

# Demographic processes limiting seedling recruitment in arid grassland restoration

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## Summary

1. Seeding is an important management tool in aridland restoration, but seeded species often fail to establish. Previous research has largely focused on the technical aspects of seeding with little effort directed at identifying demographic processes driving recruitment failures.

2. In tilled plots, in each of 3 years, we estimated life stage transition probabilities for three species commonly used in sage steppe restoration. We also took similar measurements on seed sown by managers following four major fires.

3. Point estimates and associated Bayesian confidence intervals demonstrated germination probabilities that were consistently high, averaging 0.72. However, estimates suggest only 17 and 7% of the germinated seeds emerged in the tilled plots and fire sites, respectively. Following emergence, survival across the seedling, juvenile and adult transitions averaged 0.72. This suggests the transition from a germinated seed to an emerged seedling was the major bottleneck in recruitment. Although most individuals died during emergence, this was not always the principal source of variation in recruitment across sites.

4. *Synthesis and applications.* Processes occurring after emergence, such as mortality during spring and summer drought, may contribute to site-to-site variation in recruitment but are unlikely to be the main causes of restoration failures. Instead, recruitment may largely be determined by processes occurring during emergence, such as freezing and thawing of the seedbed, development of physical soil crusts and pathogen attack on germinated seeds. Using tools such as seed coatings and soil amendments to manage processes inhibiting emergence and developing seed mixes with higher emergence probabilities are likely to greatly improve restoration outcomes in the sage steppe and similar aridland systems.

**Key-words:** annual grass, fire, great basin, invasion, life stage, seeding

## Introduction

Seedling recruitment often is a central limitation to plant community restoration (Bakker *et al.* 1996; Seabloom *et al.* 2003). Seeding native species can overcome this limitation and allow managers to direct plant community assembly (Whisenant 1999; Martin & Wilsey 2006; Foster *et al.* 2009). In arid systems, seeding is a particularly important tool because plant community recovery following disturbance can be slow (Leps, Osbornovakosinova & Rejmanek 1982; Macgillivray *et al.* 1995) and may be inhibited by invasive species (DiVittorio, Corbin & D'Antonio 2007). Although important in arid systems, seeding is an expensive practice that often fails (Epanchin-Niell, Englin & Nalle 2009). Although much research has focused on improving seeding success, most of this work has

been centred on the technical aspects of seeding (e.g. Monsen & Stevens 2004; Thompson *et al.* 2006) rather than identifying and manipulating demographic processes driving seedling establishment.

An understanding of the way in which variation in life stage transition probabilities contributes to population persistence has improved the management of rare and invasive plant species. For example, demographic comparisons of the rare *Centaurea corymbosa* showed that reintroduced populations had higher survival rates than natural populations, but not higher population growth rates (Colas *et al.* 2008). Increasing mate availability was recognized as a management option that could increase growth rates of reintroduced populations. As another example, the transition from seed to seedling was found to drive population growth rates for the invasive *Carduus nutans*, and it was determined that biocontrol integrated with grazing would be needed to lower seed production enough

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to decrease population size (Shea & Kelly 1998). Quantifying life stage transition probabilities is essential for generating hypotheses about ecological processes influencing population size and for identifying management options that can manipulate these processes. This approach may be useful for improving the outcomes of large-scale seeding efforts that seek to re-establish native plant communities following disturbance such as fire.

It is particularly important to understand the demographic processes driving seedling recruitment for improving aridland restoration efforts where invasive plants have altered fire cycles (D'Antonio & Vitousek 1992; Brooks *et al.* 2004). For example, fire is a natural disturbance in the sagebrush steppe of western North America, which spans over 40 million ha across nine states (West 1983). The spread of invasive annual grasses into these historically perennial-dominated systems has increased the continuity and amount of fine fuels (Brooks *et al.* 2004), which in turn has dramatically increased fire size and frequency (Whisenant 1990; Pyke 2003). Tens of millions of dollars are spent each year seeding landscapes following fire in an effort to facilitate plant community recovery and inhibit annual grass invasion (United States Government Accountability Office 2003; Knutson *et al.* 2009). Unfortunately, the majority of seedlings fail (United States Government Accountability Office 2006). Quantification of the life stage transitions that are limiting recruitment in these seeding efforts is a first step in identifying the ecological processes that can be managed to improve restoration outcomes.

In arid systems, juvenile mortality during summer drought is thought to be a major limitation to recruitment. For example, Pyke (1990) found mortality of grass seedlings during spring to range between 8 and 14% but mortality during the first summer reached up to 86%. Similarly, Salihi & Norton (1987) reported 30% grass seedling mortality during the first spring but 85% mortality over the first seasonal drought cycle. Other work, however, has suggested that survival probabilities of shrubs, forbs and grasses in arid systems may exceed 50% once seedlings have emerged (Chambers 2000; Huber-Sannwald & Pyke 2005; Meyer & Pendleton 2005). In some cases, germination or seedling emergence has appeared to be the major recruitment bottleneck, with the percentage of grass and forb seed sown that become established ranging from 2 to 7% (Pyke 1990; Chambers 2000). While these studies provide some insights into the demographic processes limiting recruitment, they have not quantified transition probabilities for all life stages, so it is difficult to determine the relative importance that each stage has in driving recruitment. In addition, there have been no efforts to quantify variation in life stage transitions across sites and years. Differences in environmental conditions or soil properties may cause the particular life stage transition, limiting recruitment to differ among sites and years. If this is true, then this basic information is critical in order to understand the degree to which management strategies can be transferred across different restoration scenarios.

The objectives of this study were to quantify the role of various life stage transitions in driving seeded species recruitment and to determine how variation in these transitions influences

year-to-year and site-to-site variation in recruitment in sage steppe systems. We used two approaches to address our objectives. First, we estimated transition probabilities for key life stages on three widely used restoration species sown in tilled plots at one site in each of 3 years. Secondly, to quantify variation across sites, we took similar demographic measurements on seed sown by land managers following four major fires.

## Materials and methods

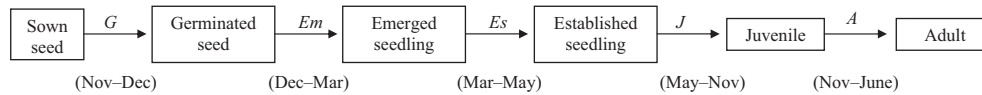
### LIFE STAGES, STUDY SITES AND SPECIES

Two experiments were conducted to address our objectives. The life stages and transitions quantified in both experiments are described in Fig. 1. The first experiment examined variation in life stage transition probabilities across years within a site and was conducted at the Northern Great Basin Experimental Range (NGBER) in eastern Oregon, USA (43°22'N, 118°22'W, 1300 m elevation). Soils are a sandy loam with 56, 24 and 20% of sand, silt and clay, respectively. Precipitation amounts and distribution during the study are shown in Table S1, Supporting Information. Measurements were taken on seeded monocultures of three widely used restoration species (Table S2, Supporting Information). *Pseudoroegneria spicata* (Pursh) A. Löve and *Elymus elymoides* (Raf.) Swezey are native perennial bunchgrasses, while *Agropyron desertorum* (Fisch. ex Link) Schult. is an introduced perennial grass native to the Eurasian Steppe. Seeds were purchased from a commercial supplier. *Elymus elymoides* is an early seral bunchgrass, while *P. spicata* is a late seral bunchgrass. While their life history and phenologies are comparable, the early seral nature of *E. elymoides* has led to the expectation that this species may have a greater ability to colonize disturbed sites compared with *P. spicata* (MacKown *et al.* 2009). *Agropyron desertorum* germinates and emerges several weeks earlier in the spring than the native grasses (Johnson 1986). These traits are thought to be key in the overall greater establishment of *A. desertorum* compared with native grasses in seeding efforts (Johnson 1986). Using this successful introduced species may provide insight into what life stage transitions most limit native plant recruitment. The second experiment evaluated site-to-site variation in life stage transition probabilities by gathering data in areas seeded by managers following four wildfire complexes that burned 80,000 ha of sage steppe in eastern Oregon in summer 2007. Fire locations and site characteristics are described in Table S3, Supporting Information. Seeds sown by managers were purchased from commercial suppliers. Prior to seeding, laboratory germination percentage was determined by germinating seed on moist filter paper at 20 °C for 4 weeks and recording the number of seeds that produced a radicle. For these grass species, the hydrothermal time accrued during these incubations was sufficient to break dormancy (Hardegree *et al.* 2010).

### EXPERIMENTAL DESIGN AND MEASUREMENTS

#### Seed sown at NGBER

In autumn 2007, 2008 and 2009, we seeded monocultures of the three species in 1-m<sup>2</sup> plots using three randomly assigned replicate plots per species per year. The seasonal timing of seeding followed standard protocol for autumn seeding. Seeding rates are listed in Table S2 and were adjusted after the first year to make final plant densities more comparable among species. Plots were tilled to a depth of 8 cm 1 month before planting. Volumetric soil moisture and temperature



**Fig. 1.** Life stages (boxes) and transitions (arrows) quantified and the months each transition spanned. 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 & Thompson (2005), individuals were considered germinated when seeds produced a radicle, emerged when coleoptiles or cotyledons appeared above the soil surface and established when possessing a fully expanded leaf. We considered juvenile plants to be those that survived to winter dormancy the first growing season and adult plants to be those that produced seed.

sensors were installed in plots, and measurements were taken hourly in the 5- and 15-cm soil layer.

Germination was measured using buried nylon bags placed in the 0- to 2-cm soil layer (Abbott & Roundy 2003). Germination bags were filled with 50 seeds mixed with field soil, paired with and buried adjacent to the 1-m<sup>2</sup> plots. Five bags of each species were excavated approximately every 2 weeks for 4 months starting 2 weeks after sowing. Bag contents were gently rinsed over a fine screen, and all seeds were scored as germinated, dormant or dead. Seeds with a radicle present at the time of harvest were scored as germinated. Seeds that were ungerminated at harvest but produced a radicle following 4 weeks of incubation on moist filter paper at 20 °C were scored as dormant. Seeds that were ungerminated at harvest, did not germinate when laboratory incubated and were visibly decomposed were scored as dead. Plots were censused weekly, and new seedlings were marked with toothpicks. Marked seedlings were followed weekly through July, and seedling status was recorded as live or dead. Marked plants surviving through leaf senescence in autumn were considered juveniles, and those producing seed the following year were considered adults.

#### Seed sown by managers following fire at four sites

The four fire sites were seeded by managers during autumn 2007 using a rangeland drill with a 30-cm row spacing (Table S3). Sixteen 2 × 2 m plots were randomly located at each site, and four drill rows within each plot were marked. Sixteen control plots that were not seeded were also marked to subtract any natural recruitment. Soil texture was analysed using the hydrometer method (Bouyoucos 1962). Soil inorganic nitrogen and potentially mineralizable nitrogen were measured following the study of Waring & Bremner (1964). Germination measurements were taken in the same manner as at NGBER. In this experiment, we were unable to distinguish species during the early stages of growth, so we report the pooled responses here for the entire seed mixture sown.

The emergence and fate of seedlings was followed through the spring and summer using an approach similar to the methods adopted at NGBER, except we were unable to track plants after the first summer owing to cattle trampling.

#### STATISTICAL ANALYSIS

We estimated survival probabilities using Bayesian statistics, where posterior distributions describe the knowledge of parameters arising from the data. We summarized the posterior distributions by their modes and 95% Bayesian confidence intervals (CIs). Bayesian confidence intervals have a simple interpretation, making them well suited for quantifying survival probabilities and other parameters (Rinella & 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 largest. Also, there is simply a 95% chance that a 95% Bayesian confidence interval brackets the fixed, unknown parameter of interest. In our case, many of the parameters of interest

were mean survival probabilities for the given combinations of site, species and year. Finally, in instances where we report the probability that one treatment exceeded another, we use the notation 'pr = .'

We used a Bayesian continuation ratio model to estimate probabilities of transitioning between  $K$  growth stages (Congdon 2001). The model for the  $(K-1) \times 1$  data vector for plot  $j$  (i.e.  $y_j$ ) was

$$p(y_j|\eta) \propto \prod_{k=1}^{K-1} \left( \frac{e^{\eta_{j,k}}}{1 + e^{\eta_{j,k}}} \right)^{y_{j,k}} \left( \frac{1}{1 + e^{\eta_{j,k}}} \right)^{n_{j,k}} \quad \text{eqn 1}$$

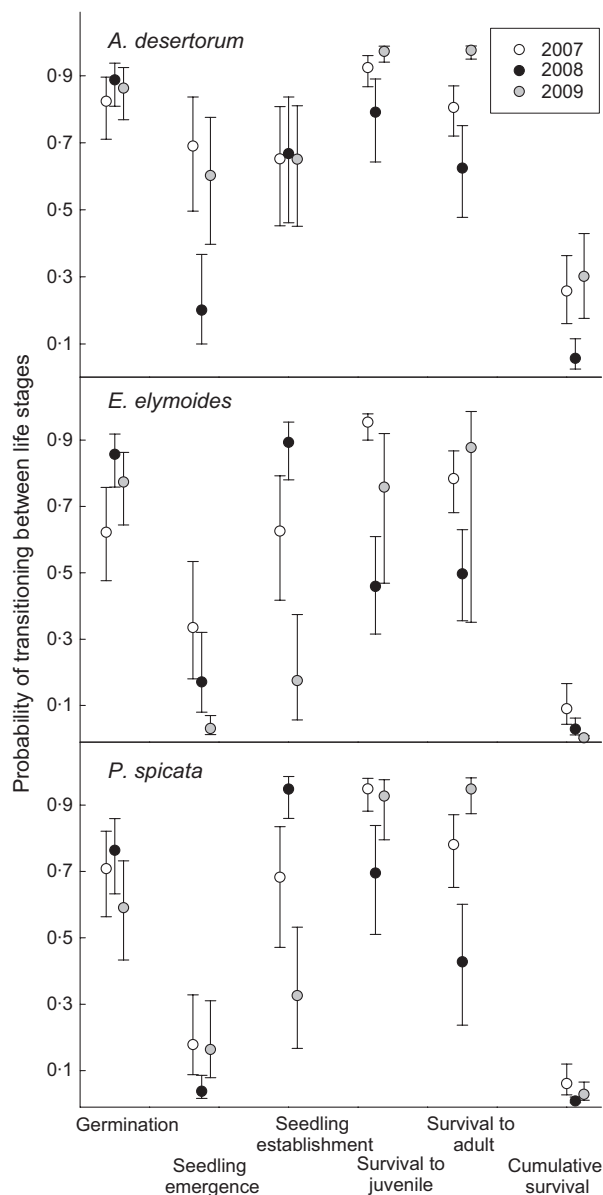
where  $y_{j,k}$  is the number of individuals entering but failing to exit stage  $k$ ,  $n_{j,k}$  is the number of individuals living beyond stage  $k$  and  $\eta_{j,k} = \text{logit}(p_{j,k}) = \log\left(\frac{p_{j,k}}{1-p_{j,k}}\right)$  where  $p_{j,k}$  is the probability of dying at stage  $k$ . We assumed  $\eta_j \sim N(X_j\beta, \Sigma)$  where  $\Sigma$  is a  $(K-1) \times (K-1)$  covariance matrix and  $X$  has columns for main effects and all possible interactions. Main effects were years, species and life stage transitions for the NGBER site, and locations and life stage transitions for the four fire sites. We assigned  $\beta$  to a uniform prior distribution and  $\Sigma$  to an inverse Wishart prior with  $K$  degrees of freedom and  $(K-1) \times (K-1)$  identity matrix as scale parameter. We used a hybrid Gibbs sampler/Metropolis algorithm to sample the joint posterior distributions (Carlin & Louis 1996) and used an algorithm of King, Tomz & Wittenberg (2000) to transform from the logit to probability scale.

Confidence intervals of Figs 2 and 3 are for individual combinations of year, site and transition. Simulated expected plant densities across life stages are shown in Figs 4 and 5 using posterior modes along with random draws from the posterior distributions. Starting densities for the simulations were representative of the study, with 500 and 376 seeds m<sup>-2</sup> being used at the NGBER and four fire sites, respectively. This simulation-based approach is useful for displaying parameter uncertainty in applications involving multiple, correlated parameters (Gelman & Hill 2007).

After identifying the transition with the lowest mean survival probability, we tested whether site-to-site and year-to-year variation in deaths during this transition was the greatest source of site-to-site and year-to-year variation in final plant density. The transitions tended to negatively covary because when the number of individuals that died during a transition exceeded the mean for that transition, fewer individuals were available to die during subsequent transitions, so subsequent transitions tended to be below their means. The transitions were not independent; hence, the decomposition of the final plant density variance involved covariances in addition to variances, and these covariances prevented the variance decomposition from being easily interpreted. Therefore, instead of relying on the variance decomposition, we computed 95% CIs on the difference between covariances. We computed CIs for

$$\text{cov}(t_1, \text{final plant density}) - \text{cov}(t_x, \text{final plant density})$$

where cov is the covariance function,  $t_1$  is the transition with the lowest mean survival probability and  $t_x$  is any one of the other transitions. A CI confined to negative values would indicate that,



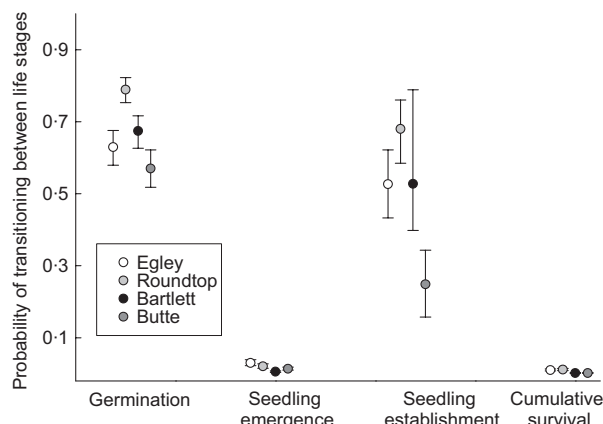
**Fig. 2.** Most likely parameter estimates (dots) and 95% confidence intervals (bars) estimating probabilities of surviving life stage transitions for the three study species seeded at Northern Great Basin Experimental Range. Categories represent transitions described in Fig. 1. Also shown is the transition from sown seed to adult plant (cumulative survival).

compared with  $t_x$ ,  $t_l$  covaried more negatively with final plant density.

## Results

### ENVIRONMENTAL CONDITIONS

Crop year precipitation varied 1.5-fold over the 3 years that plots were seeded at NGBER (see Table S1). While this variation corresponded to differences in water content and temperature profiles in the 5- and 15-cm soil layer (see Fig. S1, Supporting Information), precipitation in all 3 years was less than the long-term 283-mm average for the site, with 2009



**Fig. 3.** Most likely parameter estimates (dots) and 95% confidence intervals (bars) comparing probabilities of surviving life stage transitions for species mixtures seeded by managers following wildfires at four sites in eastern Oregon. Life stage transitions are described in Fig. 1. Also shown is the transition from sown seed to established seedling (cumulative survival).

being the wettest year (243 mm) and 2007 the driest (161 mm). Although germination at NGBER and fire sites began within 2 weeks of sowing and continued through December, emergence did not start until March (Fig. 1).

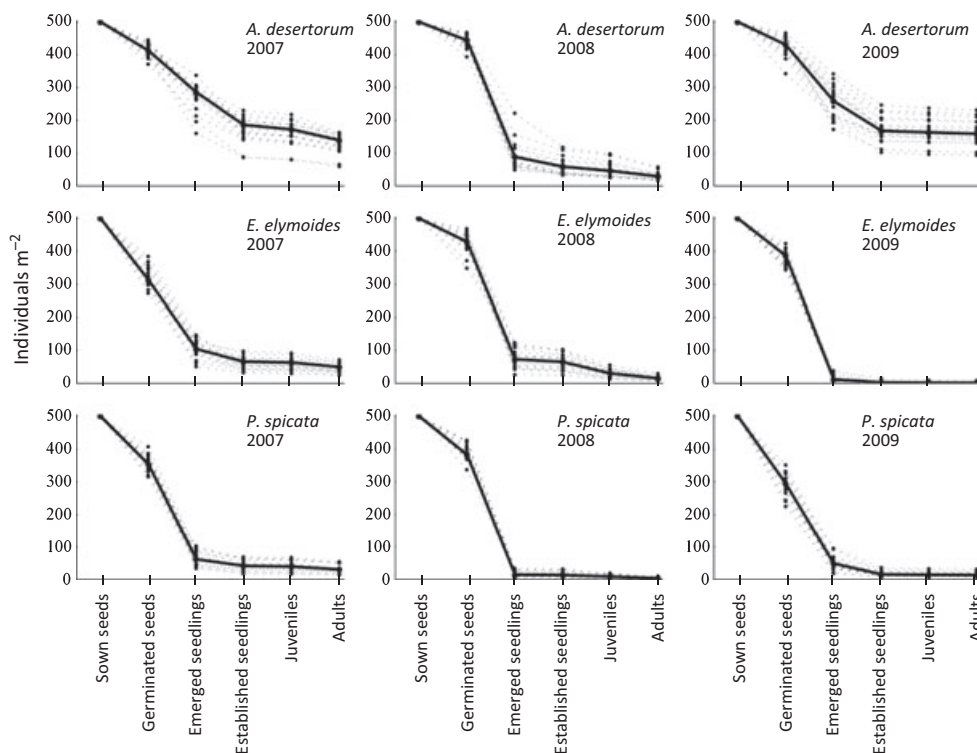
### LIFE STAGE TRANSITION PROBABILITIES

Averaged across years at NGBER, the introduced *A. desertorum* had a higher cumulative survival probability than the two native grasses ( $pr > 0.99$ ; Fig. 2). Germination probabilities were high for each species each year, with point estimates suggesting a range of 0.6–0.9 (Fig. 2). Germination in the field was lower than that in the laboratory, and this difference was attributable to seed death, not dormancy, because very few ungerminated seeds remained viable ( $< 1\%$ ) the year after seeding (Table S2). For the native species *E. elymoides* and *P. spicata*, emergence was the transition with the lowest survival probability each year ( $pr \geq 0.93$ ; Fig. 2). There was substantial year-to-year variation in survival probabilities for seedling establishment, survival to juvenile and survival to adult transitions. For example, seedling establishment probabilities for the natives were lower in 2007 than in 2008, but juvenile and adult survival probabilities were higher in 2007 than in 2008 ( $pr > 0.99$ ).

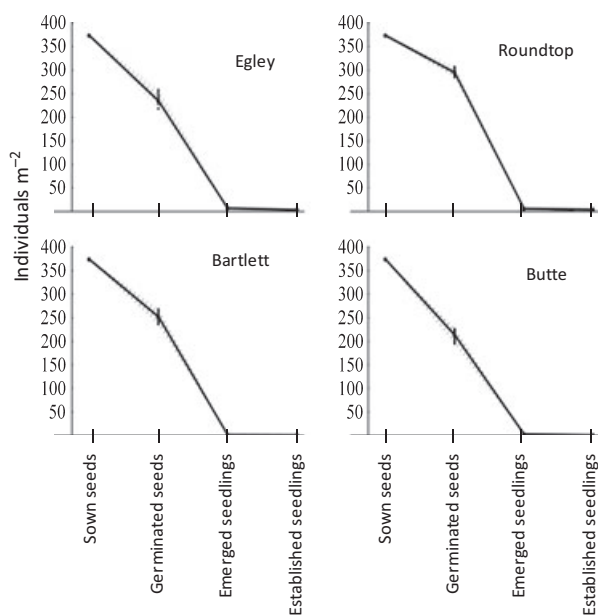
At all four fire sites, the probability that any given seed established was  $< 0.06$  (Fig. 3, cumulative survival). Averaged across the four fire sites, the germination probability exceeded all other transition probabilities ( $pr > 0.99$ ). Most of the seeds that failed to germinate died the first year (Table S3). Similar to NGBER, the transition with the lowest survival probability was emergence, which had at least a fivefold lower probability than the other transitions at each fire site ( $pr > 0.99$ ; Fig. 3).

### DENSITY AT EACH LIFE STAGE

The majority of deaths occurred before seedlings emerged regardless of year, species or site ( $pr > 0.99$ ; Figs 4 and 5).



**Fig. 4.** Estimates of expected numbers of seeded individuals surviving to various growth stages for the three study species seeded in 2007, 2008 and 2009 at Northern Great Basin Experimental Range. Seeding rates were set at 500 seeds  $m^{-2}$ . Solid lines represent most likely values (i.e. mode of posterior probability distributions) from a Bayesian model, and dotted lines represent 20 random draws from the posterior distribution. Dotted and solid lines close together indicate low uncertainty about the expected numbers.



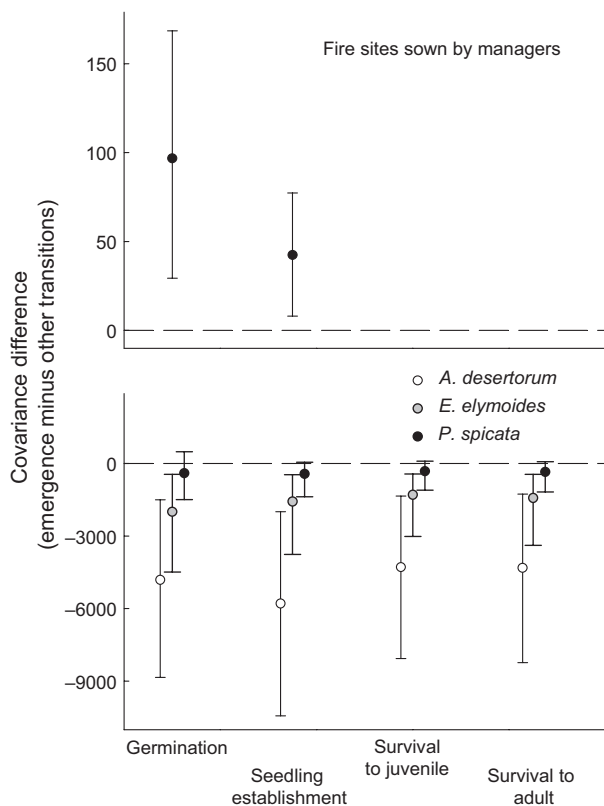
**Fig. 5.** Estimates of expected numbers of seeded individuals surviving to various growth stages for species mixtures sown by managers following wildfires at four sites in eastern Oregon. Seeding rates were set at 376 seeds  $m^{-2}$ . Line values are described in Fig. 6.

Moreover, averaged over years, the largest numbers of deaths of each species occurred during the transition from germinated seed to emerged seedling ( $pr > 0.99$ ). Following sowing of 500 seeds  $m^{-2}$  at the NGBER, averaged across years, the

number of *A. desertorum*, and native *E. elymoides* and *P. spicata* individuals that died during germination was  $75 \pm 30$ ,  $128 \pm 36$  and  $159 \pm 39$  (95% CI,  $pr > 0.99$ ), respectively. During emergence,  $214 \pm 42$ ,  $299 \pm 34$  and  $290 \pm 34$  of *A. desertorum*, *E. elymoides* and *P. spicata* individuals were lost, respectively ( $pr > 0.99$ ). During all transitions following emergence, the combined numbers of *A. desertorum*, *E. elymoides* and *P. spicata* individuals lost were  $116 \pm 30$ ,  $51 \pm 22$  and  $30 \pm 17$ , respectively ( $pr > 0.99$ ). Following sowing of 376 seeds  $m^{-2}$ , across fires,  $122 \pm 10$ ,  $248 \pm 9$  and  $3 \pm 1$  individuals died during germination, emergence and establishment, respectively ( $pr > 0.99$ ).

Averaged across years at NGBER,  $74 \pm 25$  (95% CI) more *A. desertorum* than native plants survived to adulthood (Fig. 4). This greater survival of the non-native species is mostly explained by the germination and emergence transitions. On average,  $68 \pm 33$  and  $81 \pm 47$  more natives died than *A. desertorum* during germination and emergence, respectively ( $pr > 0.99$ ).

Although emergence was always the principle bottleneck to recruitment at the NGBER and fire sites, emergence was not always the principle source of variation in final plant density. At the fire sites, site-to-site variation in final plant density was primarily driven by variation in mortality during germination and establishment ( $pr > 0.99$ ; Fig. 6, upper panel). At NGBER, on the other hand, variation in *A. desertorum* and *E. elymoides* final plant densities was mostly caused by variation in mortality during emergence ( $pr = 0.98$ ; Fig. 6, lower



**Fig. 6.** Most likely parameter estimates (dots) and 95% confidence intervals (bars) estimating effects of mortality variation at different life stage transitions on variation in final plant density. The intervals test the hypothesis that death during emergence covaries more negatively with final plant density than death during any other transition. The top panel shows confidence intervals for four fire sites seeded by managers. Only emergence minus germination and emergence minus establishment were estimated at these sites. The confidence intervals are confined to positive values, so they reject the hypothesis and suggest site-to-site variation in final plant density was primarily driven by variation in mortality during germination and establishment. (A negative covariance subtracted by a more negative covariance is positive.) The bottom panel shows the confidence intervals for three study species seeded during 3 years at Northern Great Basin Experimental Range (NGBER). Emergence minus germination, emergence minus establishment, emergence minus juvenile and emergence minus adult were measured at NGBER. The confidence intervals are mostly or wholly confined to negative values, so they support the hypothesis and suggest year-to-year variation in emergence is the most important driver of year-to-year variation in final plant density. (A negative covariance subtracted by a less negative covariance is negative).

panel). This was probably also the case for *P. spicata*, but the confidence intervals overlapped zero so the evidence is weaker for this species.

## Discussion

### LIFE STAGE TRANSITIONS INFLUENCING RECRUITMENT

Our finding that the majority of individuals are lost after germination but before emergence has important implications for understanding plant population dynamics and for identifying

which ecological processes need to be managed to increase seedling recruitment. The fact that the number of seedlings that establish represents a small fraction of seeds sown is well known (Chambers 2000; Traveset *et al.* 2003; Garrido, Rey & Herrera 2007). However, no studies have identified where, in the transition between sown seed and established seedling, the bulk of mortality occurs. We provide evidence that the majority of the mortality may be associated with the emergence of germinated seed rather than seed germination. This discovery is important because conceptual and quantitative plant demography models do not differentiate between processes and rates associated with germination from those associated with emergence (e.g. O'Connor 1991; Chambers & MacMahon 1994; Shea, Sheppard & Woodburn 2006). If the bulk of individuals are lost during emergence, then these models may fail to capture the ecological processes predominantly driving plant abundance. From an applied perspective, this distinction is important because models of plant life cycles are used to identify how ecological processes can be managed to alter plant population dynamics.

Comparisons between the transition probabilities of the introduced *A. desertorum* and the native species provide further support that emergence is a critical transition limiting native plant recruitment. In our study, *A. desertorum* emergence probability exceeded that of the natives and, in addition to germination rate, was one of the key transitions resulting in the greater recruitment of *A. desertorum* compared with the natives (Fig. 4). Greater establishment of *A. desertorum* compared with native grasses following seeding has been well documented (Johnson 1986). Our study suggests that these differences in establishment are driven mainly by differences in germination and emergence probabilities and less by juvenile and adult plant survival.

Survival probabilities for seedling establishment, juvenile and adult transitions were variable with probability rankings often changing among years (Fig. 2). While the drivers of this variation are not known, an important practical consideration is to ask what this variation in survival probability during later developmental stages means for recruitment. Life table analyses have indicated that seed mortality and germination have an overriding influence on the pattern and rate of population survivorship through time (Sharitz & McCormick 1973; Leverich & Levin 1979). In this study, when the low probability of surviving emergence is considered, reductions in survival probabilities during later life stages (Figs 2 and 3) have little impact on seedling recruitment (Figs 4 and 5). These data support early arguments (e.g. Hickman 1979) that high mortality rates in later life stages may be trivial in determining plant abundance when mortality in early life stages is considered.

One important caveat to this conclusion, however, is that seedling recruitment is only one component of population success and, as a result, patterns of seedling recruitment may not represent long-term patterns of population growth. For example, while we showed very low cumulative survival probability of sown native grasses, with point estimates ranging from 0.02 to 0.09, it is possible that high reproductive output of these survivors could result in rapid population growth. However, if we

consider the effects of initial recruitment on population success in a restoration context where invasive plants are present, we would expect these initial low recruitment rates to have substantial repercussion for long-term population success. In these situations, small differences in arrival time that establish priority effects can have long-term effects on plant community development and species abundance (Korner *et al.* 2008). In addition, failed seedlings following a disturbance give invasive species an opportunity to establish and spread, posing a major barrier to future recruitment (Standish *et al.* 2007; Abraham, Corbin & D'Antonio 2009).

While this study develops a strong case for emergence as the principle bottleneck to recruitment in aridland restoration, emergence was not necessarily the driver of recruitment variation. For the introduced *A. desertorum* and native *E. elymoides*, variation in emergence was the driver of year-to-year variation in final plant density (Fig. 6, lower panel), but variation in germination and establishment was the drivers of variation in final plant density among the fire sites (Fig. 6, upper panel). It is not possible to determine whether these contrasting results are attributable to differences between seeding methods used at NGBER and fire sites, differences in seed mixes, or whether emergence varies more year-to-year than site-to-site. All of these factors have substantial management implications and justify further researches into the spatial and temporal drivers of recruitment variation in aridland restoration.

#### LINKING RECRUITMENT LIMITATIONS TO ECOLOGICAL PROCESSES

Quantification of the life stage transition probabilities and the numbers of individuals lost at each stage can be used to develop hypotheses about which ecological processes are likely to influence seedling recruitment. Recruitment failures in arid grassland restoration have been widely blamed on mortality during spring and summer drought (Ratzlaff & Anderson 1995; Stevens 2004; United States Government Accountability Office 2006). In this study, we were able to compare the importance of mortality during this time period with that of mortality during other stages of seedling development. We found that most mortality occurred well before seedlings were exposed to spring and summer drought. While seedlings are undoubtedly lost during drought periods, when these losses are compared to mortality incurred during earlier life stages, they are small, suggesting spring and summer droughts are unlikely to be causes of recruitment failure in aridland restoration. Instead, abiotic and biotic processes occurring early in the season during emergence are likely to have the largest influences on recruitment.

In this study, seeds germinated by December but seedlings did not emerge until March (Fig. 1). During this period, seedbed temperatures were often below freezing and soil moisture often as low as levels observed during summer drought (Fig. S1, bars lower left panel). The effects of fluctuating temperature and moisture regimes on germination have been extensively examined (Baskin & Baskin 1998), and we know much about how these stresses affect established plants (Lam-

bers, Chapin & Pons 1998). However, we know little about how temperature and drought stress influence the emergence of germinated seed. Given the level and duration of stress to which germinated seeds are exposed, this stress may significantly impact emergence. In addition, freeze–thaw and wet–dry cycles during winter can cause physical crusts to form in aridland systems (Belnap 2003). Physical crusts were observed in this study (data not shown) and may have a pronounced effect on emergence.

Biotic processes also could inhibit emergence. As seeds germinate and protective seed structures are lost, plants become more susceptible to pathogens (Harper 1977). While not all studies have shown negative effects of pathogens on seedling emergence (e.g. Gallery, Moore & Dalling 2010), work in crop and wildland systems has suggested pathogens may have a large effect on emergence, particularly when soil temperatures are cool and seedling growth is slow (Harper, Landragin & Ludwig 1955; Kirkpatrick & Bazzaz 1979). Given the cold soil temperatures that persist prior to seedlings emerging and the long period between germination and emergence, pathogen attack may be an important biotic process influencing recruitment.

#### SYNTHESIS AND MANAGEMENT APPLICATION

Seeding is an important tool used by aridland managers to facilitate plant community recovery following disturbance and to prevent the spread of invasive species. The high rates of recruitment failure following seeding, however, have greatly limited the effectiveness of this practice. In this study, we found most of the seeded individuals that did not survive to adulthood died after germinating but before emerging. Therefore, seedling emergence was the transition most limiting native plant recruitment. Difference in emergence probability also was a central trait contributing to greater seedling recruitment of the non-native *A. desertorum* over the native species. Based on seedbed environmental conditions, the timing of life stage transitions and previous literature findings, we hypothesize emergence bottlenecks could be driven by mortality owing to low seedbed temperature or moisture in winter, physical crusting of soil or pathogens attacking germinated seed. If these processes are shown to inhibit emergence, then there are management options that can be used to overcome these limitations. For example, synthetic seed coats could be used to reduce abiotic stress effects on emerging seedlings, soil amendments could be used to reduce physical crusting, and fungicides could be used to reduce mortality from pathogens (Harper, Landragin & Ludwig 1955; Lehrsch, Lentz & Kincaid 2005; Turner *et al.* 2006). As a complementary approach, by identifying physiological traits resulting in differences in emergence probabilities among species, as was seen between the introduced *A. desertorum* and native grasses, it may be possible to design seed mixtures that are more effective in overcoming emergence bottlenecks. While the specific processes inhibiting emergence need to be identified and the variation in emergence probabilities among species needs to be assessed, our results suggest advances in these areas are likely to substantially increase our ability to restore sage steppe and similar aridland systems.

## References

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Figure S1.** Average daily volumetric soil moisture and temperature in the 5 and 15 cm soil layers in the plots seeded at the NGBER for each of the 3 years the study was conducted.

**Table S1.** Weather data for NGBER for the 3 years plots were sown and the 70 year average.

**Table S2.** Seed lot characteristics and seeding rates for tilled plots at NGBER.

**Table S3.** Site and seeding data for four fire sites sown by managers.

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