Effects of propagule pressure and priority effects on seedling recruitment during restoration of invaded grassland

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ABSTRACT

High disturbance frequency, low water availability, and advantageous growth mechanisms of invasive annual compared to native perennial grasses reduce native grass establishment throughout arid rangelands. Modifying seeding dispersal processes, including seeding rate and time, may increase native grass recruitment by influencing safe site occupation. A better understanding of seedling development through life history stages and the ecological processes occurring during these stages may be necessary to comprehend modified dispersal dynamics on plant community assembly. We tested the effects of spring vs. fall annual grass seeding times, adding water, and varying annual and perennial grass propagule pressure on perennial and annual grass recruitment in an eastern Oregon shrub-steppe ecosystem. Across species, survival rates were lowest between germination and emergence stages. However, perennial grass germination rates were highest when perennials were seeded with annual grasses in autumn. Perennial grass recruitment was generally low, especially when annual grass propagule pressure was higher than 150 seeds m^{-2}. Although, by the second growing season, perennial grasses had the highest density when perennials were seeded with annuals in autumn and water was added. Consequently, modifying native perennial grass dispersal, like priority autumn seeding and increasing propagule pressure, should produce higher perennial grass recruitment across arid lands.

1. Introduction

Arid lands across the western U.S. are plagued by the spread and dominance of exotic annual grass invaders (Brooks et al., 2016). These invasive species reduce the ecological integrity and function of arid ecosystems (Seastedt and Pyšek, 2011). Their invasiveness is related to physiological advantages such as higher growth rates, faster germination times, and greater allocation to roots than many native perennial grasses (Gornish and James, 2016). Resource preemption allows these invaders to capture most of the available space, water, and soil nutrients prior to the onset of native perennial plant growth. Furthermore, annual grasses have greater propagule pressure than native perennial grasses and produce, on average, 100-times more seeds annually than perennial grasses and have germination rates averaging 97% (Smith et al., 2008). Thus, most invasive annual grass-dominated sites are very resistant to restoration (Kulpa et al., 2012). A better understanding of the ecological processes, propagule pressure and priority effects may be central to restoring native perennial grasses to these regions.

Propagule pressure and priority effects can strongly influence plant assembly by influencing safe site occupation, which depends on the number and timing of seeds reaching safe sites (Satterthwaite, 2007). Species that arrive and develop first have a priority effect for accessing safe sites, or resource patches within a plant community that provide conditions suitable for seedling germination and establishment (Grubb, 1977). Where invasive annual grasses dominate, safe site availability is typically low (Aicher et al., 2011), primarily because annual grasses produce high numbers of propagules that dominate seed banks. Furthermore, annual grasses begin growth earlier than most native grasses, thus preempting available safe sites and soil resources (Chambers and Wisdom, 2009). Consequently, seeding desirable native perennial grasses at the optimal times and rates should produce higher native plant density by matching the seed availability with safe site openings.

Complicating seedling success is that water is generally the most limiting resource for seedling development in arid ecosystems (Abbott and Roundy, 2003). Furthermore, precipitation timing and availability vary through time and strongly influence safe site availability (Weltzin and McPherson, 1999). Making short-term weather predictions and seeding in a wet year should facilitate native grass seedling establishment. However, it is still undetermined how water availability interacts with priority effects and propagule pressure to influence seedling

recruitment through their life history.

To overcome the limitations to native plant recruitment, life history stages and the transitions among stages can be quantified using system-based models that quantify underlying ecosystem dynamics and relate these properties to seedling growth characteristics of both undesirable and desirable plant species (James et al., 2013). These models were created to link the independent effects and interactions among major ecological processes dominating annual grass dominated ecosystems to species life history strategies to better understand plant community assembly, especially during invasion and restoration (Brooks et al., 2016). For example, the primary temporal limitation in native grass seedling recruitment in annual grass dominated regions occurs between the seed germination and seedling emergence stages (James et al., 2011). Low seedling establishment may be because of soil pathogen destruction, graminivore consumption, and freeze-thaw cycles that increase winter mortality in germinated seedlings, especially for autumn seeded species (James et al., 2012). Modifying propagule pressure, priority effects, or water availability may increase seedling emergence and even seedling establishment, however, seedling survival will depend upon a species' ability to transition through life history stages (Adler et al., 2014). Using a systems-based model, we can better understand the limitations to native grass seedling recruitment, especially when propagule pressure, priority seeding effects, and water availability differ.

The objective of this study was to improve seeding practices by quantifying the effects of modified propagule pressure, priority seeding effects, and increased water availability on seedling life history and the transitions among life history stages. Because seedlings must successfully transition among life history stages to reach reproductive maturity and because James et al. (2011) identified that seedling mortality was greatest between the germination and emergence growth stage, we hypothesized that 1) Where perennial grass seedling emergence rates were highest, the density of all following life history stages would also be highest. However, plant population dynamics and, thus, plant community assembly, may differ by management's influence on various ecological processes that occur at each growth stage (Fridley et al., 2007). Thus, we also hypothesized that 2) Seeded perennial grass survival rates at the end of the second growing season would be highest when their seeding rates were highest, e.g. 3500 seeds m^{-2}, annual grass seeding rates were lowest, e.g. 150 seeds m^{-2}, when water was added, and when annual and perennial grasses were seeded independently, i.e. perennial grasses were seeded in autumn and annual grass seeding was delayed until spring.

2. Materials and methods

2.1. Study site

The study was conducted about 5 km south of Juntura, Malheur County, Oregon (Zone: 11, 410178 easting, 4840910 northing) in a low elevation (1033 m) shrub-steppe dominated by annual grasses. Soils at the site are sandy-loams within the Bogusrim series (fine, smectitic, mesic abruptic Xeric Argidurids) and receive an average 250 mm precipitation per year occurring primarily in winter and spring. This site has a slight southwest-facing slope and is devoid of sagebrush. Current vegetation structure is primarily medusahead (*Taniatherum caput-medusae* (L.) Nevski) growing in association with 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.).

Average daily precipitation (cm) and temperature (°C) were recorded daily from November 2011 to June 2013 using a HOBO$^{©}$ rain gauge smart sensor (Onset Comp. Inc., Cape Cod, MA, USA). Long-term (1963–1996) average daily precipitation and temperature data from Juntura were obtained from the Western Regional Climate Center (W.R.C.C., 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.

2.2. Model system

To test seeding strategies effect on 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, and a four-species mix of the native perennial grasses, which included bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), bottlebrush squirreltail, Sandberg bluegrass, and Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth). Annual grass seeds were hand-collected 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.

Prior to initiating the study, in 2011, the site was sprayed with 3.36 L ha^{-1} of glyphosate [N-(phosphonomethyl) glycine] and tilled to 100 mm to remove existing vegetation. Densities and proportions of annual grasses and perennial grasses were arranged to provide four addition-series matrices (Radosevich, 1987) and seeded in a complete randomized design with three replications of each treatment. Seeding densities of annual: perennial grasses in each matrix were 150:150, 150:1,500, 150:2,500, 150:3,500, 1500:150, 1500:1,500, 1500:2,500, 1500:3,500, 2500:150, 2500:1,500, 2500:2,500, 2500:3,500, 3500:150, 3500:1,500, 3500:2,500, and 3500:3500. Seeding rates were chosen to illustrate low, moderate, high, and very high recommended native grass seeding rates compared to likely very low, low, medium, and medium-high existing invasive grass propagule pressure. To quantify the priority effects of perennial grasses, we used a seeding matrix where 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 2012). Half of the plots were also 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 to 2.61 L added per month, depending on the month. Each matrix was replicated three-times in a completely randomized design (Table 1).

Seeding occurred 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–May) using watering cans to evenly distribute water on each water added treatment plot.

2.3. Germination

Field germination assessments were conducted in 2013 due to time and budget constraints in 2012 and measured using the buried bag technique (Abbott and Roundy, 2003). Germination bags were created to mimic field study conditions so that seeding densities of annual:

Table 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	1500	1500
		2500	2500
		3500	3500

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 perennial grass germination bags that were filled with only perennial grasses and seeded in autumn (November 2012) and annual grass germination bags that only included annual grasses and was seeded in spring (February 2013). All germination bags were harvested on 15 March 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. Germination rates were determined by dividing the total number of germinates in each germination bag by the total number of seeds per bag. We also calculated germination density by multiplying the percentage of germinated seeds by the seeding rate. Each matrix was replicated three-times in a completely randomized design.

2.4. Emergence and recruitment

Annual and perennial grass 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 13 March to 2 June 2012. Plants were individually marked with colored toothpicks as they emerged to indicate the emergence time, while seedling mortality was counted by the number of free standing toothpicks from previous sampling periods. 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. Germination, as described above, was classified as the germination growth stage, while we categorized the recruitment growth stages as emerged seedlings (coleoptile or single leaf), established (1–5 leaves), juveniles (5–10 leaves), and adults (10 + leaves), and the second-season adults were the number of seeded species in plots in June 2013.

2.5. 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 were not normally distributed. Several 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) 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 season. To determine differences in germination rates, a mixed-model ANOVA was also used to test differences in the main effects and interactions among seeding time, annual grass seeding rate, and perennial grass seeding rate on the germination rate of annual and perennial grasses. 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 (Corbin and D'Antonio, 2004; Rice and Knapp, 2008). For all models, replication was used as the random factor, means were separated using the slice procedure (Schabenberger, 2013), and F-test results with an associated *P* value of ≤ 0.05 considered significant.

3. Results

3.1. 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 (Appendix Fig. 1A and B; *P* < 0.05). Soil temperature was approximately 5 °C higher at 5 cm when water was added and fluctuated similarly to air temperature (Appendix Fig. 2A and B; *P* < 0.05). Alternatively, volumetric water content was higher in the water added plots compared to control plots and fluctuated from about 25% in November–April to about 10% in May–October (Appendix Fig. 2C and D; *P* < 0.05).

3.2. Germination

Perennial grass germination rates were over two times higher when simultaneously seeded with annual grasses compared to delaying annual grass seeding until spring (56.35% ± 0.02 vs. 25.18% ± 0.01 perennial grass germination rates) (Fig. 1A and B; *P* < 0.001). When annual and perennial grasses were simultaneously seeded in autumn, seeding 150 perennial grass seeds m^{-2} at the three-highest annual grass seeding rates (1500–3500 annual grass seeds m^{-2}) produced higher perennial grass germination rates compared to 3500 perennial grass seeding rates (Fig. 1A; *P* < 0.001). In general, annual grass seeding rates did not affect perennial grass germination rates (*P* = 0.709). However, when only 150 annual and 150 perennial grasses were simultaneously seeded, perennial grass seeding rates were over 10% lower than when 1,500, 2,500, or 3500 annual grass seeds m^{-2} were simultaneously seeded with 150 perennial grass seeds m^{-2} (Fig 1A; *P* < 0.001). Furthermore, when annual grass seeding was delayed until spring at the highest perennial grass seeding rates (3500 perennial grass seeds m^{-2}), perennial grass seeding rates were almost twice as high when 3500 annual grass seeds were added m^{-2} (35.83% ± 0.01) compared to only seeding 150 annual grass seeds m^{-2} (18.98% ± 0.01) (Fig. 1B; *P* < 0.001).

Annual grass germination rates were higher at the lowest annual grass seeding rates (150 annual grass seeds m^{-2}) compared to the highest annual grass seeding rates (3500 annual grass seeds m^{-2}) across seeding times when only 150 perennial grass seeds m^{-2} were added and when annual grass seeding was delayed until spring and 1500 perennial grass seeds m^{-2} were added (Fig. 1C and D; *P* < 0.001). While annual grass germination rates were not generally affected by the annual grass seeding rate and time interactions (*P* = 0.157), there were two cases where similar annual grass seeding rates yielded different annual grass germination rates. For example, simultaneously seeding 1500 annual grass seeds m^{-2} and 3500 perennial grass seeds m^{-2} in autumn only yielded 60.00% ± 0.01 annual grass germination rates, compared to 79.17% ± 0.01 annual grass germination rates when annual grass seeding was delayed until spring (Fig. 1C and D; *P* = 0.014). Similarly, when 150 annual grass seeds
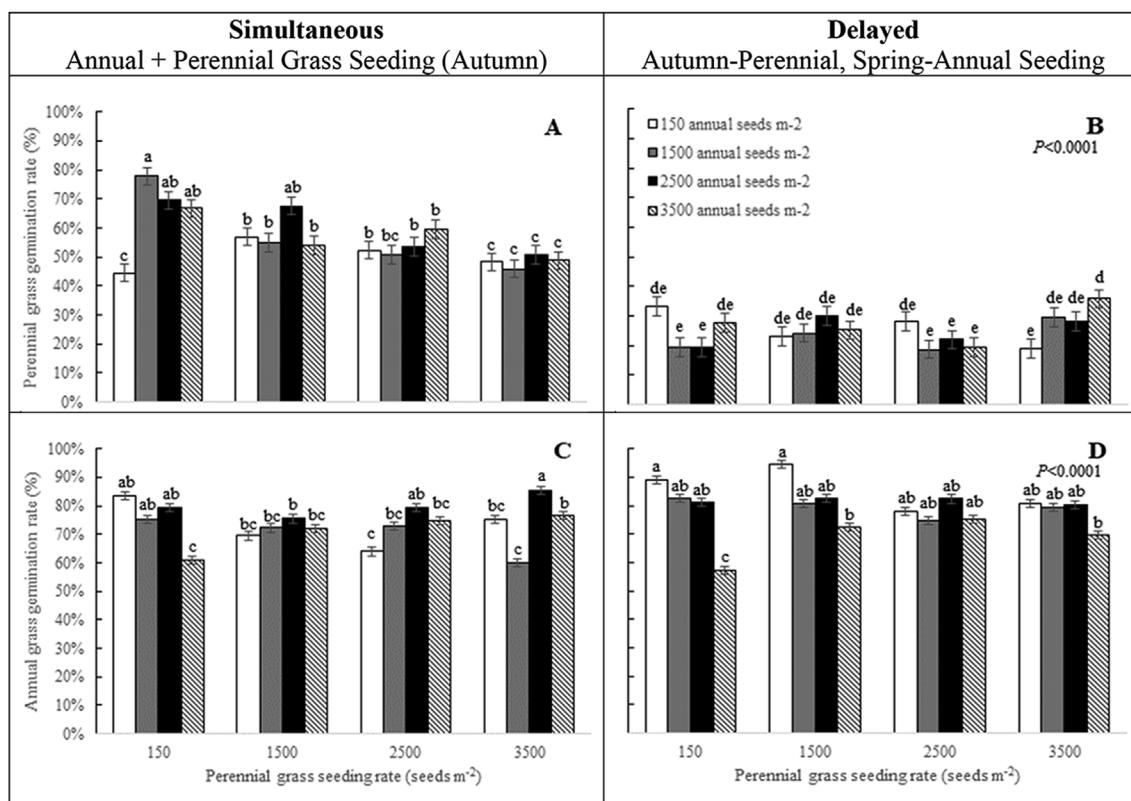
Fig. 1. Means and standard error of perennial grass ($P < 0.0001$) and annual grass ($P < 0.0001$) germination rates: Figure A and B represent perennial grass germination rates, where Fig. A represents when annual and perennial grasses were simultaneously seeded and Fig. B represents when annual grass seeding was delayed until spring seeding. Figure C and D represent annual grass germination rates where Fig. C represents annual grass germination rates when annual and perennial grasses were simultaneously seeded and Fig. D represents when annual grass seeding was delayed until spring seeding. Letters indicate differences among seeding rate treatments ($P \leq 0.05$).

m^{-2} and 1500 perennial grass seeds m^{-2} were seeded in autumn, annual grass germination rates were only 69.45% $\pm$ 0.01 compared to 94.44% $\pm$ 0.01 annual grass germination rates when annual grass seeding was delayed seeding until spring (Fig. 1C and D; $P = 0.004$).

3.3. Life history

The greatest reduction in perennial (Fig. 2; $P = 0.002$) and annual (Fig. 3; $P = 0.027$) grass density occurred between the germination and emergence life history stages, where only an average of 10% of germinated perennial and annual grasses emerged. However, the highest perennial grass seeding rates, 3500 seeds m^{-2}, yielded over three times as many emerged perennial grass seedlings as the lowest perennial grass seeding rates, 150 seeds m^{-2} ($P < 0.001$). Furthermore, delaying annual grass seeding until spring coupled with seeding at least 1500 perennial grass seeds m^{-2}, produced approximately 4 times as many emerged perennial grasses compared to delaying annual grass seeding until spring and only seeding 150 perennial grass seeds m^{-2} ($P = 0.034$).

Following seedling emergence, perennial grass density slightly decreased (Fig. 2; $P = 0.013$), and the greatest decrease in perennial grasses density through their life history occurred when annual grasses were seeded in autumn ($P = 0.005$) and when annual grass seeding rates were high ($P = 0.075$). Temporally, perennial grasses did not transition from the emergence growth stage to later growth stages until late-April, early-May (Table 3) and did not begin developing into juveniles until mid-May. By the end of the first growing season, only 1% of seeded perennial grasses developed into adults.

Annual grasses had relatively constant density from the emergence to juvenile life history stages at approximately 135 $\pm$ 8.2 plants m^{-2} (Fig. 3). Annual grass density was lower in the adult life history (116.8 $\pm$ 8.2 plants m^{-2}) stage compared to the juvenile life history

stage (135.3 $\pm$ 8.2 plants m^{-2}) ($P = 0.060$) and this effect was especially apparent when annual grasses were delayed seeding until spring ($P = 0.003$). Annual grass density differed between growth stages more at the highest compared to the lowest annual grass seeding rates ($P < 0.001$). For example, at the lowest annual grass seeding rates, the difference in annual grass density from the emergence to adult life history stages was 0.7 $\pm$ 15.8 plants m^{-2}, but was 107.3 $\pm$ 21.3 plants m^{-2} at the highest annual grass seeding rates ($P = 0.002$). Furthermore, delaying annual grass seeding until spring produced greater differences between growth stages than simultaneous annual and perennial grass seeding in autumn ($P < 0.001$) and adding water magnified this effect ($P = 0.002$). Annual grasses transitioned quickly among growth stages (Table 4). By mid-April 82% of emerged annual grasses transitioned to established individuals. By late-April to early-May, annual grass seedlings were generally evenly distributed between the establishment and juvenile stages. However, only about 25% of annual grasses reached the adult life history stage by the first year of this study.

Across all seeding treatments, perennial grass density was similar when perennial grass seeding rates were lowest (Fig. 2; $P = 1.00$). While the independent effects of annual grass seeding rates did not affect perennial grass density ($P = 0.279$), adding water increased perennial grass seedling density by approximately 3.8 $\pm$ 1.4 plants m^{-2} (Table 2; $P = 0.056$). Furthermore, perennial grass density was 1.5 times higher when annual grasses were seeded at the lowest rate, 150 seeds m^{-2}, and perennial grasses were seeded at the highest rates, 3500 seeds m^{-2}, compared to seeding the lowest rate of annual grasses with the second highest, 2500 seeds m^{-2}, of perennial grasses ($P = 0.024$). Alternatively, when annual grasses were seeded in autumn at the lowest annual grass seeding rates, 150 annual grass seeds m^{-2}, perennial grass density was two times higher than when annual grasses were seeded at 1500 annual grass seeds m^{-2} ($P = 0.034$).
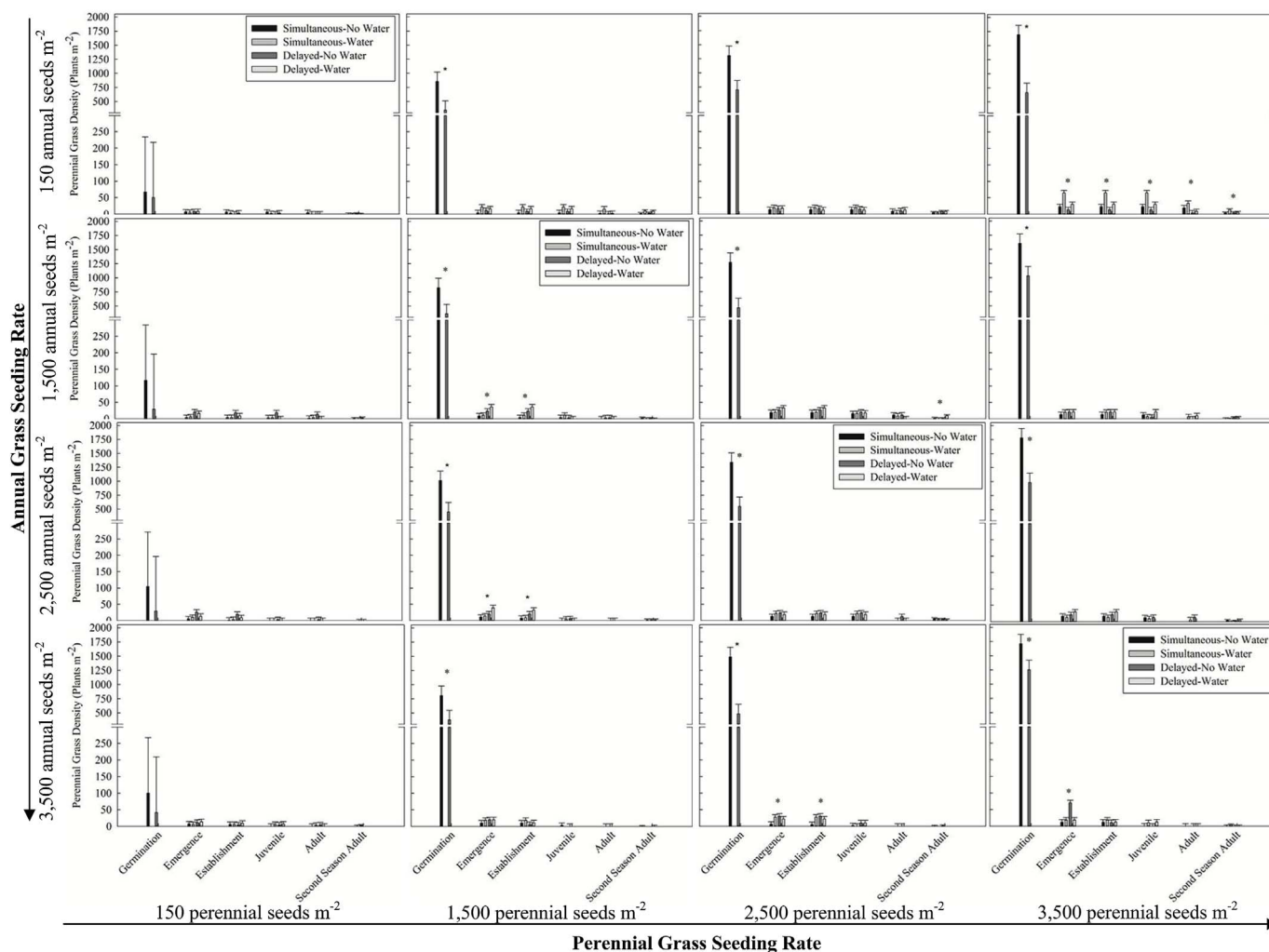
Fig. 2. Least squared means and standard error of perennial plant density (density m^{-2}) by life history stage including the seeding rate, germination, emergence, established, juvenile, adult, and second year-adult. Germination did not include a watering treatment due to the difficultly of administering water in the winter months. Asterisks represent a significant difference within a life history stage ($P \leq 0.05$).

The number of adult perennial grasses from the first growing season did not differ from the number of surviving adults in the second growing season (Fig. 2; $P = 0.925$). However, there were 16 times more surviving adult perennial grasses in the lowest compared to the highest annual grass seeding rates ($P = 0.033$). Furthermore, the highest perennial grass seeding rates produced the highest number of surviving adult perennial grasses, at 6.2 ± 1.4 seedlings m^{-2} ($P = 0.033$). By the second growing season, adult perennial grass density was highest when perennial grass seeding rates were highest ($P = 0.017$). Conversely, when annual grass seeding rates were lowest, perennial grass density in the second growing season was over seven times higher than when annual grass seeding rates were highest ($P = 0.001$). While there was no interaction between annual grass seeding times and perennial grass seeding rates on perennial grass density ($P = 0.695$), perennial grass density in the second growing season was over four times higher when planting of 1500 annual and 2500 perennial grass seeds m^{-2} was delayed until spring compared to simultaneous annual and perennial grass seeding in autumn ($P = 0.035$). In addition, seeding 150 annual and 3500 perennial grass seeds m^{-2} in autumn yielded approximately 1.7 times more second season adult grasses compared to delaying annual grass seeding until spring ($P = 0.015$).

Annual grass density was not affected by any treatments when annual grass seeding rates were lowest (Fig. 3; $P = 1.000$). However, adding water, delaying annual grass seeding until spring, and adding the highest annual grass seeding rates, 3500 annual grass seeds m^{-2} all

produced more annual grass plants than ambient water, simultaneous seeding, and the lowest annual grass seeding rates, 150 annual grass seeds m^{-2} (Table 2; $P < 0.001$). Annual grass density was about 70 plants m^{-2} $\pm$ 13.6 higher when annual grass seeding was delayed until spring and water was added compared to simultaneous annual grass seeding in autumn in ambient water conditions ($P = 0.047$). Delaying annual grass seeding until spring coupled with the highest annual grass seeding rates produced over ten-times as many annual grasses compared to simultaneous annual grass seeding in autumn at the lowest annual grass seeding rates ($P < 0.001$). Furthermore, annual grass density was highest 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 which produced 277.3 ± 38.0 annual grasses m^{-2} ($P = 0.028$).

The density of annual grasses in the second growing season was higher than density of annual grasses in the previous year (Fig. 3; $P = 0.078$). By the second growing season, simultaneous annual and perennial grass seeding in autumn yielded 1.5-times more annual grasses m^{-2} than when annual grass seeding was delayed until spring ($P < 0.001$). Annual grass density in the second growing season was highest at the highest annual grass seeding rates at approximately
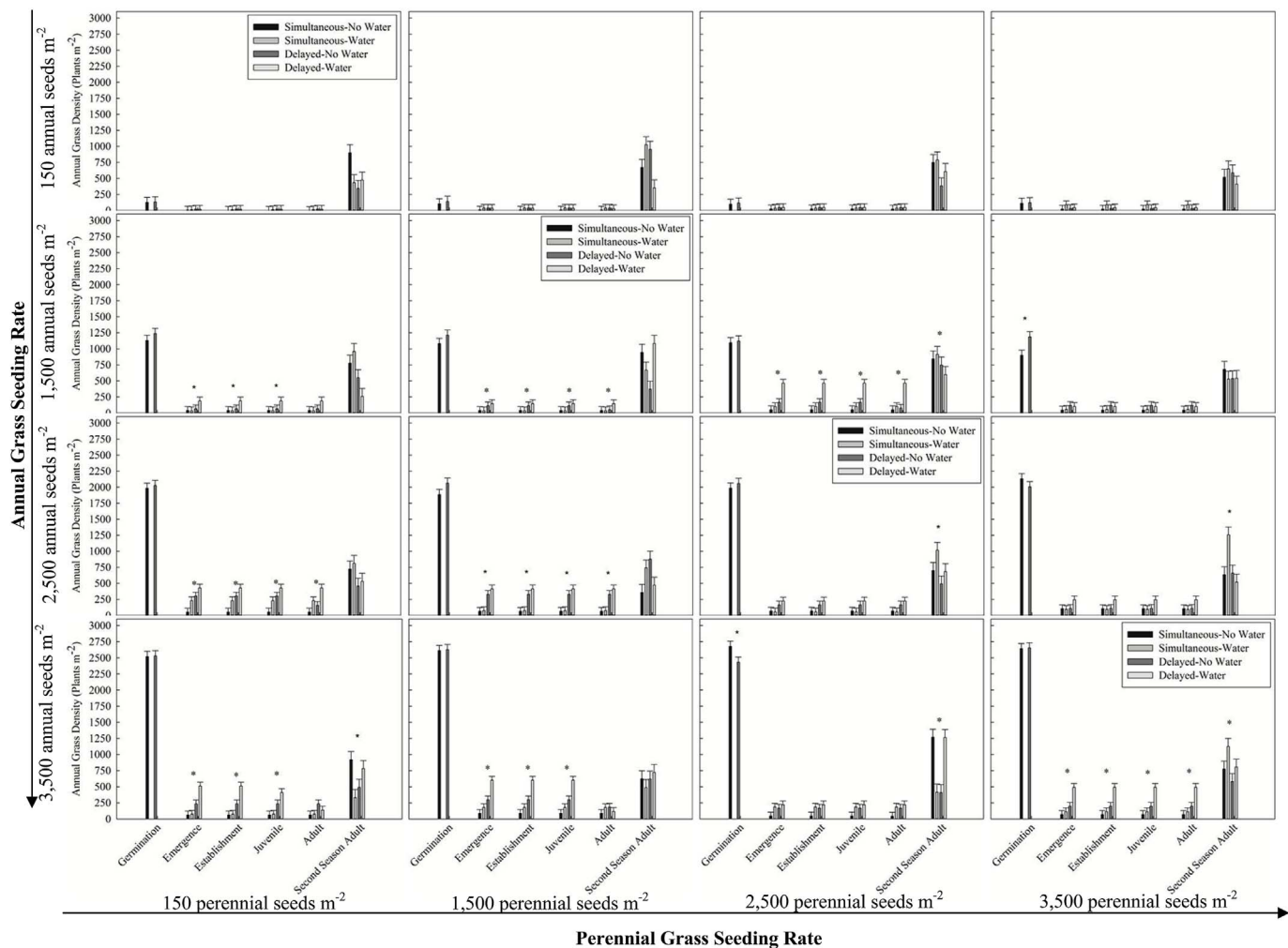
Fig. 3. Least squared means and standard error of annual grass density (density m^{-2}) by life history stage including the seeding rate, germination, emergence, established, juvenile, adult, and second year-adult. Germination did not include a watering treatment due to the difficultly of administering water in the winter months. Asterisks represent a significant difference within a life history stage ($P \leq 0.05$).

762.2 $\pm$ 55.6 ($P < 0.001$). While the interaction between annual and perennial grass seeding rates did not affect annual grass density ($P = 0.401$), when annual and perennial grass seeding rates were high and annual and perennial grasses were simultaneously seeded in autumn there were several cases where annual grass density was higher than these same seeding rates when annual grasses were delayed seeding until spring. For example, seeding 1500 annual and 2500 perennial grasses m^{-2} in autumn produced 1005.3 $\pm$ 155.1 plants m^{-2} compared to only 742.7 $\pm$ 155.1 plants m^{-2} when annual grasses were delayed seeding until spring ($P = 0.019$) and when 3500 annual and 2500 perennial grasses m^{-2} were seeded in autumn, annual grass density was 954.7 $\pm$ 155.1 plants m^{-2} compared to only 356.0 $\pm$ 155.1 plants m^{-2} when annual grasses were seeded in spring ($P = 0.030$).

4. Discussion

Forecasting plant community assembly when seeding times and rates 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. 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 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 (DiVittorio et al., 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 restoration approach (James et al., 2013).

4.1. Seedling germination

Germination has historically been thought to be the limiting growth stage for plant recruitment (Young and Evans, 1977). However, germination rates ranged from 60 to 94% of initial seeding rates, regardless of initial seeding rate or time throughout this study. Similarly, Boyd and James (2013) suggested that seedling growth is not limited during the seedling germination stage, but instead, the transition stage between germination and emergence (James et al., 2011, 2012). Madsen et al. (2012) suggested that agglomerating seeds together increases germination rates because the grouping of germinated seeds increases heat and thereby favorable germination conditions for neighboring seedlings. In contrast, we found that higher perennial seeding rates

Table 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 at $P \leq 0.05$.

Effects and Interactions	*df*	Annual Density		Perennial Density	
		F-Value	*p*-Value	F-Value	*p*-Value
water	8	26.91	**0.0008**	5.56	0.0564
timing	16	87.46	**< 0.0001**	5.69	**0.0345**
water + timing	16	5.78	**0.0287**	3.66	0.0800
annuals (ann)	96	33.79	**< 0.0001**	1.31	0.2789
water + ann	96	2.76	**0.0465**	2.07	0.1119
timing + ann	96	10.91	**< 0.0001**	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	**< 0.0001**
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	**< 0.0001**	0.96	0.4544
timing + per + stage	288	5.78	**0.0287**	1.03	0.4084
water + timing + per + stage	288	33.79	**< 0.0001**	1.02	0.4116
ann + per + stage	288	2.76	**0.0465**	1.52	0.0860
water + ann + per + stage	288	10.91	**< 0.0001**	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 3
Percentage of perennial grasses 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
Percentage of annual grasses 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%

produced lower germination rates, but only when annual and perennial grasses were simultaneously seeded and comparing the lowest (150 seeds m^{-2}) to the three highest (1,500, 2,500, or 3500 seeds m^{-2}) perennial grass seeding rates. However, in arid rangelands, higher seeding rates may be necessary to ensure enough germinate to break through soil crusts since the inability to break through soil crusts has been thought to increase seedling mortality between the germination and emergence life history stages (James et al., 2012).

Annual grasses gain priority in shrub-steppe ecosystems by beginning growth earlier than perennial grasses (Abraham et al., 2009).

Thus, if annual grasses are chemically treated in autumn and perennial grass seeding occurs following herbicide treatment in autumn, perennial grasses may be able to overcome the limitations of preemptive annual grass growth. However, we found that annual grass germination rates were similar when annual grasses were seeded in autumn or spring. Access to resources are scarcely limited during the germination stage (James et al., 2011, 2012), and Leger and Espeland (2010) found that neighboring annual grasses even facilitate perennial grass growth rates in early growth stages. Similarly, in this study, when perennial grasses were simultaneously seeded with annual grasses in autumn, perennial grass germination rates were over two times higher than delaying annual grass seeding until spring. Orrock and Christopher (2010) suggested that when competing seeds are seeded together, the time to initiate germination is shorter. Consequently, earlier annual grasses germination likely accelerate perennial grass germination times in the germination stage when seeded with neighboring annual grasses (Wainwright et al., 2012).

5. Life history

It has been clearly demonstrated that the bottleneck in seedling survival occurs between the germination and emergence stages (James et al., 2011). Similarly, in support of our first hypothesis, our data suggest that where seedling emergence was highest perennial grass density in the following life history stages remained high through to the second growing season. This was especially apparent when annual grass seeding was delayed until spring, where perennial grass emergence density was almost 4-times higher than when annual and perennial grasses were simultaneously seeded in autumn. Low emergence rates may be because the extended time spent underground before emerging can increase seedling mortality on perennial grass seedlings (Boyd and James, 2013). Seedling germinates may also be prone to mortality prior

to emergence because they are unable to break through hard soil crusts. Madsen et al. (2012) identified that agglomerating seeds increased native plant recruitment because the grouped germinates provided the pressure necessary to break through soil crusts. Similarly, we found that perennial grass emergence rates were higher at higher densities and especially when they were seeded with low densities annual grasses in autumn. However, when annual grass propagule pressure reached 1500 seeds m^{-2} or more, perennial grass density remained low, regardless of seeding time or water availability (Fig. 3). Higher perennial grass densities when seeded with low numbers of annual grasses suggest that low numbers of neighboring annual grasses likely facilitate perennial grass production by serving as nurse plants (Lortie and Turkington, 2008). However, there appears to be a limit between 150 and 1500 annual grass seeds m^{-2} added where annual grass propagule pressure will limit perennial grass recruitment regardless of seeding time or water availability.

Theoretically, higher propagule pressure should yield higher plant densities (Lortie and Turkington, 2002), but this is dependent on competitor seed densities and safe site availability (Aicher et al., 2011). Contrary to our second hypothesis, perennial grass survival at the end of the second growing season was not necessarily highest at their highest propagule pressures (3500 seeds m^{-2}), the lowest annual grass propagule pressures (150 seeds m^{-2}), when water was added, and when they were seeded independently. For example, life history stage was not as important as competitor densities since perennial grasses only had higher density in the second growing season when annual grasses were delayed seeding until spring. Furthermore, perennial grass density was low in this study when annual grass seeding rates were higher than 150 seeds m^{-2}. These results suggest that perennial grasses are unlikely to develop in areas that have high annual grass propagule pressure (Larios et al., 2013). Similarly, in a previous study, we found that if the annual grass seeding rate exceeded 150 seeds m^{-2}, the likelihood of perennial grass survival was low because of annual grass preemption of resources (Schantz et al., 2015). Annual grass preemption of safe sites and soil resources from perennial grasses can be high in annual grass dominated systems (Abraham et al., 2009). However, annual grass density may also be self-limiting since increasing annual grass seeding rates past 1500 seeds m^{-2} did not affect annual grass density. It appears that annual grass propagule pressure limits both annual and perennial grass growth, even in the first growing season; first by occupying safe sites in early life history stages, then by acquiring a majority of soil resources in later life history stages (Goldberg et al., 2001).

Earlier seeded species can have higher individual plant production because they have greater access to soil resources (Lortie and Turkington, 2002). In this study, providing perennial grasses a priority effect by seeding perennial grasses prior to annual grasses yielded higher perennial grass density through their life history. Earlier perennial grass emergence may have allowed these species to access necessary soil resources prior to annual grass growth (Verdu and Traveset, 2005). Alternatively, annual grasses had higher densities when seeded simultaneously with perennial grasses in both the first and second growing season. Annual grasses have been known to benefit from the stability of perennial grasses which are better equipped to survive in harsh environmental conditions (Arredondo et al., 1998). Furthermore, adding water magnified these effects for both annual and perennial grasses.

Areas with high water availability generally have higher total plant density, soil nutrient availability, safe site abundance, and lower competition for resources (Burke et al., 1998). However, we found that adding water only increased annual and perennial grass density when annual and perennial grass seeding rates were lower than 2500 seeds m^{-2} suggest that safe site availability becomes limited when seeding rates exceed 2500 seeds m^{-2} for both annual and perennial grasses (Clark et al., 2007). Thus, regardless of water availability, safe sites for plant growth will still be limiting for both annual and perennial grasses

if annual grass seed banks exceed 2500 seeds m^{-2}.

Two-times higher annual grass density in the second-growing season compared to the adult life history stage in the first growing season suggests that annual grass interference with its neighbors likely increases by the second growing season (Hirsch-Schantz et al., 2014). 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 when initial seeding rates were higher than 1500 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). However, because established perennial grasses can limit annual grass expression, getting perennial grasses to establish in the first year can exclude annual grass spread in later growing seasons (Orloff et al., 2013).

5.1. Conclusions and management implications

A systems based management approach can be advantageous for forecasting the effect of ecological processes on plant growth. In this study, we found regardless of seeding strategy, 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. However, we also found that native perennial grass growth through their life history stages was strongly dependent on seeding time and rate interaction with existing propagule pressure and water availability. For example, providing native perennial grasses a priority seeding effect by delaying annual grass seeding until spring produced lower perennial grass germination rates compared to simultaneous annual and perennial grass seeding, suggesting that perennial grasses are facilitated by neighboring annual grasses at early life history stages. However, following seedling emergence, delaying annual grass seeding until spring resulted in higher perennial grass densities through the first growing season, but only when annual grass propagule pressure was 1500 seeds m^{-2} or higher. Furthermore, while seeding higher rates of native perennial grasses generally increased recruitment, we found that seeding more than 2500 seeds m^{-2} did not significantly increase native perennial grass density, especially if annual grass density is higher than 150 seeds m^{-2}. Alternatively, while high water availability benefited the growth of all species, it did not strongly interact with propagule pressure or priority effects to benefit species through their life history. While these findings suggest that modifying seeding strategies, such as increasing seeding rates and providing perennial grasses a priority seeding effect, can increase perennial grass recruitment; it is prudent to quantify the existing annual grass propagule pressure as well as forecast seeding for a wet year prior to seeding to ensure native perennial grass recruitment.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.

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