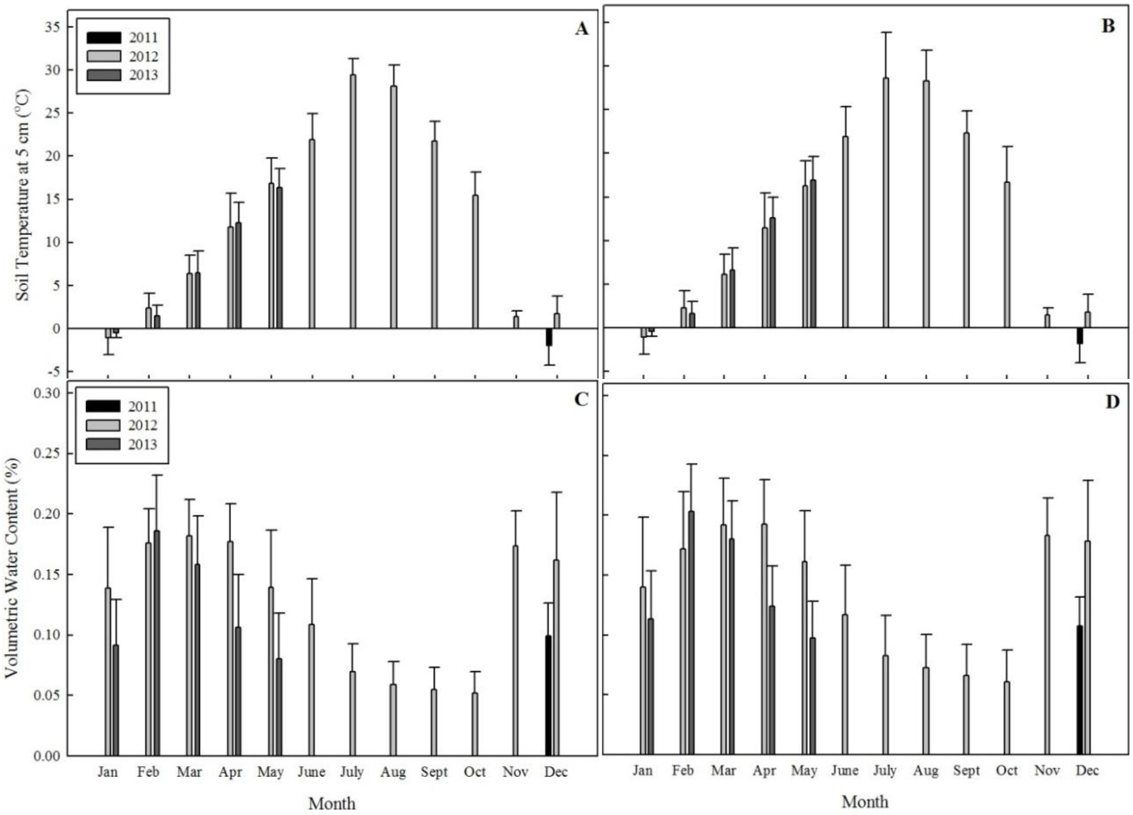


Fig. 4-3 Soil temperature at 5 cm (˚C) and volumetric water content at 5 cm (%) measured from December, 2012-May 2013. Figure A represents the means and standard deviation of soil temperature in the no water treatments, Figure B represents the means and standard deviation of soil temperature in the water added treatments, Figure C represents the means and standard deviation of volumetric water content in the no water treatments, and Figure D represents the means and standard deviation of volumetric water content in the water added treatments.

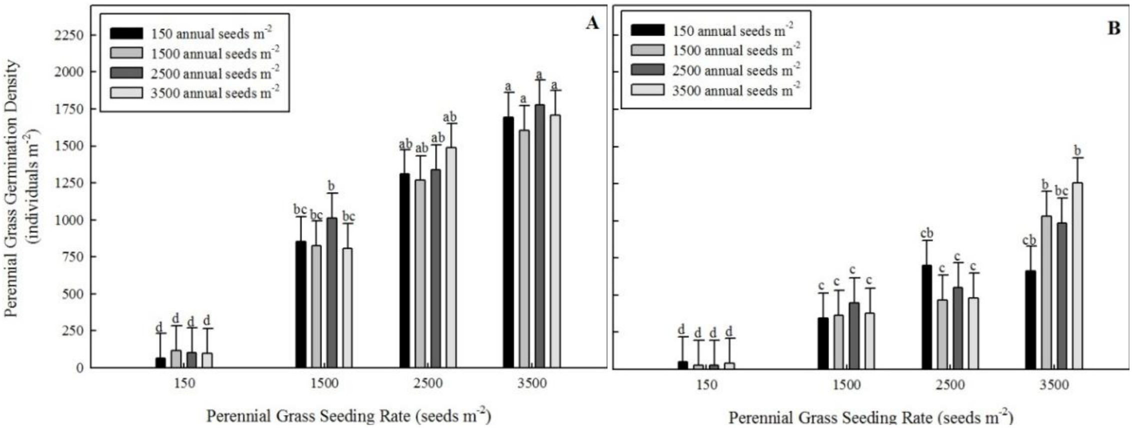


Fig. 4-4 Means and standard error of perennial grass germination: Figure A represents when annual and perennial grasses were simultaneously seeded. Figure B represents when annual grass seeding was delayed until spring seeding.

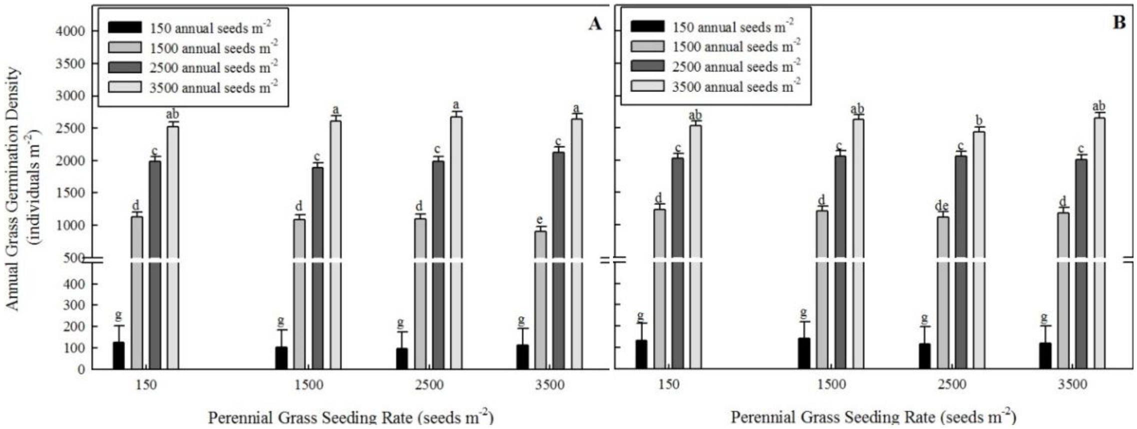


Fig. 4-5 Means and standard error of annual grass germination: Figure A represents when annual and perennial grasses were simultaneously seeded. Figure B represents when annual grass seeding was delayed until spring seeding.

Fig. 4-6 Least squared means and standard error of perennial plant density (density m^{-2}) by life history stage including the seeding rate, germination, emergence, established, juvenile, adult, and second year-adult. Germination did not include a watering treatment due to the difficultly of administering water in the winter months. Asterisks represent a significant difference within a life history stage ($P \leq 0.05$). (Continued on next page)

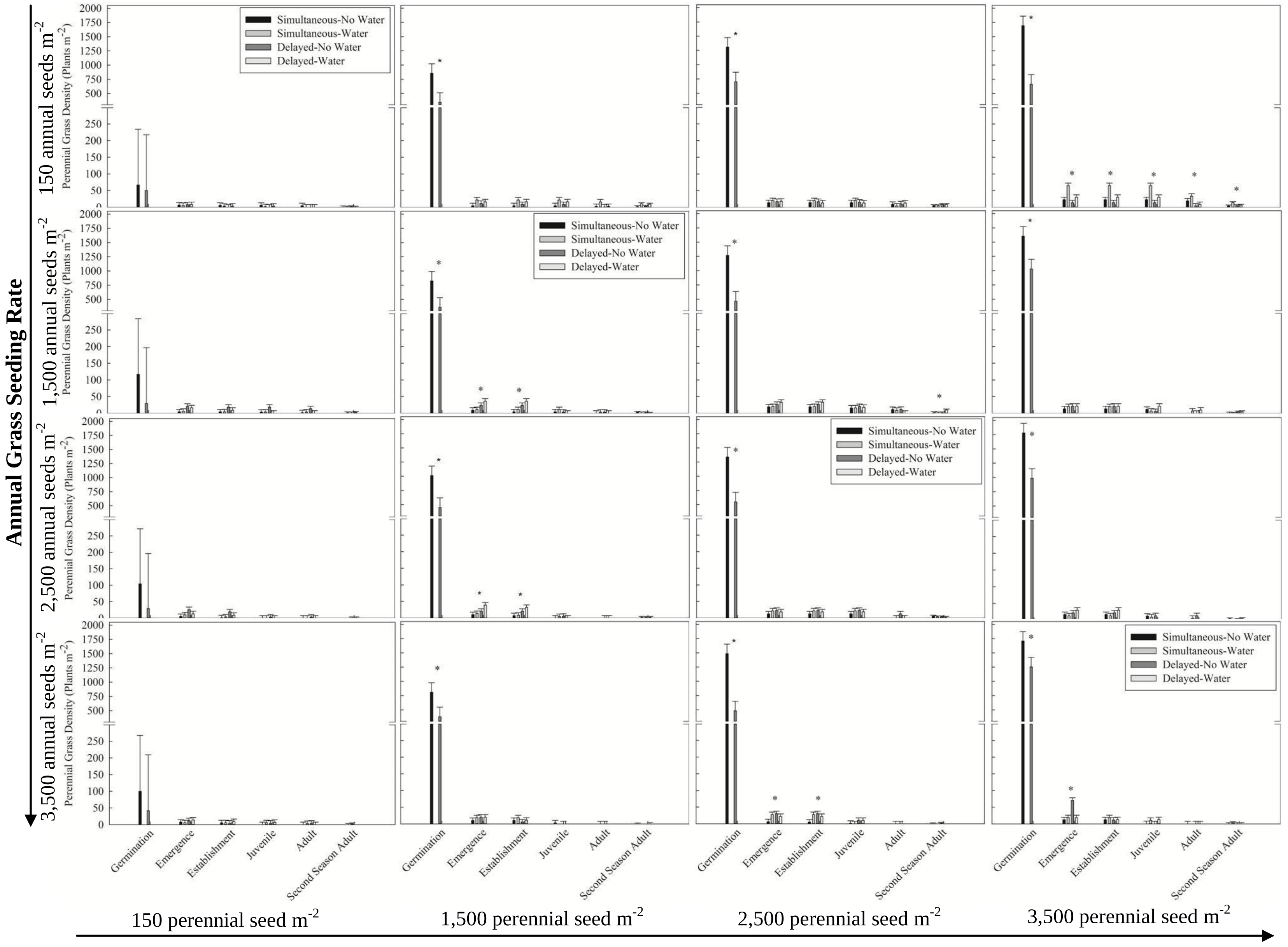
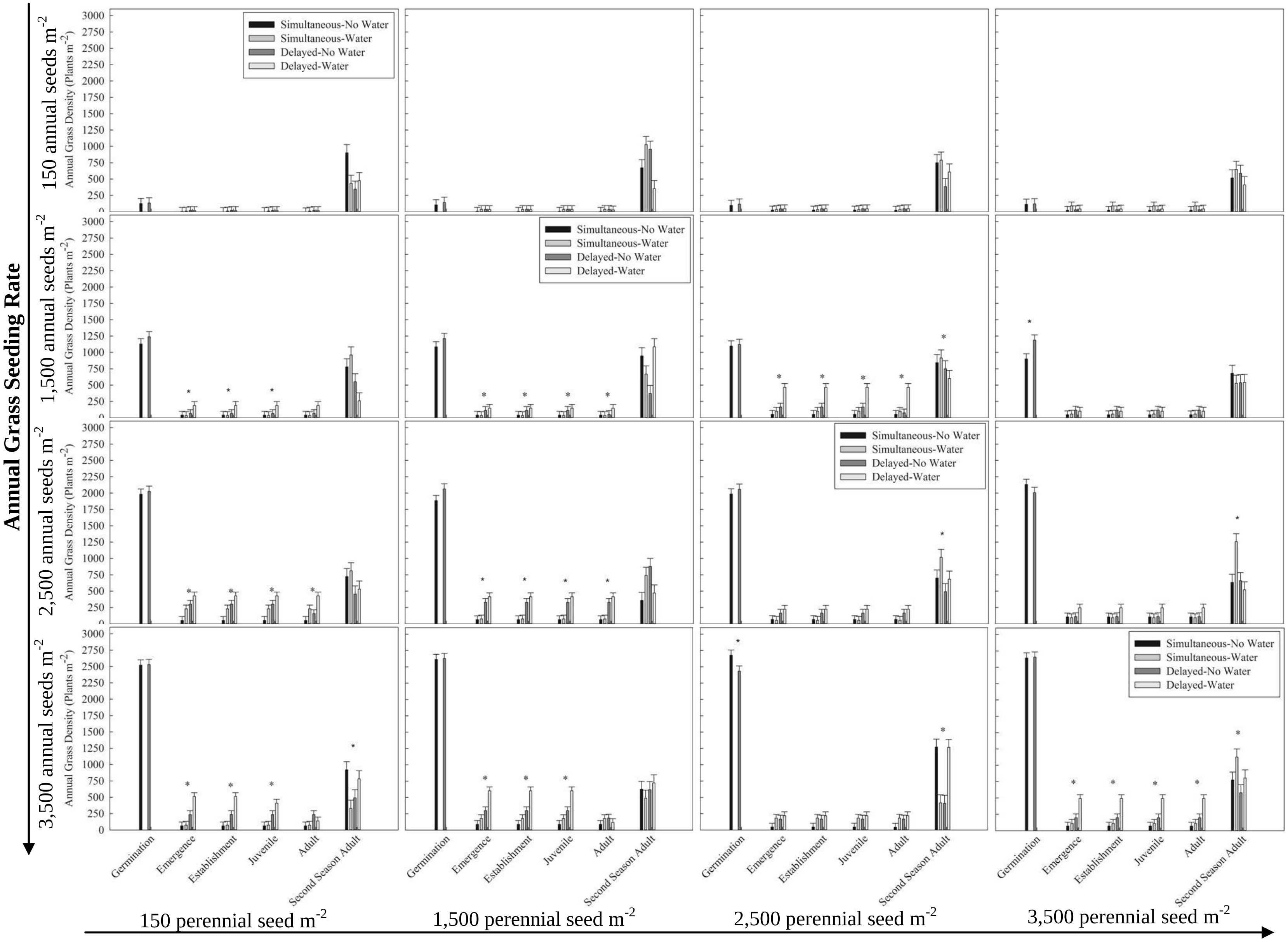

Annual Grass Seeding Rate
150 annual seeds m-2
1,500 annual seeds m-2
2,500 annual seeds m-2
3,500 annual seeds m-2
Perennial Grass Density (Plants m-2)
Simultaneous-No Water
Simultaneous-Water
Delayed-No Water
Delayed-Water
0
50
100
150
200
250
500
750
1000
1250
1500
1750
2000
*
Germination
Emergence
Establishment
Juvenile
Adult
Second Season Adult
150 perennial seed m-2
1,500 perennial seed m-2
2,500 perennial seed m-2
3,500 perennial seed m-2

Fig. 4-7 Least squared means and standard error of annual grass density (density m^{-2}) by life history stage including the seeding rate, germination, emergence, established, juvenile, adult, and second year-adult. Germination did not include a watering treatment due to the difficultly of administering water in the winter months. Asterisks represent a significant difference within a life history stage ($P \leq 0.05$). (Continued on next page)


Annual Grass Seeding Rate
150 annual seeds m^{-2}
1,500 annual seeds m^{-2}
2,500 annual seeds m^{-2}
3,500 annual seeds m^{-2}
Annual Grass Density (Plants m^{-2})
0
250
500
750
1000
1250
1500
1750
2000
2250
2500
2750
3000
Simultaneous-No Water
Simultaneous-Water
Delayed-No Water
Delayed-Water
*
Germination
Emergence
Establishment
Juvenile
Adult
Second Season Adult
150 perennial seed m^{-2}
1,500 perennial seed m^{-2}
2,500 perennial seed m^{-2}
3,500 perennial seed m^{-2}

5 General Conclusions

5.1 Summary of main dissertation findings

On landscapes dominated by invasive plants, restoration is central to fostering desired vegetation structure and function (Montoya et al. 2012). Seeding is a restoration technique that accelerates desirable species establishment into invasive plant dominated communities (Newman and Redente 2001). Given the current knowledge and technology, attempts to establish desirable species into areas that are dominated by invasive plants by seeding typically produces patchy plant populations that are unable to survive among the existing 'weedy' species (Montoya et al. 2012; Sheley and James 2014). Overcoming limitations to restoration requires a basic understanding of ecological processes that direct vegetation dynamics, together with the knowledge of the establishment and persistence of invasive species (Sheley et al. 2006). One of the grand challenges in the western United States is to identify and manipulate the ecological processes directing successional dynamics to restore annual grass invaded ecosystems (Eliason and Allen 1997; Sheley and Larson 1996). Seed dispersal strongly influences plant community assembly and seedling life history dynamics following restoration (DiVittorio et al. 2007; Larios et al. 2013). The research presented in this dissertation uses various experimental approaches to investigate the role of dispersal dynamics, specifically propagule pressure and priority effects, influencing the initial establishment, growth, and life history of invasive annual grasses and desired perennial grasses during restoration of invaded shrub-steppe.

In Chapter 2, we sought to evaluate the role propagule pressure and priority effects by testing the effects of seeding annual grasses in autumn or spring, adding water, and varying annual and perennial grass seeding rate by 150, 1,500, 2,500, or 3,500 seeds m^{-2} on perennial and annual grass seedling emergence and final density and biomass. We hypothesized that species which arrive earliest and have the highest seeding rate will produce the highest density. We also hypothesized that water additions would increase the density of perennial and annual grasses, and would ultimately favor both functional groups' establishment. Some of our key findings included that native perennial grass recruitment into invasive annual grass dominated sites depended on the interaction among dispersal timing, propagule pressure and water availability. In support of our hypotheses, we found that providing perennial grasses a priority effect by delaying annual grass seeding until spring initially facilitated perennial grass density; however this effect did not persist into the second-year following seeding. Similarly, our finding that when annual grass propagule pressure exceeded 150 seeds m^{-2}, an ecological threshold was crossed which limited perennial grass recruitment regardless of perennial grass seeding rate, support our hypotheses. When water availability was high, perennial grass establishment was high because safe site availability increased, but perennial grass establishment was dependent on annual grass propagule pressure. Because adding water increased the density of both annual and perennial grasses, we found support our hypothesis that water would favor the development of both annual and perennial functional groups. Collectively, our results suggest that propagule pressure, priority effects, and water availability strongly affect plant community establishment following seeding.

In Chapter 3, perennial grass seeding time and frequency, annual and perennial grass seeding density, and water availability were modified to evaluate the effect of priority effects and propagule pressure on seedling establishment. We hypothesized that perennial grass seed dispersal split between the autumn and spring would result in higher perennial grass density and biomass compared to seeding native grasses exclusively in either period. In addition, we hypothesized that perennial grass density and biomass in seasonally split applications would be higher when perennial propagule pressure was high and annual grass propagule pressure was low. We also hypothesized that adding water would increase perennial grass density and biomass, especially in plots with seasonally split seeding and high perennial grass propagule pressure. In support of these hypotheses, we found increasing the frequency of perennial grass seeding to autumn and spring or delaying perennial grass seeding until spring produced higher perennial grass density and biomass than seeding in autumn. Increasing perennial grass seeding rates also support our hypotheses because perennial grass density and biomass were higher when perennial grass seeding rates were high and this effect was especially apparent when seeding frequency and water availability were higher. However, our finding that there was a threshold between 150-1500 annual grass seeds m^{-2}, where regardless of perennial grass seeding strategies, perennial grass density and biomass were low, contradict our hypotheses that increasing perennial grass seeding frequency or delaying perennial grass seeding until spring would increase perennial grass density. In support of our hypotheses, higher water availability increased perennial grass establishment, but only when annual grass propagule pressure was low. This study confirms that modifying dispersal dynamics can increase the probability of a perennial grass seed reaching a safe site. However, because high annual grass propagule pressure limits perennial grass density and biomass, perennial grass recruitment will depend upon existing annual grass propagule pressure.

In Chapter 4, a life history approach was used to quantify population demographics when annual grass seeding times varied (autumn or spring), annual and perennial grass propagule pressure was modified by 150, 1,500, 2,500, or 3,500 seeds m^{-2}, and watering occurred (ambient or water added treatments). Our hypotheses for this study were that seeding perennial grasses at high seeding rates and prior to annual grass seeding would increase perennial grass density by providing these species a priority effect for accessing safe sites and reducing invasive species interference in later life history stages. In addition, we hypothesized that higher water availability would increase perennial grass density through their life history because higher resource availability can initially increase the number of available safe sites and reduce competition for resources in later life history stages. In this study, we found that all species had low emergence rates, even though seedling germination was relatively high which, based on prior research, suggests that freeze-thaw cycles, pathogen attack, and soil crusts strongly inhibit plant growth from the germination to emergence growth stages. Alternatively, contrary to our hypothesis that providing perennial grasses a priority seeding effect would increase perennial grass density, we found that perennial grass germination rates were higher when they were seeded with annual grasses in autumn compared to delaying annual grass seeding until spring. This finding suggests that perennial grasses are facilitated by neighboring annual grasses during germination. Following seedling emergence, we found support for our hypothesis that providing perennial grasses a priority seeding effect by delaying annual grass seeding until spring would yield higher perennial grass density and this effect was especially apparent from the emergence to the juvenile life history stages. However, delaying annual grass seeding until spring only provided perennial grasses a priority effect when annual grass propagule pressure was high. When annual grass propagule pressure was low, seeding perennial grasses in autumn yielded the highest perennial grass density through their life history. Consequently, perennial grasses appear to be facilitated by low numbers of neighboring annual grasses through their life history. We found support for our hypotheses that water availability would facilitate the growth of all species because both annual and perennial grasses had higher density when water was added. By the second growing season, annual grass density was two-times higher than initial annual grass seeding rates and over four-times higher than perennial grass density, suggesting that annual grass interference by the second growing season was high. Collectively, these results suggest that early seedling development is highly vulnerable to the ecological processes surrounding seedling development, especially for perennial grasses. Based on these findings; applying management, such as targeted grazing, preemergent herbicides, or prescribed fire, prior to seedling emergence and using adaptive management strategies to facilitate plant establishment following the first winter should increase desirable plant density.

5.2 Future Research

Plant community assembly following seeding of resource poor environments, such as the shrub-steppe, requires a keen understanding of the processes that limit seedling establishment together with the knowledge of management inputs that will increase seedling success. Based on the findings from my dissertation research, it appears that seedling establishment is limited by annual grass interference of safe sites and soil resources. Systems-based management approaches increase our understanding of ecological processes on population demographics; yet extrapolating these effects to multi-species, sites, soils, climate across years are not included in the current models. To manage these dynamic ecosystems, these models should included site, soils, climate, and all species into a systems-based model because quantifying plant community assembly in a variety of conditions will increase our ability to restore dynamic ecosystems.

5. 3 Citations

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