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Propagule pressure and priority seeding effects on the demography of invasive annual and native perennial grass species

Merilynn C. Schantz [a], Roger L. Sheley[b] and Jeremy J. James[c]

aDepartment of Animal and Rangeland Sciences, Oregon State University, Corvallis, OR, USA; bUSDA-Agricultural Research Service, Burns, OR, USA; cSierra Foothills Research and Extension Center, University of California Division of Agriculture and Natural Resources, Browns Valley, CA, USA

ABSTRACT

Background: Annual grass invasion and dominance creates a self-sustaining cycle that promotes wildfires and reduces forage abundance. Restoring native plant species to annual grass-invaded ecosystems is fundamental to fostering self-sustaining native plant communities.

Aims: We sought to clarify varying restoration strategies on invasive annual and native perennial grass assembly, including strategically modified seeding times, seeding rates, and added water.

Methods: We tested the effects of seeding perennial grasses in autumn, spring, or seeding half in autumn and the remaining half in spring, adding water, and varying annual and perennial grass seeding rates on annual and perennial grass life history.

Results: While varying perennial grass seeding times did not affect perennial grass germination rates, annual grass germination rates were highest when perennial grasses were seeded in autumn. Seeding perennial grasses in spring produced the highest adult perennial grass density in the first-growing season, but adult perennial grass density in the second-growing season was greatest when seeding occurred in autumn. Second-growing season perennial grass density was highest where annual grass seeding rates were lowest and perennial grass seeding rates were highest. Adding water in the first-growing season produced almost two-times more second-year adult perennial grasses compared to where water was not added.

Conclusions: High water availability during the seeding year appears to be the most important factor for retaining perennial grasses in annual grass-invaded ecosystems.

Introduction

Directing plant community assembly of rangelands invaded by annual grasses toward native perennial grass dominance requires an understanding of the ongoing abiotic and biotic properties occurring in the invaded site along with the knowledge of management inputs necessary to overcome the feedbacks sustaining invasive species (Seabloom 2011). Annual grass invasiveness is likely related to physiological advantages such as higher growth rates, faster germination times, and greater allocation to root growth than many native perennial grasses (Piemeisel 1951; Arredondo et al. 1998). Resource pre-emption allows these invaders to capture most of the available space, water, and soil nutrients prior to the onset of native perennial plant growth (Grime 1977; Wedin and Tilman 1993). Furthermore, annual grasses have greater propagule pressure than native perennial grasses and produce, on average, 100-times more seeds per plant annually than perennial grasses and have germination rates averaging 97% (Smith

et al. 2008). Once dominant, sites invaded by annual grasses are resistant to native plant restoration (Corbin and D'Antonio 2004).

Increasing native perennial grass cover to stabilise soils and soil resource availability is fundamental to restoring rangelands invaded by annual grasses (Seabloom et al. 2003). However, seeding success varies depending upon multiple controlling processes, including access to desirable seed (DiVittorio et al. 2007), existing propagule pressure (Fridley et al. 2007), seedling development rates (Moles and Leishman 2008), soil resource availability (James et al. 2006), and their interactions. In a previous study, we found that regardless of the management strategy, perennial grass recruitment was low if annual grass propagule pressure exceeded 1,500 seeds m^{-2} (Schantz et al. 2016). Furthermore, plant communities dominated by annual grasses are resistant to management inputs (Humphrey and Schupp 2004). Overcoming the limitations to restoration requires an understanding of: (1) seeded species development and ecological processes directing vegetation

CONTACT Merilynn C. Schantz ✉ redrresources@gmail.com

dynamics and (2) knowledge of how perennial grasses may promote the establishment and persistence of invasive species (Evans 2012).

Models of plant population growth are a quantitative tool used to forecast plant community assembly by accounting for the growth of species from seed to reproductive adult (Evans et al. 2012). These models are valuable for disciplines like restoration ecology because they can quantify plant growth under a variety of starting conditions (James et al. 2013). However, species have differing life history strategies, including dispersal time, seed dormancy, germination speeds, growth rates, leaf characteristics, and time to reproduction (Adler et al. 2014). Furthermore, the ecological processes that affect life history stages and the transition among stages vary through time (Benton et al. 2006). Germinated seedlings are vulnerable to soil pathogens and herbivores (Moles and Westoby 2006), as well as freeze-thaw cycles that increase winter mortality of seedlings (James et al. 2012). Moreover, for seedlings to emerge, they must break through soil crusts (James et al. 2011). Because of the processes that seedlings must endure to become reproductive adults, James et al. (2013) proposed using a 'systems framework' to restore invaded ecosystems.

Systems-based management frameworks build from many other plant population models by accounting for the ecological processes driving plant growth through time and can provide a quantitative assessment of plant community assembly (Grime 1977; Lavorel and Lebreton 1992; Davis et al. 2000; Evans et al. 2012). Unlike conceptual and phenomenological models, systems models account for the underlying mechanisms and processes driving model behaviour, such as climate, life history stage, or invasive species presence (Bansal and Sheley 2016). 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, such as the interaction of annual grass priority effects and propagule pressure on seeded native perennial grass recruitment (James et al. 2013). This is key for restoration because when we know the processes limiting seedling development, we can target management inputs to address the given processes and thereby increase recruitment. However, the applicability of using a systems-management approach is largely unknown, especially when pre-seeding restoration inputs vary.

Abundant existing annual grass propagule pressure can limit safe site availability for seedling recruitment (DiVittorio et al. 2007). Safe sites, such as resource patches, support diverse plant populations and provide conditions suitable for seedling germination and establishment (Grubb 1977). Safe sites are generally less available in ecosystems invaded by annual grasses because annual grasses germinate earlier than native perennial grasses (Deering and Young 2006; Abraham et al. 2009), perennial grass growth from seed is slow compared to annual grasses (Montoya et al. 2012), and annual grasses can produce up to 28 times more seeds per individual plant following the first-growing season compared to perennial species (Kulpa et al. 2012). In addition, regions invaded by annual grasses are resource limited and when water availability is low, native grass seedling recruitment is low (James and Svejcar 2010). Because of the limitations to perennial grass seedling recruitment through time, modifying the temporal arrival of perennial grass seed relative to annuals could provide perennial grasses a priority effect for accessing safe sites prior to annual grass development (Stella et al. 2006; Young et al. 2017). However, the relative effects of seeding time, varying seeding rates, seeding year water addition and their interactions on plant community assembly following restoration have yet to be quantified.

Using a systems approach may allow managers to quantify the limitations to seeded plant community development. Our objective was to test the usefulness of a systems-management approach by quantifying the role of seeding time, seeding rate, and water availability on the demography of annual and perennial grasses. Based on the fact plant community assembly is directly affected by management inputs and various ecological processes at each growth stage (Goldberg et al. 2001); our hypotheses were that (1) perennial grasses would be least affected by limiting ecological processes of safe site and water acquisition throughout their life history when perennial grass seeding frequency and seeding rates were highest and (2) water additions would decrease the effect of limiting ecological processes, and ultimately favour both functional groups establishment. Systems-based management approaches should increase our ability to manage invasion, especially during restoration by identifying where, in species life history, seedlings are most limited and to identify potential ecological processes that might be responsible for the barrier to establishing desirable seeded plant communities.

Materials and methods

This study was conducted in south-eastern Oregon, ca. 5 km south of Juntura, at a latitude and longitude of 43.715,689, −118.115,122, in a low-elevation (1,033 m) sagebrush-steppe ecosystem in 2013. This study was conducted on the same study site as Schantz et al. (2016) and adjacent to that reported in Schantz et al. (2015) where we described the effects of annual and perennial grass seeding rate, seeding time, and water availability on plant establishment and growth. Unlike these previous studies, this study evaluates the effects of modified propagule pressure, perennial grass seeding times, and water availability on annual and perennial grass demography from germination to second-growing season adult life history stages. Detailed materials and methods, including vegetation and soil properties, climate data, the model system, propagule pressure, and dispersal timing and frequency, are fully described in supplementary information (Appendix S1).

Model system

To test seeding strategy effect on species density through their life history, we used a model system consisting of locally collected invasive annual grasses, cheatgrass (*Bromus tectorm* (L.) and medusa head (*Taeniatherum caput-medusae* (L.) Nevski) (50–50 mixture, by seed number) as the invaders. The desired native system was represented by an equal mix of purchased perennial grasses blue bunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve), bottlebrush squirrel tail (*Elymus elymoides* (Raf.) Swezey), Sandberg bluegrass (Poa secunda J. Presl), and Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth). All perennial grasses were purchased from Granite Seed Company ® in Lehi, UT, USA in autumn 2011. Seeding rate was applied on a per weight basis so that each plot received 100% pure-live seeds per plot.

Propagule pressure and dispersal timing and frequency

Densities and proportions of annual grasses and perennial grasses were manipulated to provide four addition-series matrices to identify the effects of propagule pressure on seedling life history. Seeding rates of annual and perennial grasses were 150, 1,500, 2,500 or 3,500 seeds m^{-2}. These seeding rates were chosen to represent 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 (Humphrey and Schupp 2001; Barr et al. 2017). There were two seeding treatments: (1) annual grasses were seeded in autumn (November 2011), and perennial grass seeding was delayed until spring (February 2012), or (2) all annual grasses and half of the allotted perennial grasses were seeded in autumn and the remaining half of perennial grasses seeded in spring. Seeds were all hand broadcast onto the soil surface of 1 m^2 plots and covered with 2-cm of sifted topsoil collected from the site. We added water weekly at twice the historical average precipitation, which averaged 2.5 L added m^{-2} month^{-1}. Watering was administered weekly during the growing season in Year 1 (March–May) using watering cans to evenly distribute water on each water added treatment plot. Approximately 0.55 L of water were added to each plot weekly. This study design fully crossed these factors in a 3 × 2 x 4 × 4 design, with three replicates of each in a completely randomised design yielding 288 1-m^2 plots (Table 1).

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 adjacent to seeded plots. 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 either autumn-seeded matrices, where all annual and perennial grasses were seeded in November 2012, or spring-seeded matrices where all annual grasses were seeded in one germination bag that was planted in November 2012, while perennial grasses were

Table 1. Seeding factors and their combinations evaluated during this study (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	1,500	1,500
November + February		2,500	2,500
		3,500	3,500

delayed seeding into a separate germination bag that was planted adjacent to each monitoring plot in February 2013. All germination bags were harvested on 15 March 2013 because previous studies in nearby regions found that the majority of germination had occurred by this time (James et al. 2011). Germination bag sampling involved washing the contents of the bag through a 710 μm screen, collecting seeds, and scoring seeds as germinated or not. Germination bags did not include a November and February seeding treatment because seeding into a planted germination bag would have caused destruction and bias and the factorial combinations of annual to perennial grasses were already represented in the treated matrices. In addition, a watering treatment was also not included for germination because of the difficulty of administering watering in the winter months.

Life history analysis

Plant density was counted within the centre 0.5 m x 0.5 m of the plot for perennial species and the centre 0.25 m x 0.25 m for annual species biweekly during the first-growing season, from March 13, to 2 June 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 coloured 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 bi-weekly for average leaf number to indicate the average growth stage of seedlings through time. Growth stage was estimated by counting the number of leaves on five randomly chosen plants by the week they emerged and averaging these leaf numbers. We categorised 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).

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, USA). Germinated annual and perennial grasses were normally distributed, but annual and perennial grass density from germination to the second life history growth stages were not normally distributed. Several transformations were attempted but did not improve model fit for annual or perennial grass density. However, when the germination and second-season adult life history stages were eliminated from the repeated measures, normality across growth stages for annual and perennial grass density was achieved.

Density of annual and perennial grass life history stages were evaluated using SAS (SAS Institute Inc., Cary, NC, USA). Germination and second-season adult life history stages were found by testing for the main effects and interactions among seeding time, annual grass seeding rate, and perennial grass seeding rate with replication used as the random effect on the number of germinates and the density of adults in the second-growing season using a mixed-model ANOVA. A repeated-measures analysis of variance (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. Those data from emergence to adult life history stages were analysed using an RM-ANOVA because of their biological importance across these life history stages, while germination and second-season adult life history stages were analysed as a mixed-model ANOVA. In all models, means were separated using the slice procedure (Schabenberger, 2013), and F-test results with an α with an associated P-value of ≤ 0.05 considered significant.

Results

Environmental conditions

Temperature was consistent with long-term averages, while precipitation was generally 10% lower than the 30-year mean in the summer months and average throughout the rest of the year (Figure S1). Temperature and precipitation are further described in Schantz et al. (2016) and Supplementary Material (S1).

Germination to emergence

Perennial grass germination rates ranged from 49 to 56% of initial seeding rates, yet were not affected

the individual effects or interactions among seeding time or annual grass seeding rate (Figure 1(a, b)). However, perennial grasses did have somewhat lower germination rates at higher perennial grass seeding rates: seeding 150 seeds m^{-2}, produced 56.0 ± 3.1% germination, while the highest seeding rates of 3,500 perennial grasses yielded only 49.3 ± 0.01% perennial grasses germination ($F_{3, 49} = 295.2$; $P < 0.0001$).

Annual grasses were significantly affected by varying seeding rates and modified perennial grass seeding times (Figure 1(c,d); $P < 0.0001$). Annual grass germination rates were highest when annual and perennial grass seeding rates were lowest ($F_{3, 20} = 408.2$; $P < 0.0001$). Alternatively, when perennial grasses were seeded in autumn, annual grass germination rates were lower than when perennial grasses were seeded in spring ($F_{1, 20} = 52.1$; $P < 0.0001$). Adding 3,500 seeds m^{-2} annual grass seeding rates and seeding perennial grasses in the spring yielded higher annual grass germination density than these same seeding rates when perennial grasses were seeded in autumn ($F_{3, 20} = 6.8$; $P = 0.0024$). Annual grass density was highest when perennial grass seeding rates were also highest ($F_{3, 48} = 4.93$; $P = 0.005$). In addition, at high annual and perennial grass seeding rates and spring perennial grass seeding times, annual grass germination density was greater than when perennial grasses were seeded in autumn ($F_{9, 48} = 2.36$; $P = 0.027$).

Life history

Perennial grass density was most limited between the germination to emergence life history stage (Figure 2(a–d), Figure S3; $F_{25, 96} = 33.95$; $P < 0.0001$). Adding water and seeding perennial grasses in the spring produced a greater difference between emergence and adult life history stages compared to when perennial grasses were seeded in autumn and spring or when perennial grasses were simultaneously seeded with annual grasses in autumn ($P = 0.0005$). In general, the transition from the emergence growth stage to later growth stages did not occur until mid-April (Table S1). Furthermore, perennial grasses did not begin developing into juveniles until late-April. By the end of the first-growing season 34% of all perennial grass seedlings had reached the juvenile growth
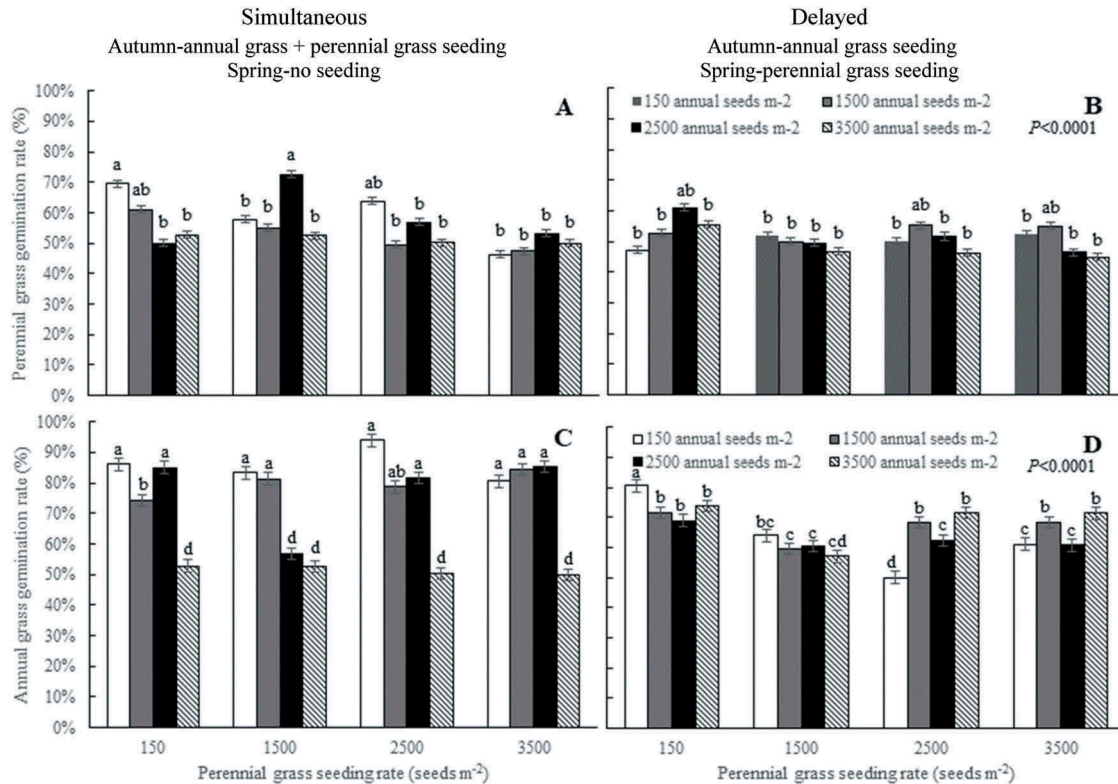

Figure 1. Means and standard error of perennial grass ($P < 0.0001$) and annual grass ($P < 0.0001$) germination rates. Perennial grass germination rates: (A) when annual and perennial grasses were simultaneously seeded and (B) when annual grasses were seeded in autumn and perennial grass seeding was delayed until spring. Annual grass germination rates: (C) annual grass germination rates when annual and perennial grasses were simultaneously seeded and (D) when annual grass seeding was seeded in autumn and perennial grass seeding delayed until spring. Letters indicate differences among seeding rates within a functional group (P?0.05).
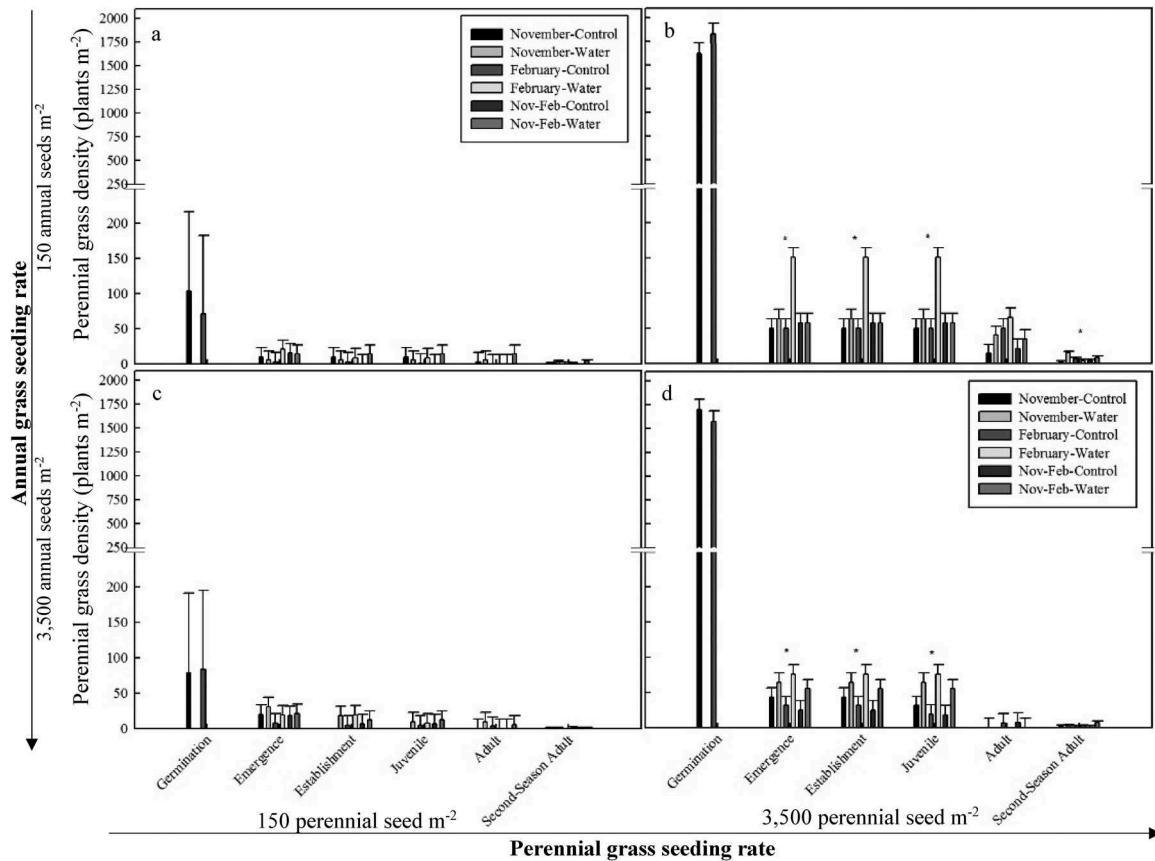
Figure 2. Least-squared means and standard error of perennial plant density (density m^{-2}) by life history stage including the seeding rate, germination, emergence, established, juvenile, adult, and second-year adult. Germination did not include a watering treatment due to the difficultly of administering water in the winter months. (a) represents where 150 annual and 150 perennial grass seeds m^{-2} were seeded, (b) refers to plots seeded with 150 annual and 3,500 perennial grass seeds m^{-2}, (c) refers to sites seeded with 3,500 annual grasses and 150 perennial grass seeds m^{-2}, and (d) represents areas seeded with 3,500 annual and 3,500 perennial grass seeds m^{-2}. Within each figure, perennial grass density (plants m^{-2}) increases along the y-axis and life history stage (germination to second-year adult increases along the x-axis. Asterisks represent a significant difference within a life history stage (P < 0.05).

stage and 15% were considered adults. The number of surviving perennial grass adults in the second-growing season was less than the surviving adults from the first-growing season and only averaged 2.45 ± 0.3 perennial grasses m^{-2} (Figure 2; $F_{12,\ 288}$ = 2.70; P = 0.024). Perennial grasses that survived until the second-growing season had two times greater densities when water was added during the first-growing season ($F_{1,\ 6}$ = 29.99; P = 0.002). Moreover, seeding perennial grasses in autumn and spring produced the highest perennial grass density in the second-growing season ($F_{2,6}$ = 7.24; P = 0.025). Perennial grass density was also greatest when annual grass seeding rates were lowest ($F_{3,36}$ = 13.88; P < 0.0001) and when perennial grass seeding rates were highest ($F_{3,144}$ = 17.55; P < 0.0001). Furthermore, the combination of adding water and low annual grass seeding rates yielded higher perennial grass density compared to when annual grass seeding rates were high and water was ambient ($F_{3,36}$ = 3.06; P = 0.040).

Annual grasses had the greatest reduction in density between the germination and emergence growth stages (Figure 3(a–d); Figure S4; $F_{23,\ 96}$ = 66.15; P < 0.0001). Seeding treatments did not influence annual grass density across growth stages. Collectively, annual grasses transitioned quickly across growth stages (Table S2). By mid-April, over 50% of emerged annual grasses transitioned to established species, while 17% had proceeded to the juvenile stage. In late-April, early-May, individual annual grass species were evenly distributed among the establishment, juvenile, and adult stages. By the end of the first-growing season about 50% of annual grasses were considered adults. The density of annual grasses in the second-growing season was over four-times higher than the adult life history stage from the previous year ($F_{28,\ 288}$ = 3.03; P < 0.0001). Annual grass density in the second-growing season was not influenced by any independent effects or interactions among perennial grass seeding time, perennial grass
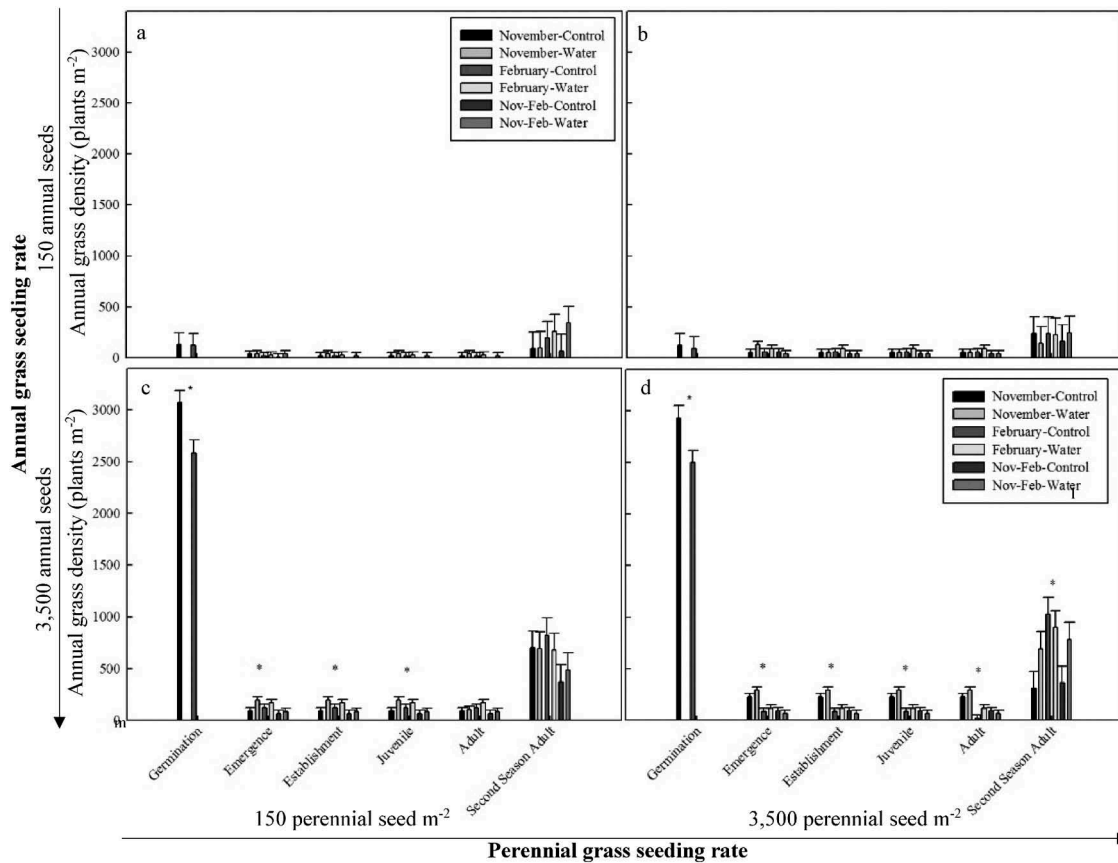
Figure 3. Least-squared means and standard error of annual plant density (density $m-2$) by life history stage including the seeding rate, germination, emergence, established, juvenile, adult, and second-year adult. Germination did not include a watering treatment due to the difficultly of administering water in the winter months. (a) represents where 150 annual and 150 perennial grass seeds $m-2$ were seeded, (b) refers to plots seeded with 150 annual and 3,500 perennial grass seeds m -2, (c) refers to sites seeded with 3,500 annual grasses and 150 perennial grass seeds $m-2$, and (d) represents areas seeded with 3,500 annual and 3,500 perennial grass seeds $m-2$. Within each figure, perennial grass density (plants $m-2$) increases along the y-axis and life history stage (germination to second-year adult increases along the x-axis. Asterisks represent a significant difference within a life history stage (P ? 0.05).

seeding rates, or watering. However, high annual grass seeding rates produced high annual grass density in the second-growing season that averaged 586 ± 39 plants m^{-2} ($F_{3, 36} = 29.4$; $P < 0.0001$).

Seeding treatments

Perennial grass density was similar across all seeding treatments when perennial grass seeding rates were lowest (Figure 2(a,c); Figure S3; $F_{92, 432} = 0.528$; $P = 0.833$). However, perennial grass density was highest when water was added (Table S3; $P < 0.0001$), perennial grass seeding was delayed until spring ($P = 0.02$), and perennial grass seeding rates were higher than 1,500 seeds m^{-2} ($P < 0.0001$). The combination of high perennial grass seeding rates, adding water, and seeding perennial grasses in spring produced the highest perennial grass density ($P = 0.015$). High annual grass seeding rates and water addition, and high perennial grass seeding

rates and adding water yielded 2.6 and 1.9 times higher perennial grass density compared to low annual grass seeding rates in ambient water ($P = 0.0040$) and low perennial grass seeding rates in ambient water ($P = 0.001$).

When annual grass seeding rates were lowest, annual grass density was similar across treatments (Figure 3(a,c); Figure S4; $F_{92, 432} = 1.01$; $P = 0.514$). Annual grasses had the highest densities when water was added (Table S3; $P = 0.004$), when perennial grass seeding occurred in autumn ($P < 0.0001$), when annual grass seeding rates were high ($P < 0.0001$), and when perennial grass seeding rates were high ($P = 0.0002$). When water was added and annual and perennial grass seeding rates were high, annual grass density was over three-times higher than when annual and perennial grass seeding rates were low and water was not added ($P = 0.001$). Annual grass density was highest when annual and perennial grass seeding rates

were high and perennial grasses were seeded in autumn ($P = 0.024$).

Discussion

Systems-based management

Quantifying seedling life history from germination to reproductive adult using system-based models should increase the ability to forecast plant population dynamics after imposing management inputs by identifying the suite of processes limiting seedling development (Evans 2012). Systems-management approaches are so effective because they identify the effect of ecological processes within model components, such as life history growth stages (James et al. 2013). Quantifying the limitations to seedling establishment by better understanding the link between species development through time and management inputs should increase management success rates (Cornwell and Ackerly 2010). While we previously quantified the advantages to modifying perennial grass seeding times and frequencies on the initial seedling emergence (Schantz et al. 2016); in this study, we used a systems-management approach to monitor annual and perennial grass life history to the second-growing season when perennial grass seeding times, seeding rates, and water availability varied.

Germination to emergence

The germination stage has historically been thought to be the limiting growth stage for developing seedlings (Kitchen and Monsen 1994). However, James et al. (2011) reported that the primary limitation to seedling recruitment occurs between germination and emergence growth stages (James et al. 2012). Similarly, we found that germination rates ranged from 70 to 90% of initial seeding rates (in bags), yet only 5–6% of germinated seedlings emerged (in plots). Processes, mechanisms, and conditions limiting seedling emergence include freeze-thaw cycles, where seedlings will emerge only to be frozen at a later date (Boyd and Lemos 2013); physical soil crusts, which are common in recently disturbed soils (Elmarsdottir et al. 2003); and/or soil pathogens that are prevalent in wet winter conditions (Mordecai 2012). During early life history stages, when competition for resources is at its lowest, Madsen et al. (2012) suggest agglomerating seeds to increase emergence since grouped seedlings have greater abilities to

break through soil crusts. However, we found that increasing seeding rates decreased germination rates, especially when seeding rates exceeded 2,500 seeds m^{-2} and we did not find evidence that higher perennial grass seeding rates led to higher seedling emergence rates. There are likely not enough resources in this environment to support seeding densities higher than 2,500 seeds m^{-2}, at least beyond initial seedling emergence (Spotswood et al. 2017). Similarly, it appears that perennial grass seedling emergence is limited more by the number and availability of safe sites rather than the number of available seeds (Owens et al. 1995).

Life history

In general, seeds are subject to 'the law of diminishing returns' (Clark et al. 2007). This is because the availability of safe sites (i.e. water and nutrient) availability is limited, especially in arid ecosystems (Aicher et al. 2011). Our finding that adding more than 2,500 perennial grass seeds m^{-2} did not produce higher perennial grass plant density at the end of this study clearly illustrates these 'density independent' effects (Spotswood et al. 2017). However, annual grasses do not appear to be limited by safe site availability since higher annual grass seeding rates produced higher annual grass density from emergence to second-year adult stages. Furthermore, annual grasses maintained high density throughout this two-year study even at moderate, 1,500 annual grass seeds m^{-2}, seeding rates. Annual grasses have characteristics that support their growth and development, such as higher relative growth rate (Svejcar 1990), resource acquisition (Svejcar and Sheley 2001), and root growth (Monaco et al. 2003) than native perennial grasses. Annual grasses also germinate and emerge earlier than perennial grasses (Abraham et al. 2009). Thus, safe site availability appears to be sufficient for annual grass seedling development, even at the highest annual and perennial grass seeding rates. Furthermore, because annual grasses had higher density at high perennial grass seeding rates; annual grasses are likely facilitated by neighbouring perennial grasses (Leger and Espeland 2010) and/or perennial grasses are ineffective competitors, which allows annual grass density to be unrestricted in these regions (Yelenik and D'Antonio 2013).

Annual and perennial grass density decreases from seedling emergence to adult life history stages (Sheley and Larson 1994). However, seedling

survival was not significantly different across life history transition stages following initial seedling emergence for both annual and perennial grasses. In a companion paper, we suggest that if perennial grasses reached the juvenile life history stage in the first-growing season, they would likely survive into the second-growing season (Schantz et al. 2016). However, the fact that perennial grass density in the second-growing season was lower than the juvenile or adult life history stages in the first-growing season suggests that perennial grass seedling survival is not dependent on which growth stages perennial grasses reach in the first-growing season. Furthermore, perennial grasses had higher density in the second-growing season when seeded in autumn or when seeding frequency was increased to autumn and spring. These findings suggest that seeding perennial grasses in autumn may have allowed these species to acclimate through the winter and readily emerge in the spring (Dyer et al. 2010). Consequently, while modifying seeding times and frequency may increase perennial grass recruitment in the short-term, it may be necessary to track perennial grass recruitment for more than two growing seasons to identify whether overwintering during the first-growing season will affect perennial grass recruitment.

Seeding treatments

Modifying perennial grass seeding frequency and seeding rates may alter the ecological processes that direct seedling recruitment (Wainwright et al. 2012). In support of our first hypothesis, delaying perennial grass seeding until spring or seeding half of perennial grass seeds in autumn and the remaining half in spring yielded higher adult perennial grass density. The higher perennial grass recruitment when seeding occurred in spring or in autumn and spring may be because seeded species are not resource limited (i.e. water) during these times of the year and the initial resource availability allows these species to reach later life history stages (Dyer et al. 2000). Alternatively, annual grass density was highest when perennial grass density was highest and especially when perennial grasses were seeded in autumn, suggesting that annual grass performance is highest when seeded with high numbers of perennial grasses in autumn (Goldberg et al. 2001). Seedlings can experience accelerated germination when seeded together (Tielborger and Prasse 2009). Yet, because annual

grasses germinate earlier and grow more quickly than perennial grasses (Abraham et al. 2009), seeding annual and perennial grasses together benefits annual grasses more than simultaneously seeded perennial grasses (Corbin and D'Antonio 2004). Thus, delaying perennial grass seeding until spring or increasing perennial grass seeding in autumn and spring may simultaneously limit annual grass density while promoting native perennial grass density in these environments.

Annual grass cover and density are generally far greater two-years following management inputs (Munson et al. 2015). This is likely because space and resources are still readily available from initial management inputs, while annual grass seedbanks are able to reproduce during the first-growing season (HilleRisLambers et al. 2010). Similarly, we found that annual grasses yielded two-times more density in the second-growing season compared to the first-growing season and annual grass density was highest when perennial grasses were seeded in autumn. Thus, getting perennial grasses established in the first-growing season can be critical to limiting annual grass interference on perennial grass growth in later growing seasons (Eliason and Allen 1997). Annual grass density in the second-growing season was greatest when perennial grasses were seeded in spring, which may be because during the first-growing season annual grass density was highest when perennial grasses were seeded in autumn and this high annual grass density may have depleted resource availability even into the second-growing season. Humphrey and Schupp (2001) found that where annual grass density is high, their seed banks can return to pre-management conditions and interfere with perennial grass establishment. Alternatively, regardless of annual grass interference Vaughn and Young (2015) suggest that initial establishment of perennial grasses can eventually lead to native perennial grass colonisation. Thus, providing perennial grasses a priority seeding effect, such as seeding perennial grasses in autumn, may yield more perennial grasses in later life history stages, but only when annual grass propagule pressure is low.

Greater water availability during the seeding year can facilitate the growth of all plant species by increasing soil nutrient availability during initial seedling growth and development (Elmarsdottir et al. 2003). In support of our second hypothesis, both annual and perennial grasses benefited from water addition during the first-growing season. However, perennial grasses benefitted from adding

water more than annual grasses and the fitness of perennial grasses was highest when water was added, and perennial grasses were seeded in autumn. These effects are likely because annual grasses tend to pre-empt available resources from perennials by growing earlier and faster than simultaneously seeded perennial grasses (Kulpa et al. 2012). Furthermore, annual grasses can reach adult life history stages on limited water while perennial grasses generally require steady water availability (Everard et al. 2010). Because annual grasses do not need to store resources for post-reproductive growth and development (Petru et al. 2006), it appears that water availability is sufficient for annual grass production in this system in this year. When precipitation is abundant, seeding perennial grass should yield higher native perennial grass recruitment.

Conclusions and management implications

Forecasting the effect of ecological processes on plant growth is possible when using a systems-based model. For example, while seedling germination was relatively high for both annual and perennial grasses, only 5–6% of germinated seedlings emerged in this study. However, following seedling emergence, the effect of limiting ecological processes on plant growth were low during Year one, yet over-wintering effects between Year one and Year two reduced plant growth. It appears that management inputs should focus on the transition between the germination and emergence growth stages following seeding, and managers should use adaptive management strategies to facilitate plant establishment following the first winter.

Modifying management inputs strongly influenced the trend in plant community assembly throughout this study. Our finding that annual grasses had higher germination rates and seedling density during the first-growing season when perennial grasses were seeded in autumn suggests that dispersal of annual grasses in autumn (which occurs naturally in nature and was experimentally manipulated by seeding in our study) likely accelerates annual grass germination. Higher perennial grass density when perennial grass seeding was delayed until spring or increased to autumn and spring appeared to initially provide perennial grasses a priority effect for accessing safe sites in the first-growing season; yet low perennial grass density in the second-growing season when perennial grass seeding occurred in spring may be because perennial grass fitness increases when

they over winter during the first-growing season. Alternatively, the low perennial grass density in the second-growing season may be because annual grass density in the second-growing season was almost two-times higher than initial annual grass seeding rates, especially in plots where perennial grass seeding was delayed until spring. Collectively, these findings suggest that while perennial grasses are strongly affected by the ecological processes surrounding seedlings early in their life history, annual grasses are mostly affected by the environmental fluctuations like annual weather patterns.

Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributor

Merilynn C. Schantz is Owner and Research Ecologist for Red Rock Resources LLC in Miles City, MT.

ORCID

Merilynn C. Schantz 🄳 http://orcid.org/0000-0002-7740-2345

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