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

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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

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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 1992). 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 versus 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.

Materials and methods

Study site

This experiment was conducted on a low elevation (1,033 m), heavily infested sagebrush-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 457 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.).

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.

Study design

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 196 1m^{-2} plots (Table 1, Fig. 1).

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.

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.

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
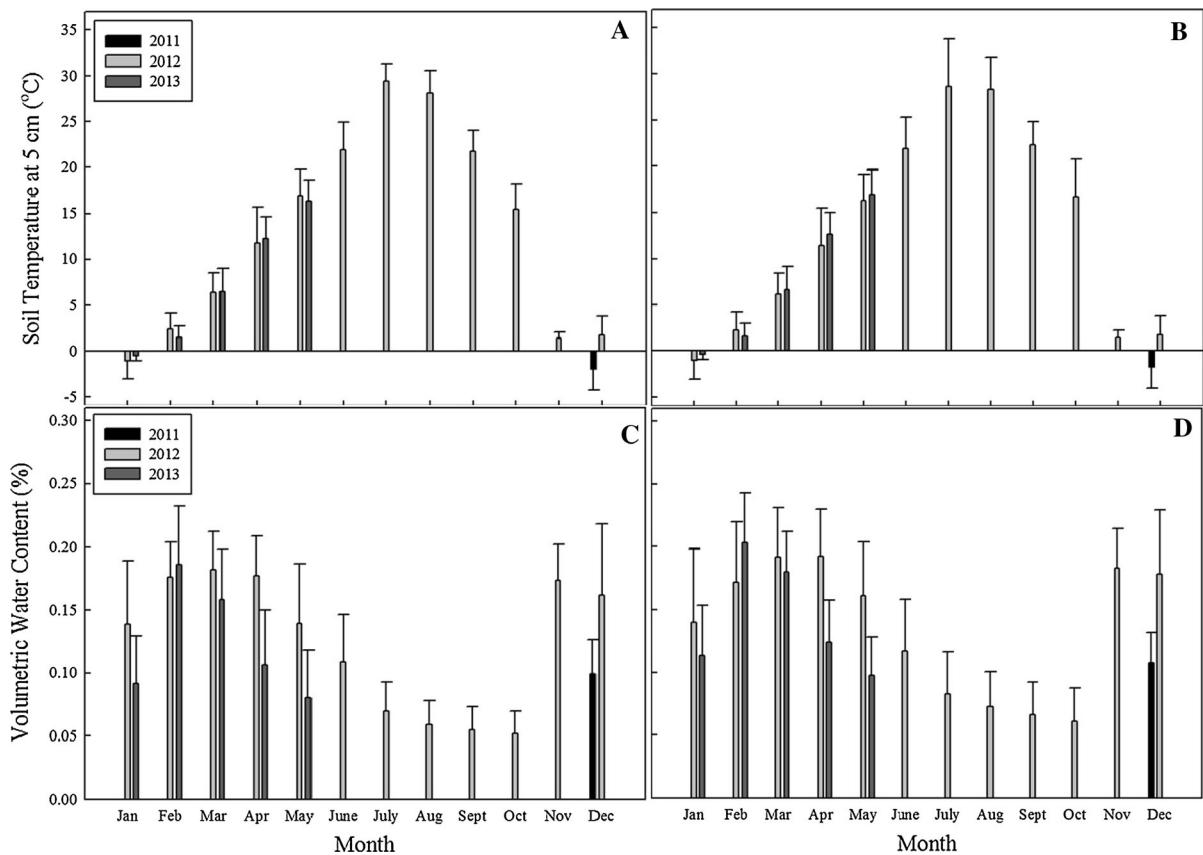
Fig. 1 Means and SD of soil temperature at 5 cm (°C) and volumetric water content at 5 cm (%) during the study period (December 2012–May 2013). **a** represents soil temperature in the no water treatments, **b** represents soil temperature in the water added treatments, **c** represents volumetric water content in the no water treatments, and **d** volumetric water content in the water added treatments

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 $P \leq 0.05$.

Results

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 (Appendix
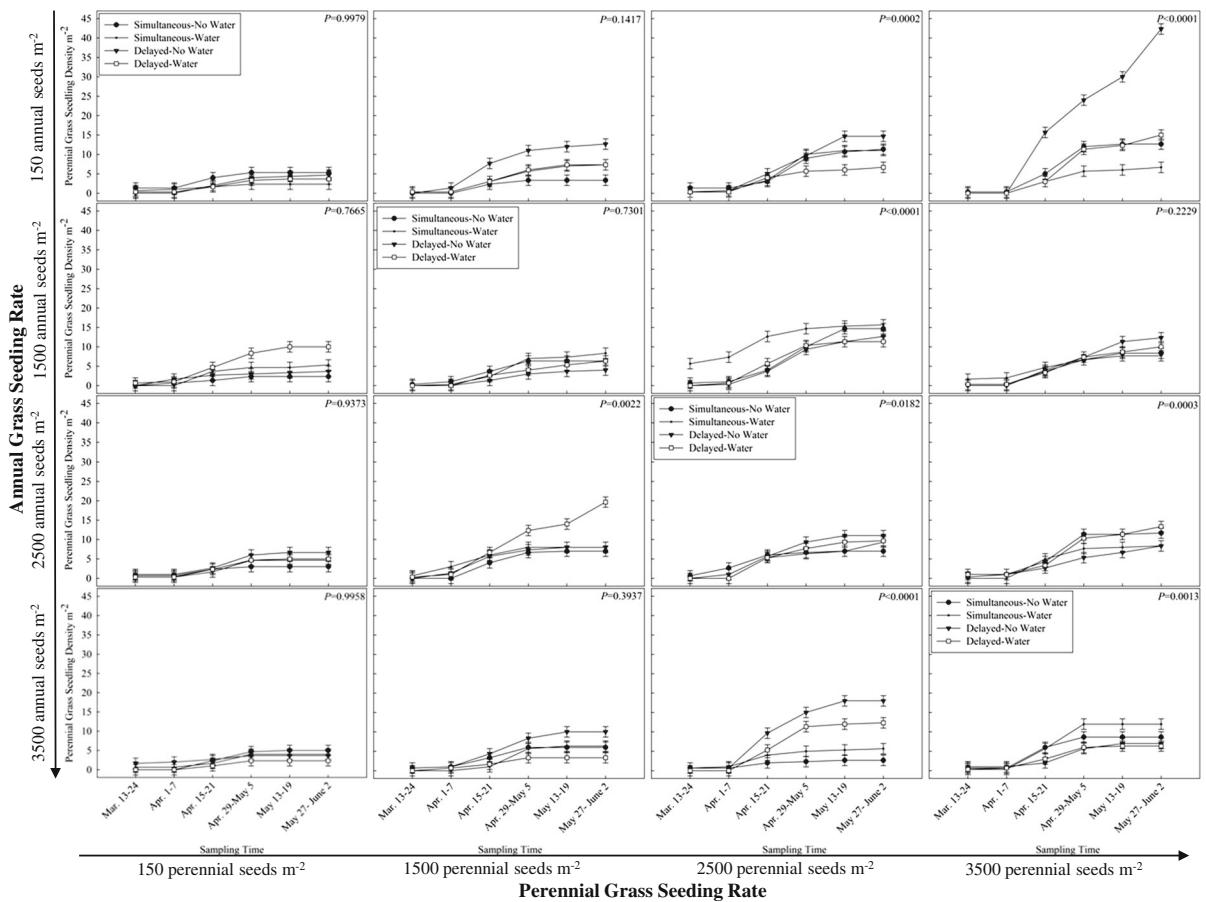
Fig. 2 Least squared means and SE of perennial grass seedling density (density m^{-2}) at 6 sampling times in 2012 by seeding time and watering interaction for each annual and perennial grass propagule pressure ($P < 0.05$). The *panel of figures* represents the difference in propagule pressure where 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 SE

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. 1). Average daily volumetric water content fluctuated from a high of 17 % from November–April to a low of 7 % from May–October (Fig. 1a, 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. 1b, c).

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. 2). 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. 3). At the three higher seeding rates, delaying annual grass
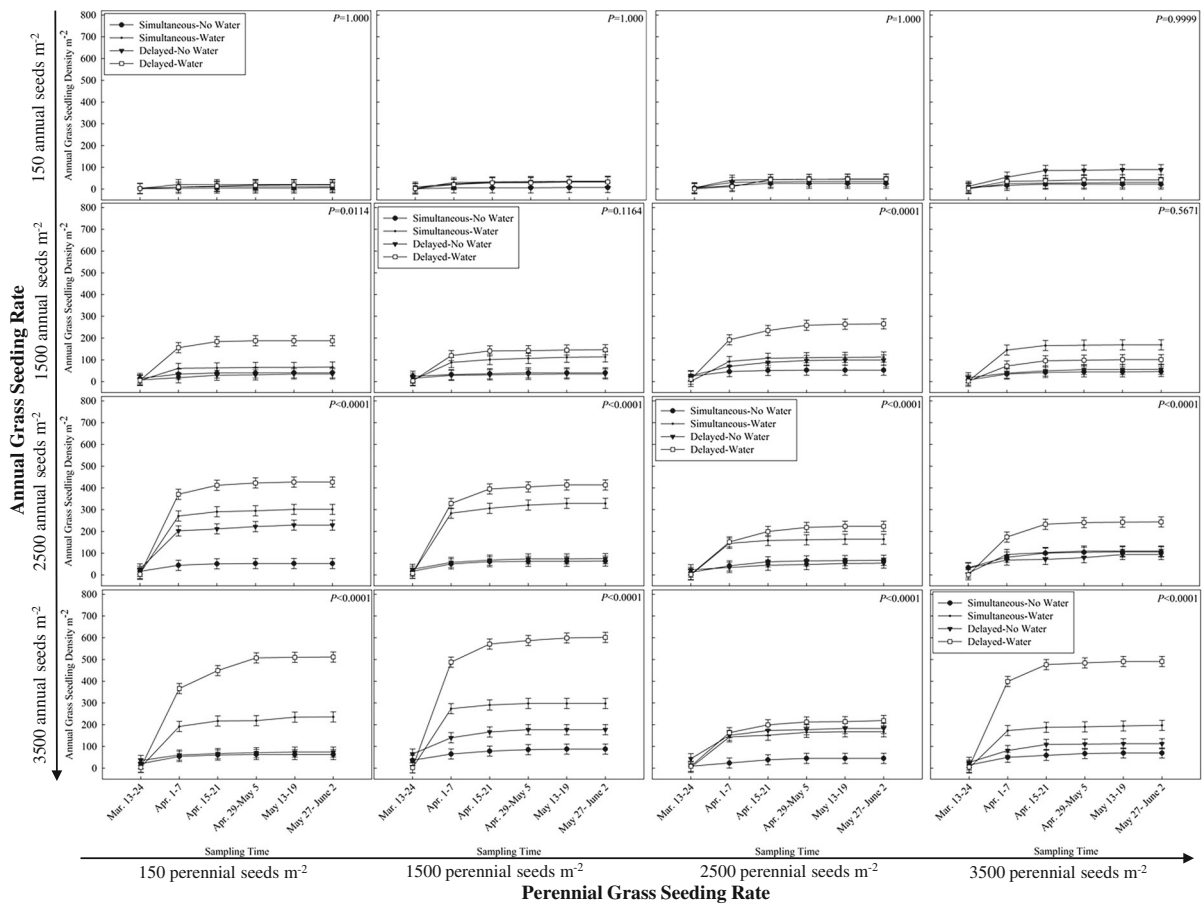
Fig. 3 Least squared means and SE of annual grass seedling density (density m^{-2}) at 6 sampling times in 2012 by seeding time and watering interaction for each annual and perennial grass propagule pressure ($P < 0.05$). The panel of figures represents the difference in propagule pressure where perennial 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 SE

Table 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

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 (Table 1).

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

Table 2 ANOVA table of main effects and interactions of treatment effects in 2013 ($P < 0.05$; n = 192)

Effects and interactions	df	p value			
		Perennial grass		Annual grass	
		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	0.342
Timing + perennial	6	0.679	0.4166	0.1182	0.7548
Water + perennial	3	0.8074	0.6745	0.2857	0.067
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

Table includes density degrees of freedom (*df*), final annual grass density and biomass, and final perennial grass density and biomass. Bold numbers are significant
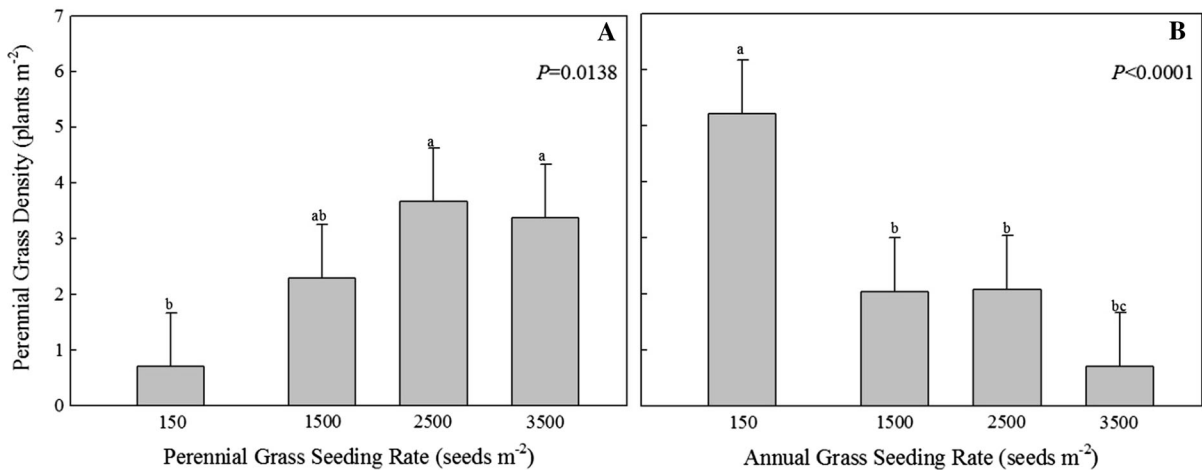

Fig. 4 Least squared means and SE of perennial plant density (density m^{-2}) in 2013. **a** perennial grass seeding rate ($P = 0.0138$). **b** annual grass seeding rate ($P < 0.0001$). *Letters* indicate significant differences

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. 4a; $P = 0.014$). 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. 4b; $P < 0.0001$).

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
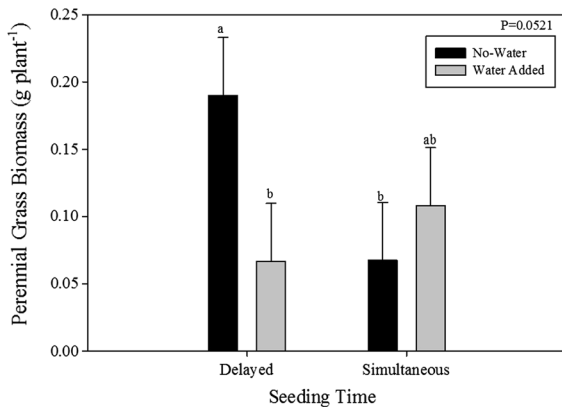
Fig. 5 Least squared means and SE of individual perennial plant biomass (g plant^{-1}) in 2013 by watering and seeding time ($P = 0.0521$). *Letters* indicate significant differences

spring and water was added (Fig. 5; $P = 0.052$). 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. 6a; $P < 0.0001$). The combination of adding water and increasing perennial grass seeding rate also

produced higher annual grass density (Fig. 6b; $P = 0.065$). 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. 7; $P = 0.067$). Alternatively, annual grasses had the highest biomass when water was not added, especially at the highest perennial and lowest annual grass seeding rates (Fig. 8; $P = 0.048$). 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. 8a). 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. 8b). Annual grass biomass was
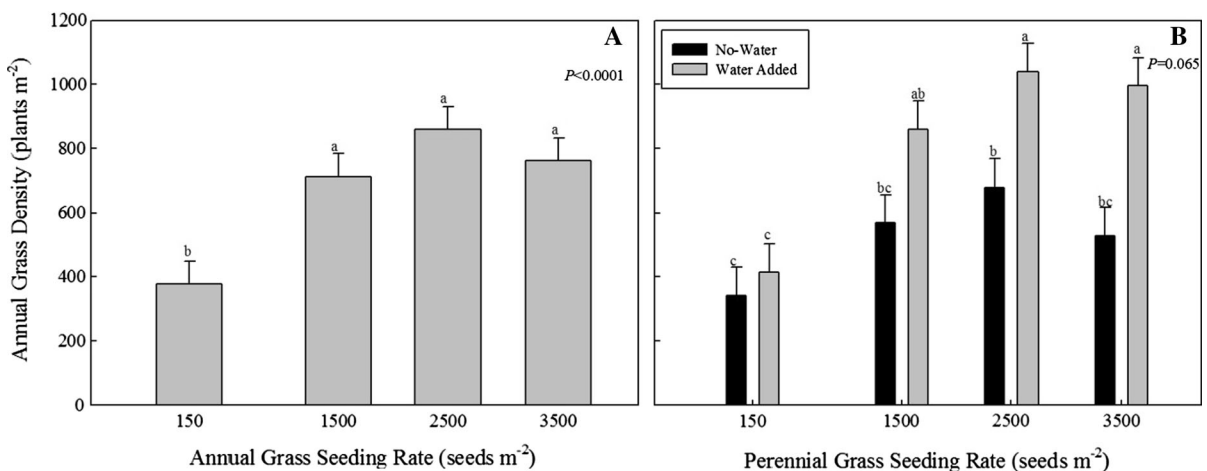

Fig. 6 Least squared means and SE of annual plant density (density m^{-2}) in 2013. **a** annual grass seeding rate ($P < 0.0001$). **b** seeding time and perennial seeding rate interaction ($P = 0.065$). *Letters* indicate significant differences
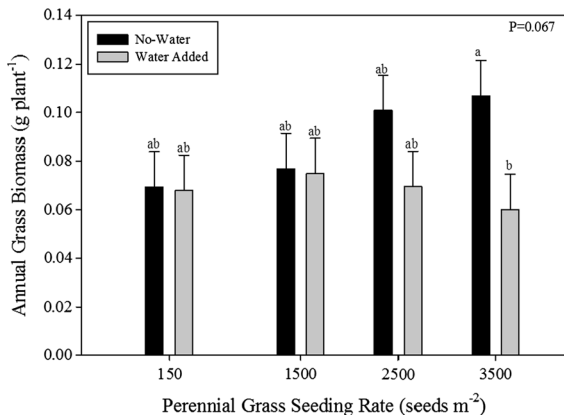
Fig. 7 Least squared means and SE of individual annual plant biomass (g plant^{-1}) 2013 based upon the timing and perennial seeding rate treatment interactions ($P = 0.067$). *Letters* indicate significant differences

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.

Discussion

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 these 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
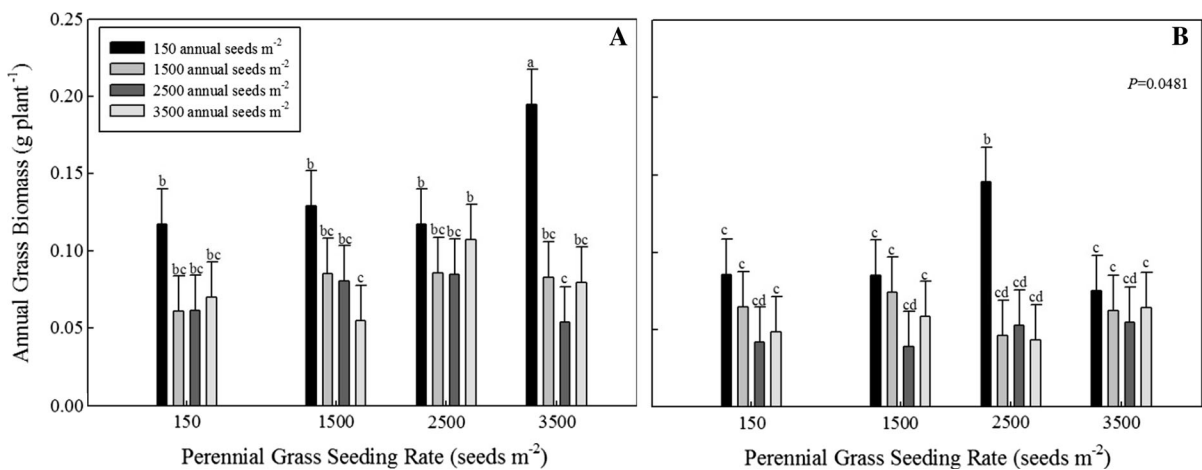

Fig. 8 Least squared means and SE of individual annual plant biomass (g plant^{-1}) in 2013 by water availability, annual grass propagule pressure, and perennial grass propagule pressure

interaction ($P = 0.0481$). **a** The no-watering treatment. **b** The watering treatment. *Letters* indicate significant differences

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.

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). Coincidentally, 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 abide by 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.

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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