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Abstract

Seeding is a key management tool for arid rangeland. In these systems, however, seeded species often fail to establish. A recent study in Wyoming big sagebrush steppe suggested that over 90% of seeded native grass individuals die before seedlings emerged. This current study examines the timing and rate of seed germination, seedling emergence, and seedling death related to this demographic bottleneck. We seeded monocultures of two native perennial bunchgrasses, *Pseudoroegenaria spicata* (Pursh) Á. Löve and *Elymus elymoides* (Raf.) Swezey, and one introduced bunchgrass, *Agropyron desertorum* (Fisch. ex Link) Schult., in 2007, 2008, and 2009 and tracked sown seed and seedling fate. Across the study years and species we found that germination was rapid and high, with species obtaining 50% germination by December, less than 2 mo after planting. Emergence of germinated seed did not occur until late February for *A. desertorum* and March for the two native grasses. In 2007 the majority of emergence and death was constrained to several weeks, whereas in 2008 and 2009 emergence and death was distributed across several months. The timing of seedling emergence did not influence survival probability or midday plant water potential (probability of exceedance < 0.05). Survival probabilities once seedlings emerged were greater for native species (0.71) than *A. desertorum* (0.51) in 2 of the 3 study yr (probability of exceedance > 0.98). The early germination of grasses following fall seeding, and the long 2- to 3-mo period that germinated grass seed remain in the soil before emerging, support the hypothesis that seedling recruitment might be limited largely by ecological processes and conditions during winter or early spring (such as soil freeze–thaw events, seed pathogens, or physical crusts). Delaying seeding to early winter or spring and other management tools that mitigate these factors driving this bottleneck might greatly improve restoration outcomes in these systems.

Resumen

Las resiembras son una herramienta clave de manejo para pastizales áridos. En estos sistemas, sin embargo, las especies sembradas a menudo no se establecen. En un estudio reciente en un pastizal de Artemisia en Wyoming se sugiere que más del 90% de los individuos sembrados de pastos nativos mueren antes que la plántula germine. Este estudio examina la época y tasa de germinación de las semillas, la aparición de la plántula, y la muerte de plántula relacionadas con el cuello de botella demográfico. Se sembraron monocultivos de dos especies nativas de pastos amacollados, *Pseudoroegenaria spicata* (Pursh) Á. Löve y *Elymus elymoides* (Raf.) Swezey, y también un pasto amacollado introducido, *Agropyron desertorum* (Fisch. ex Link) Schult., durante 2007, 2008, y 2009 y se le dio seguimiento a las semillas sembradas así como el destino de las plántulas. A través de los años de estudio y especies se vio que la germinación fue rápida y alta, con la obtención de la germinación del 50% en diciembre, menos de 2 meses después de la siembra de especies. La aparición de semillas germinadas no ocurrió hasta finales de febrero para *A. desertorum* y en marzo para las dos especies de pastos nativos. En 2007 la mayoría de aparición y muerte estaba limitada a varias semanas mientras que en 2008 y 2009 el surgimiento y la muerte se distribuyeron a través de varios meses. El tiempo de aparición de las plántulas no influyó en la probabilidad de la supervivencia o al potencial de agua de la planta al mediodía o (probabilidad de superación < 0.05). Las probabilidades de supervivencia una vez que surgieron las plántulas fueron mayores para las especies nativas (0.71) que *A. desertorum* (0.51) en dos de los tres años de estudio (probabilidad de superación > 0.98). La germinación temprana de gramíneas después de que cae la semilla y el periodo tardo de dos a tres meses la semilla germinada permanece en el suelo antes de emerger y apoya la hipótesis que el reclutamiento de plántulas puede estar altamente limitado por el proceso ecológico y las condiciones durante el invierno o el inicio de la primavera tales (como la descongelación del suelo, los patógenos de la semilla, o las costras físicas). Retrasando la siembra a principios del invierno o primavera y usando otras herramientas de manejo que mitiguen los factores que impulsan este cuello de botella se puede mejorar considerablemente los resultados de la restauración en estos sistemas

INTRODUCTION

Seeding rangeland is a critical tool used by land managers to stabilize soils following disturbance, inhibit the spread of invasive plants and direct plant community change toward desirable states (e.g., Allen-Diaz and Bartolome 1998). In the Wyoming big sagebrush steppe of western North America, land managers spend tens of millions of dollars each year seeding rangeland (USGAO 2003; Knutson et al. 2009). Despite these efforts, however, seeded species often fail to establish (USGAO 2006). In addition to economic losses, failed seedings have an ecological cost because they provide invasive species a window of opportunity to establish and spread.
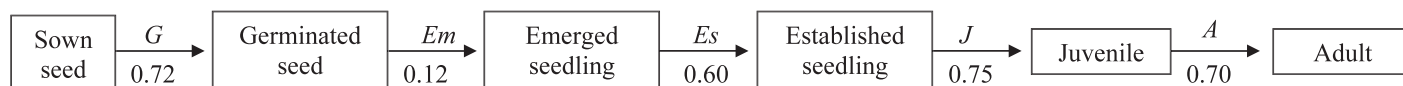
Figure 1. Life stages (boxes) and transitions probabilities (arrows) quantified for seeded native grasses *Pseudoroegenaria spicata* and *Elymus elymoides* (James et al. 2011). Numbers below arrows indicate the probability of native grasses transitioning between life stages. Values are averaged over the 3 study yr (James et al. 2011). The transitions included germination (*G*), seedling emergence (*Em*), seedling establishment (*Es*), seedling survival to the juvenile stage (*J*), and juvenile survival to the adult stage (*A*). Following the definitions of Fenner and Thompson (2005), individuals were considered germinated when seeds produced a radical, emerged when coleoptiles or cotyledons appeared above the soil surface, and established when possessing a fully expanded leaf. Juvenile plants were plants that survived to winter dormancy the first growing season and adult plants to be those that produced seed.

Given the importance seeding plays in restoring sagebrush steppe systems and the high risk of seeding failures, it is not surprising that much research has been directed toward improving seeding success. The bulk of this research, however, has focused on the technical aspects of seeding (e.g., Beukes and Cowling 2003; Monsen and Stevens 2004; Thompson et al. 2006). Although this line of work has been valuable, there has been substantially less research directed at identifying demographic processes driving patterns of seedling recruitment in Wyoming big sagebrush steppe systems. Plant demography research has been widely used to improve management of invasive and rare plant species (Parker 2000; Traveset et al. 2003; Jongejans et al. 2006; Colas et al. 2008). In these efforts, researchers identify the major demographic processes limiting population establishment and persistence. Based on these results it is then possible to identify management strategies or tools most likely to alter the particular demographic process limiting population size. This approach might be useful for identifying management strategies and tools to improve outcomes of large scale seeding efforts in Wyoming big sagebrush steppe.

Multiple demographic processes can influence restoration outcomes. Once seeds are sown by managers, they can germinate, die, or remain viable but dormant in the soil (Chambers and MacMahon 1994). To recruit into the adult population, germinated seeds must emerge from the soil, establish enough photosynthetic area to support survival independent of seed or cotyledon energy reserves, and survive the juvenile phase (Fenner and Thompson 2005). In arid systems, drought is commonly thought to be a major limitation to recruitment. For example, Pyke (1990) and Salihi and Norton (1987) documented over 80% grass seedling mortality during summer drought. Other work, however, has reported over 50% survival of shrubs, forbs, and grasses in arid systems once seedlings emerge (Chambers 2000; Huber-Sannwald and Pyke 2005; Meyer and Pendleton 2005). In some cases, a substantial amount of mortality in aridland seedings has been observed prior to seedling emergence. For example, Pyke (1990) and Chambers (2000) found that the percent of sown seeds that emerged was 2% and 7%, respectively. In these cases, seedling survival might depend on emergence timing, with earlier-emerging populations or species having greater survival probability (Miller 1987; de Luis et al. 2008).

Most studies examining demographic processes influencing seedling establishment on rangeland do not follow seed and plant fate through all key demographic stages (Fig. 1). As a consequence, it is difficult to determine the relative importance each demographic stage plays in driving recruitment patterns. In a recent study where we followed the demography of sown grass seed through critical stages spanning germination to adult plant survival, we found strong and consistent evidence that demographic processes occurring very early in seedling development were a major bottlenecks to native plant recruitment in Wyoming big sagebrush steppe (Fig. 1; James et al. 2011). Across experimentally disturbed plots and four sites burned by wildfires and seeded by managers, we found that over 90% of the sown native grass individuals died before seedlings emerged from the soil surface. Germination probability was high, averaging 0.72 across species and years, but emergence probability was low for native species, averaging 0.12. The nonnative perennial grass *Agropyron desertorum*, had germination probabilities comparable to native grasses but *A. desertorum* emergence probability averaged 0.49. Following emergence, survival probability through to adulthood for native grasses and the nonnative *A. desertorum* was high, averaging 0.68. Thus, in the northern Wyoming big sagebrush steppe systems, the transition between a germinated seed to an emerged seedling was the main demographic bottleneck limiting native plant recruitment and the key transition contributing to the greater seedling establishment of the nonnative *A. desertorum* over native grasses.

The broad objectives of this study were to examine the timing and rate of seed germination, seedling emergence, and seedling death of commonly seeded grass species. Quantifying these patterns will allow mechanistic hypotheses to be developed that can improve understanding of the strong and reoccurring demographic bottlenecks driving grass seedling recruitment. To do this, we made repeated observations through time on sown seed and emerged seedling on two native perennial bunchgrasses *Pseudoroegenaria spicata* and *Elymus elymoides* and the introduced bunchgrass *A. desertorum*. Measurements were made in the Northern Great Basin Experimental Range in eastern Oregon on the same plot in which survival probabilities for different demographic transitions were previously estimated (James et al. 2011). We predicted that the higher survival probabilities of *A. desertorum* would be associated with earlier germination and emergence of *A. desertorum* compared to the two native grasses, and that for both native grasses and *A. desertorum*, seedling cohorts that emerged earlier would have greater survival probability.

METHODS

Study Site, Species, and Demographic Stages Measured

The experiment was conducted at the Northern Great Basin Experimental Range in eastern Oregon (43°22′N, 118°22′W,

Table 1. Weather data for the 3-yr study period and long-term 70-yr average for the study site.

	2007	2008	2009	70 yr ave.
Crop-year precipitation (1 October–30 September)				
Total precipitation (mm)	161	162	243	283
No. rain events >2mm	24	22	24	28
Average event size (mm)	6.7	7.3	10.2	9.5
Spring precipitation (1 March–31 May)				
Total precipitation (mm)	32	54	67	78
No. rain events >2mm	6	9	5	8
Average event size (mm)	5.5	9	13	6.9
Temperature				
Average crop-year (1 October–30 September, °C)	7.4	7.5	8.5	7.6
Average winter (1 December–28 February, °C)	−1.7	−1.8	−1.0	−2.2
Average spring (1 March–31 May, °C)	7.1	4.7	5.7	6.2

1 300 m elevation). Vegetation at the site is representative of the Wyoming big sagebrush steppe dominated by a mixture of shrubs and perennial bunchgrasses. Soils are Xeric Haplargids with a surface AB horizon (0–15 cm) and a subsurface Bt horizon (15–30 cm) that terminates in a duripan at 30 cm, and texture is a clay loam. Average crop-year and growing season precipitation totals, precipitation event frequency, and precipitation event size, as well as average seasonal air temperature are shown in Table 1, along with the environmental conditions for 2007, 2008, and 2009, the 3 yr during which demographic measurements were made.

Demographic measurements were made on monocultures of three widely used restoration species (Table 2). *Pseudoroegenaria spicata* (germplasm Anatone) and *Elymus elymoides* (germplasm Toe Jam Creek) are native perennial bunchgrasses whereas *Agropyron desertorum* (type Hycrest II) is an introduced perennial grass native to the Eurasian steppe. Seeds were purchased from a commercial supplier and pure live seed value was recorded from the seed lot tag and retested each year of the 3 study yr. Pure live seed was evaluated in lab germination trials using light tables to evaluate seed fill, 4-wk incubations at room temperature to quantify germination, and dissections to determine if ungerminated seed was dead or viable but dormant. The same seed lot was used for each of the 3 study yr.

Although the native bunchgrasses have comparable life histories, phenologies, seedling growth rates and biomass allocation, and widely co-occur throughout the Wyoming big sagebrush steppe (James 2008a, 2008b), *Elymus elymoides* is thought to be a more early seral bunchgrass than *P. spicata*, which has lead to the expectation that this species might have a greater ability to colonize disturbed sites compared to *P. spicata* (MacKown et al. 2009). The introduced *Agropyron desertorum*, on the other hand, has a well-demonstrated ability to establish better than native grasses in reseeding efforts (Johnson 1986).

Experimental Design and Measurements

In fall 2007, 2008, and 2009 we seeded monocultures of the three study species in 1-m^2 plots using three replicate plots per species per year. Seeding rates are listed in Table 2 and were adjusted after the first year in an effort to make final plant densities more comparable among species and minimize confounding effects of interspecific competition on plant demography. Although this limits the degree to which we can compare absolute numbers of seedlings among years, it still is possible to make year comparisons when data are standardized by the number of seeds sown (e.g., germination or other transition probabilities). Species and year were randomly assigned to plots. To keep the intensity of disturbance and

Table 2. Seed and seeding rate for the three study species for each of the 3 study yr.

Year	Species	PLS[1] (%)	Germinated seed[2] (%)	Dormant seed[2] (%)	Dead seed[2] (%)	Seeds sown (seeds · m^{-2})
2007	*Agropyron desertorum*	99 ± 1	82 ± 2	—	—	500
2007	*Elymus elymoides*	99 ± 1	62 ± 4	—	—	500
2007	*Pseudoroegenaria spicata*	99 ± 1	71 ± 6	—	—	500
2008	*A. desertorum*	99 ± 1	89 ± 2	0 ± 0	11 ± 1	350
2008	*E. elymoides*	99 ± 1	86 ± 3	0 ± 0	14 ± 3	650
2008	*P. spicata*	99 ± 1	76 ± 5	1 ± 1	23 ± 5	650
2009	*A. desertorum*	92 ± 1	86 ± 2	0 ± 0	14 ± 2	350
2009	*E. elymoides*	93 ± 1	77 ± 2	0 ± 0	22 ± 2	650
2009	*P. spicata*	92 ± 1	59 ± 2	8 ± 1	33 ± 2	650

[1]PLS indicates pure live seed. Each seed fate category was adjusted for PLS rate sown. Numbers are mean ± SE.
[2]Germinated, dormant, and dead seed are the percentage of seeds in germination bags that germinated, remained dormant, or died by the end of first growing season; — indicates no data collected.
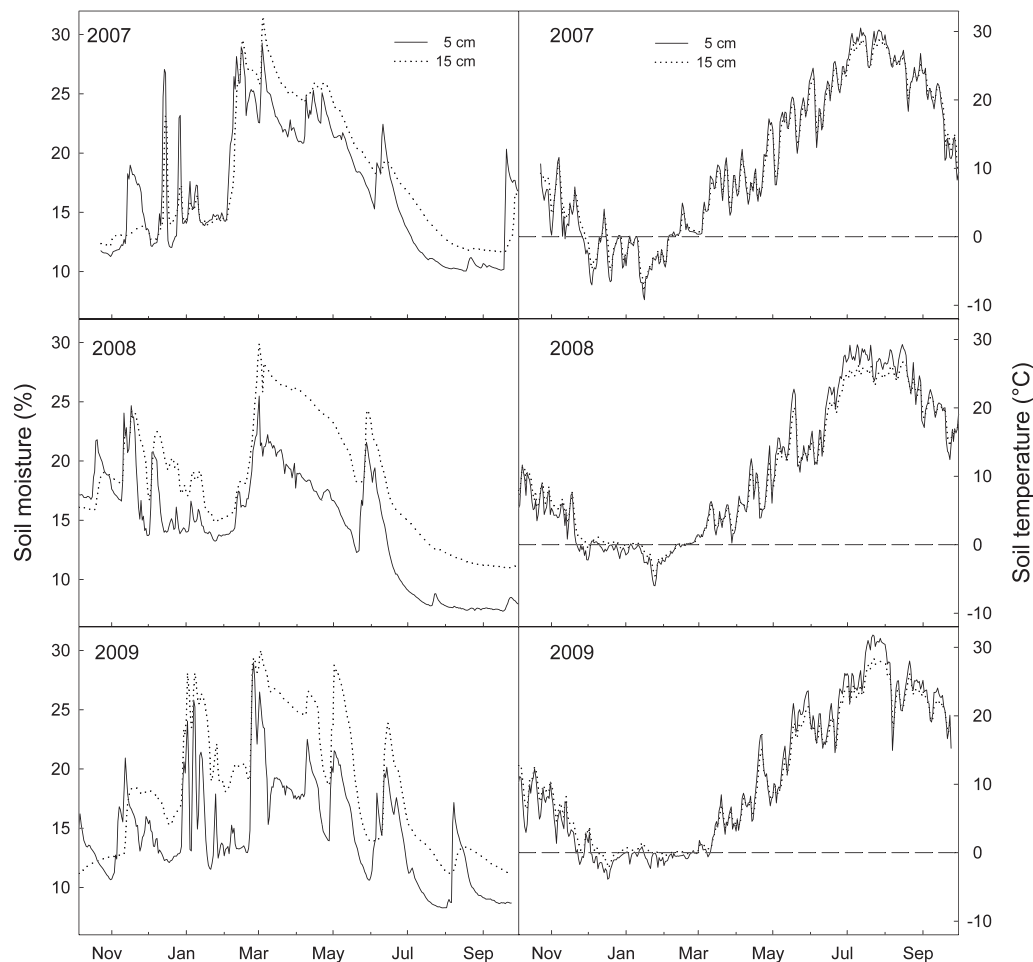
Figure 2. Volumetric soil moisture and soil temperature at 5- and 15-cm soil depth for each of the 3 yr of the study. Data are average daily values for three sensors at each depth.

seed bed conditions comparable among years, plots were tilled to a depth of 8 cm and existing vegetation removed approximately 1 mo before planting. Seeds were sown at 2-cm depth in late October following conventional seeding practices. Volumetric soil moisture and temperature sensors were installed at three randomly selected locations within the study area and measurements were made hourly in the 5-cm and 15-cm soil layer.

Timing and rate of germination was measured using the buried bag technique (Platenkamp 1991; Abbott and Roundy 2003). For each species and year, 40 bags were randomly paired with the seeded 1-m² plots and planted in the fall at the same time the plots were seeded. Five bags of each species were pulled at each harvest. The timing of harvest differed among years depending on environmental conditions and the expected impact on changes in germination (i.e., fewer harvests over cold dry periods with snow cover and more frequent harvests as snow melted and soils warmed. In 2007, the first harvest was made in February, whereas in 2008 and 2009 the first harvest was made 2 wk following seed sowing in late October. We adjusted the timing of the first harvest based on the unexpected observation in the 2007 that seeds rapidly germinated (see results). Following snow melt, the timing and rate of seedling emergence and death was tracked weekly on the seeded plots.

Seedlings that emerged in the same week were categorized as the same cohort and were marked with different-colored toothpicks so cohort survival probability could be tracked through time. Each toothpick was relocated weekly through July of each year and seedling status scored as live or dead, and any newly emerged seedlings marked. Plants were relocated the subsequent years to count the number of individuals that reached the juvenile and adult phases, respectively. For all years and species, plants surviving to the second growing season were capable of producing viable seeds. To examine the effects of emergence timing on seedling fitness, we measured survival probability and midday plant water potentials during summer on a subset of cohorts that emerged at different times during the growing season. Water potential was measured using a Scholander-type pressure chamber (PMS, Corvallis, OR) following the procedures of Turner (1988).

Statistical Analysis

Our statistical estimates were 95% Bayesian confidence intervals (CIs). Bayesian confidence intervals have a simple interpretation and are well-suited for quantifying survival probabilities and other parameters (Rinella and James 2010). When two 95% confidence intervals do not overlap, the

probability is greater than 0.95 that the treatment with the larger-valued interval is larger than the other treatments. In instances where we report the probability that one treatment exceeded another, we use the notation "pr."

Confidence intervals estimating percent germination by particular dates were computed from a linear mixed model with indicator terms for year, species, replication, date, and species × date. All factors were modeled as random, except year and species, which were modeled as fixed effects. CIs estimating the percent of individuals transitioning between life stages were computed from a generalized linear model based on the multinomial distribution. Specifically, we used a Bayesian continuation ratio model to estimate percentage of individuals transitioning between K growth stages (Congdon 2001). The seedling density, survival probability, and water potential data did not meet assumptions of standard statistical models, so we did a bootstrap analysis to compute the CI for these data (Dixon 2001). For each response variable, we calculated the mean of r (number of replications) response variable values that were drawn randomly and with replacement. We repeated the random drawing and mean calculations to derive 10,000 bootstrap samples for each response variable. The 95% bootstrap CIs were estimated by computing quantiles from the bootstrap samples. All computations were performed in FORTRAN (IntelCorporation, Santa Clara, CA).

RESULTS

Crop-year precipitation for each of the 3 study yr was lower than the long-term average (Table 1). Crop-year and spring precipitation varied 1.5- and 1.8-fold, respectively, over the 3 yr plots were seeded, with 2009 receiving the most crop-year and spring precipitation. The frequency and size of spring precipitation events also varied across study years with 2008 having the most frequent spring precipitation events and 2009 having the largest average event size. Patterns of volumetric soil–water content and temperature at 5- and 15-cm soil depth reflected the differences in timing and amount of precipitation among years (Fig. 2). The greater precipitation in 2009 did not correspond to greater germination of the study species (Fig. 3) or survivorship following germination and emergence (Fig. 4). Thus, over the 3 study yr there was no clear ranking between seedling establishment and crop year or spring precipitation.

Following fall seeding, germination of all species reached 50% by December in 2008 and 2009 (Fig. 3). Germination bags were not pulled in December 2007. During spring, most species in most years demonstrated additional germination, but in most cases, these increases were modest, representing about an additional 10% more germination compared to the December harvests (Fig. 3). The probability that *A. desertorum* had greater cumulative germination than the two native species was > 0.98 for all 3 study yr. Across years, germination for the study species was relatively high, with point estimates suggesting cumulative germination during the growing season ranged between 60% to 90%. Field germination rates, however, were lower than lab rates. Differences between field and lab germination rates were due to seed death, not dormancy, because very few ungerminated seeds remained viable (< 1%) the year after seeding (Table 2).
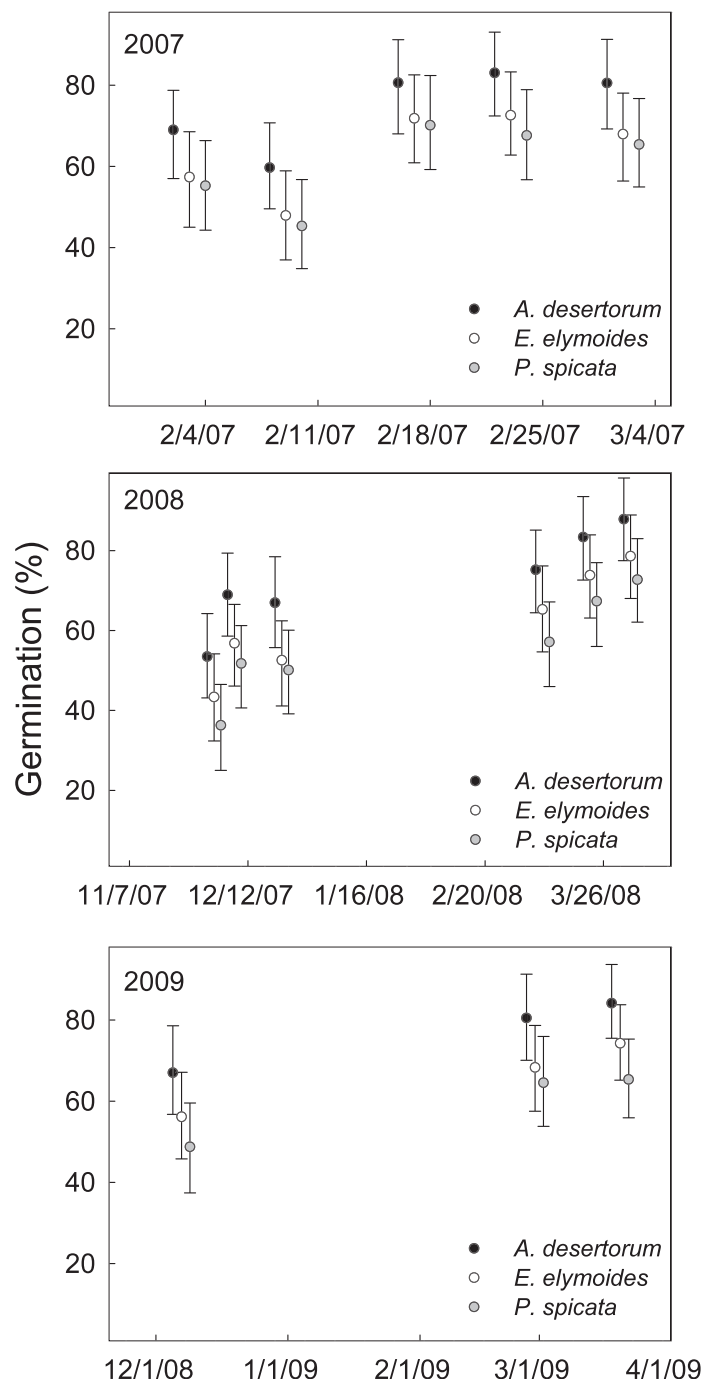

Figure 3. Germination of the three study species following planting of seeds in fall. Harvest intervals differed among the 3 yr of the study. Germination data were adjusted for number of pure live seed sown. Data are most-likely parameter estimates (dots) and 95% confidence intervals (bars).

The introduced *A. desertorum* generally reached maximum seedling emergence earlier than the two native grasses (Emergence, Fig. 4). Although the patterns of emergence and death varied among years, this variation was generally comparable among species. For example, in 2007, 97 ± 1, 91 ± 2, and $79 \pm 10\%$ (95% CI) of seedlings emerged for *A. desertorum*, *E. elymoides*, and *P. spicata*, respectively, within a 4-wk period (Fig. 4). Likewise, in 2007, 56 ± 3, 56 ± 12, and $56 \pm 4\%$ of deaths for *A. desertorum*, *E. elymoides*, and *P.*
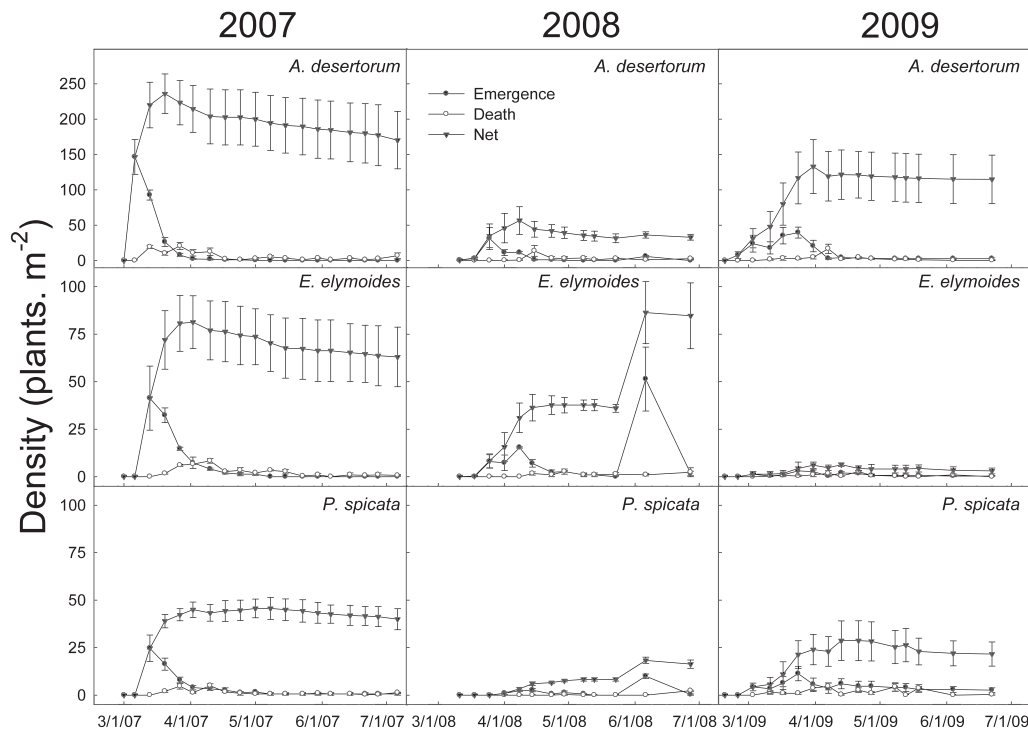
Figure 4. Patterns of seedling emergence and death and net seedling density for the three study species in each of the 3 study yr. Data are means ± SE.

spicata, respectively, occurred the first 4 wk after emergence began. However, in 2009, only 44 ± 17, 27 ± 27, and 41 ± 16% of seedlings for *A. desertorum*, *E. elymoides*, and *P. spicata*, respectively, emerged within the first 4 wk after emergence began. In addition, in 2009, 14 ± 10, 17 ± 17, and 26 ± 12% of deaths for *A. desertorum*, *E. elymoides*, and *P. spicata*, respectively, occurred the first 4 wk after emergence began.

Within a species, there was little evidence to suggest seedling survival differed greatly among cohorts that differed in emergence timing (Fig. 5). Averaged across cohorts, there was evidence that *A. desertorum* seedlings had a lower survival probability (pr) than the native grasses in 2007 (pr=0.92) and 2008 (pr=0.99) and greater survival probability than the native grasses in 2009 (pr=0.99). The data provide little evidence that midday water potentials varied greatly among the three cohorts of native grass seedlings (Fig. 6A) whereas water potential for *A. desertorum* seedlings was lower for the third cohort compared to the first and second cohort (pr > 0.97). For the first two seedling cohorts, *A. desertorum* seedlings maintained a higher water potential than native grass seedlings (pr=0.94). By the juvenile stage, differences in water potential among cohorts and species had become less apparent (Fig. 6B). Averaged across all life stages, *A. desertorum* maintained a higher water potential than the native grasses (pr=0.99), mostly due to native grasses showing a lower water potential in adult plants compared to seedling or juveniles (pr > 0.99) (Fig. 6C).

DISCUSSION

Seeding is an important management tool for arid and semiarid rangeland because plant community recovery following distur-

bance is slow (Leps et al. 1982; MacGillivray et al. 1995) and often inhibited by invasive species (DiVittorio et al. 2007). The study presented here reports several important demographic patterns for three common grass species used in Wyoming big sagebrush steppe restoration that are valuable in understanding and managing seeding outcomes. For example, we show that germination is not a central limitation to grass seedling establishment. Much of the rangeland seed ecology literature focuses on germination characteristics of different species and populations (e.g., Young and Evans 1977; Haferkamp et al. 1995; Limbach and Call 1996). For grass species, this line of work has focused on the degree days necessary to allow germination and how this differs among species. Implicit in these investigations is the assumption that differences in germination characteristics have ecological implications. In this study, we found that germination of these grass species was rapid and high, with germination reaching 50% 3 to 4 wk following fall plantings. Given that germinated seed do not emerge as seedlings until spring, there appears to be ample time for seeded populations to obtain the needed degree-day requirements for germination. Therefore, modest differences among species in degree-day requirements to achieve germination do not appear to be ecologically relevant for these grass species.

Germination patterns of these grass species also contradict two widely held notions about the fate of seed sown in Wyoming big sagebrush steppe restoration efforts. First, conventional notions in Wyoming big sagebrush steppe systems assume that fall-sown seed are dormant seedings (i.e., seeds sown in fall remain dormant over winter and germinate in spring when soils warm; Hull 1948; Stewart 1950; Young et al. 1969). Even under the very cool conditions of the northern Great Basin, this general assumption appears to be false. The
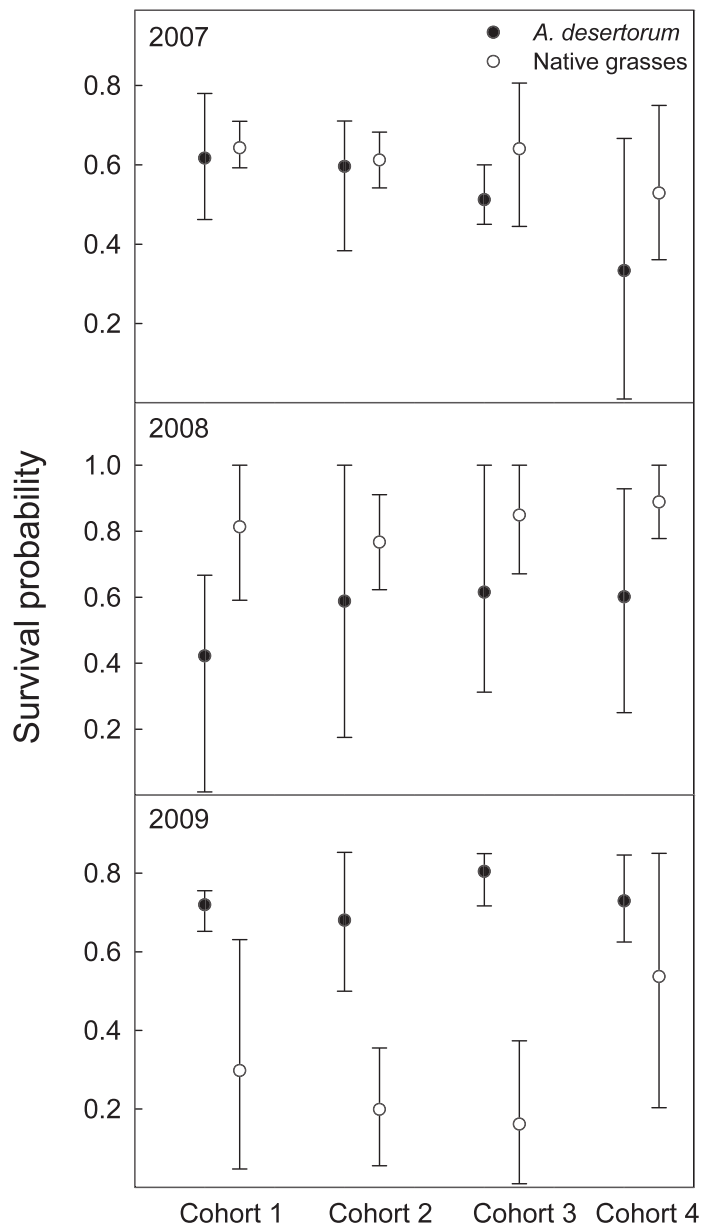
Figure 5. Survival probability of the first four seedling cohorts that emerged at different times during the growing season. Cohorts for most years are separated by 1-wk intervals. In 2008 for Cohort 4 we had to combine cohorts for 2 adjacent wk for the native grasses to obtain a sufficient sample size. Smaller numbers represent earlier-emerging cohorts. Because of the relatively low numbers of native seedlings that emerged each year, *Pseudoroegenaria spicata* and *Elymus elymoides* seedlings were grouped together for analysis. Data are most-likely parameter estimates (dots) and 95% confidence intervals (bars).

Figure 6. Midday water potential of (**A**) the first three cohorts sampled and (**B**) cohorts of juvenile plants that established at different times the previous year. Smaller numbers represent earlier emerging cohorts. (**C**) Midday water potential of seedlings, juvenile, 1-yr-old adult and 2-yr-old adult plants. Because of the relatively low numbers of native seedlings that emerged each year, *Pseudoroegenaria spicata* and *Elymus elymoides* seedlings were grouped together for analysis. Data are most-likely parameter estimates (dots) and 95% confidence intervals (bars)

few warm and wet periods in fall, although brief, appear to be sufficient to allow at least half the seed population to germinate. These germinated seeds must survive extreme cold and potential drought during the winter months before emerging in spring. In most cases, it is likely fall dormant seedings are not achieved. A second widely held notion is that it often takes several years for a species to fully establish following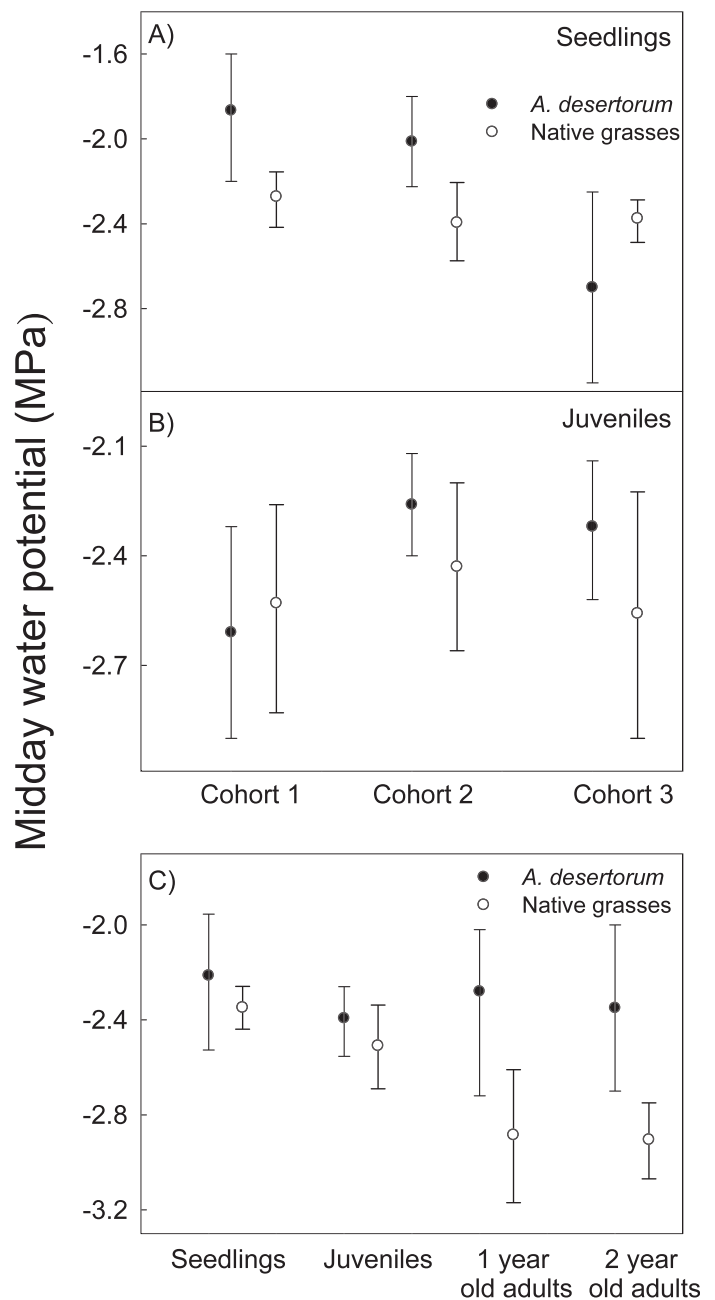 seeding. This implies that seeded species might spread out risk associated with germination by staggering germination timing through the population. Although some plant species have demonstrated the value of these strategies (Childs et al. 2010), particularly hard-seeded species (Metz et al. 2010), the perennial grass species examined here showed little evidence to suggest germination is spread over multiple years. The first growing season following seeding, germination

can reach up to 80%; the bulk of the seeds that remain ungerminated were dead. This suggests, for these and other grass species that have similar germination cues and requirements, that there is little carryover of the sown seedbank to subsequent years.

Our initial study (James et al. 2011) demonstrated that emergence, the transition between a germinated seed to an emerged seedling, was the major demographic bottleneck limiting native grass seedling recruitment. Once seedlings emerged, percent survival to the adult stage was comparatively high, with only about 8% of the emerged native seedlings dying as they transitioned to an adult plant. In this study, we showed that the timing of seedling emergence closely corresponded to the timing of seedling death. In 2007, emergence and death was confined to a short period of several weeks in early spring, whereas in 2008 and 2009, emergence and death was spread out over several months. This demonstrates that years having widely different patterns of precipitation inputs might not necessarily have large differences in patterns of seedling survival. However, the close patterning of emergence and death across years suggests that the abiotic conditions that favor emergence also correspond to timing of conditions that increase likelihood of seedling death. Alternatively, it might suggest that seedlings are most susceptible to mortality shortly after emergence but quickly become less susceptible to death through time.

Contrary to much of the seedling ecology literature, early emergence of seedlings within a species was not associated with an increase in survival probability. Although specific environmental and biotic stresses determine the adaptive value of early vs. late emergence, studies in old fields, forests, Mediterranean scrubland, and Wyoming big sagebrush steppe have reported a positive relationship between early emergence and survival (Mack and Pyke 1983; Miller 1987; Jones et al. 1997; de Luis et al. 2008). It would seem that early emergence would have an adaptive value for these arid-land perennial grasses as well. In our study, within a species, seedling cohorts that differed in emergence timing by several weeks did not differ in survival probabilities or water relations. However, this does not exclude the importance of differences in emergence timing between species. The introduced *A. desertorum* reached peak emergence earlier than the two native grasses and also had a much higher percentage of germinated seed that emerged compared to the natives. Although this study did not determine if greater emergence probability of *A. desertorum* was due to timing of emergence, the success of *A. desertorum* and invasive annuals such as *Bromus tectorum* L. have been attributed in part to their ability to emerge earlier in the growing season than natives (Harris 1967; Johnson 1986).

IMPLICATIONS

Recruitment failures in rangeland restoration have been widely blamed on mortality during spring and summer drought or competition from weeds (Ratzlaff and Anderson 1995; Stevens 2004; USGAO 2006). The early and rapid germination of grass seed that we showed in this study, coupled by the low survival probability of germinated seed shown in our initial study (James et al. 2011), strongly suggest that processes and conditions occurring over winter and early spring before seedlings emerge are a major drivers of restoration failures. Once seedlings emerge, survival probability is high, regardless of emergence timing. Potential key ecological processes and conditions that might drive large mortality of germinated seed include freeze–thaw or wet–dry cycles in winter that can mechanically damage germinated seeds, pathogen attack on germinated seed, or soil physical crusts (Harper 1977). Several management tools and strategies could be helpful in mitigating the large number of seedling deaths that occur very early in the season. These include sowing as late as possible in fall to increase likelihood of winter dormancy, or seeding in spring if feasible. Likewise, minimizing disturbance and physical crusting can increase seedling survival in soils with high silt content. Lastly, development of seed coats that delay winter germination could be extremely helpful in decreasing seedling mortality over winter. Although experimental manipulations of these putative factors are needed to determine the degree to which each influences emergence, our study strongly suggests that research and management tools that focus on overcoming emergence bottlenecks will lead to the greatest increases in our ability to restore Wyoming big sagebrush steppe and similar aridland systems.

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