RESEARCH ARTICLE

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Increased soil temperature and decreased precipitation during early life stages constrain grass seedling recruitment in cold desert restoration

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Abstract

1. Seed-based restoration is one of the most difficult challenges for dryland restoration. Identifying environmental conditions that drive variation in seed and seedling mortality across similar restoration efforts could increase understanding of when and where restoration outcomes are likely to be favourable and identify new tools and strategies to improve outcomes.

2. We asked how variation in a suite of environmental predictors influenced germination, emergence, seedling establishment and juvenile survival of four commonly sown perennial grass species across 33 seeding experiments distributed over an ~160,000-km^2 area of the Great Basin, a cold desert system in the western United States.

3. Across experiments, we observed wide variation in the rates of four demographic transitions and wide variation in environmental conditions experienced by plants at each stage. For all species, higher precipitation during the first 30 days following seeding was associated with an increase in germination. Conversely, higher soil temperature over this same time period was associated with a significant decrease in germination and emergence, and soil temperature was associated with a substantial portion of the variation in germination and emergence probabilities observed across our seeding experiments.

4. Within the range of precipitation variation observed, we were unable to detect a significant relationship between seedling establishment the first growing season and cumulative precipitation the first year, precipitation during the first spring growing season or annual climatic water deficit (CWD) the first year. Higher CWD the second growing season reduced seedling survival over that time period.

5. *Synthesis and applications.* Our results show higher soil temperature negatively impacts grass seedling establishment. Restoration efforts should be prioritized when seasonal or subseasonal temperature forecasts indicate likely periods of below average temperatures. These results also indicate that climate warming will make

restoration even more difficult, with our model estimates suggesting the 2°C increase in temperature expected in the Great Basin over the coming decades will decrease germination and emergence by about 30%. Lastly, while our field-based approach provided insight into short-term drivers of mortality, it did not provide insight into drivers of longer term survival, suggesting a need for further work on predicting long-term restoration outcomes.

KEYWORDS

annual grass, bunch grass, great basin, invasive plant, life stage, population dynamics, restoration, seeding

1 | INTRODUCTION

The urgent need to improve dryland restoration efforts across the globe is well documented (Millennium Ecosystem Assessment, 2005; UNCCD, 2012). In most parts of the world, rates of dryland degradation drastically outpace our ability to restore even basic attributes of ecosystem function, let alone specific components of biodiversity (Duniway, Palmquist, & Miller, 2015; UNCCD, 2012). While there are well-described sociopolitical and economic barriers to restoration, even the most well-supported dryland restoration efforts frequently fail because we lack the understanding and ability to manage the processes driving restoration outcomes (Menz, Dixon, & Hobbs, 2013). Such understanding is needed for moving restoration towards a predictive science, allowing managers to better decide how to deploy limited resources and guiding development of new restoration tools that ameliorate ecological barriers to dryland restoration (Brudvig et al., 2017; Davies, Boyd, Madsen, Kerby, & Hulet, 2018; Perring et al., 2015).

Understanding processes driving outcomes of seed-based restoration is among the greatest challenges facing dryland restoration (Kildisheva, Erickson, Merritt, & Dixon, 2016). Multiple biotic and abiotic stressors influence seed and seedling survival, and the importance of these stressors changes as plants transition through life stages (Fenner & Thompson, 2005). We know plant establishment in dryland restoration is often greater at higher elevation sites with lower heat load and at sites with greater mean annual precipitation, and that establishment can vary greatly within sites among years (Hardegree, Jones, Roundy, Shaw, & Monaco, 2016; Knutson et al., 2014). However, we have little understanding of the specific environmental conditions that drive this observed variation in restoration outcomes. Most seeded species mortality in restoration occurs during early life stage transitions and aggregate measures of environmental conditions may not reflect the specific environmental drivers of seedling mortality (James, Svejcar, & Rinella, 2011; Leger & Goergen, 2017). To forecast conditions favouring seedling survival and design strategies that buffer against unfavourable environmental conditions, we need to understand effects of environmental variation at time-scales in which seed and seedling mortality occurs.

The Great Basin floristic province of the western United States represents a major dryland system where environmental conditions greatly limit seed-based restoration. This 50 million-ha province was historically dominated by perennial species but is now extensively invaded by non-native annual species such as cheatgrass (*Bromus tectorum* L.). These invasive plants have drastically increased the size and frequency of catastrophic fire, altered ecosystem functions and eliminated habitat for a number of threatened species (Pyke, 2003). Almost 60% of this land is federally owned and more than 100,000 ha is typically sown each year following fire in an attempt to stabilize soils and restore native perennial communities (Pilliod, Welty, & Toevs, 2017). Unfortunately, the majority of these seeding efforts fail (Knutson et al., 2014). While year to year variation in environmental conditions is known to influence seedling establishment (Hardegree, Jones, et al., 2016), short-term variation in environmental conditions immediately following seeding may also influence seeding recruitment in the Great Basin. Simulations of daily seedbed microenvironmental conditions, for example, show that the probability and duration of drought and freezing temperatures following seeding vary significantly among years (Hardegree, Sheley, et al., 2016) and altering seeding timing by as little as 4 weeks has resulted in a threefold change in seedling recruitment (Boyd & James, 2013). Neither earlier nor later seeding consistently increases recruitment. Instead, the effects of seeding timing on recruitment appear to depend on how seeding timing alters exposure of seeds and seedlings to abiotic stress (Hardegree, Sheley, et al., 2016). To further improve our ability to forecast and manage seed-based restoration outcomes, we need to understand how environmental conditions across multiple time-scales and plant life stages drive seedling recruitment.

Here, we asked how variation in a suite of key environmental predictors influenced germination, emergence, seedling establishment and juvenile survival of four commonly sown perennial grass species across 33 seeding experiments distributed over an ~160,000-km^2 area of the Great Basin. We identified environmental predictors expected to be strong drivers of survival probability across different life stages in this system based on the literature (Table 1). We hypothesized that germination and emergence would be greater under warmer and wetter conditions as this would lower seed and seedling exposure to drought and freezing stress and allow more rapid plant growth when soil water

TABLE 1 Predictors and predictor values (mean ± *SD*) hypothesized to affect plant life stage transition probabilities

Predictors	Predictor values	Life stage transition
Total precipitation (mm) within 30 days after germination initiation	23 ± 12	Germination, emergence
Mean soil temperature (°C) within 30 days after germination initiation	3.0 ± 2.2	Germination, emergence
Total precipitation (mm) from February to June of first growing season	86 ± 33	Establishment
Cheatgrass density (plants/m^2) in April of first growing season	116 ± 137	Establishment
CWD (mm) in first water year	693 ± 165	Establishment, juvenile survival
Sand (%)	52 ± 18	Establishment, juvenile survival
Total precipitation (mm) from February to June of second growing season	71 ± 42	Juvenile survival
CWD (mm) in second water year (mm)	676 ± 157	Juvenile survival

Note: Precipitation and soil temperature were measured on-site with sensors while cumulative annual climatic water deficit, CWD, was calculated following (Dilts et al., 2015)

availability is high (Aguirre & Johnson, 1991; Brabec, Germino, & Richardson, 2017). We hypothesized that seedling establishment and juvenile survival would be greater under higher spring precipitation and lower cumulative annual climatic water deficit (CWD, a representation of drought stress experienced by plants, Dilts, Weisberg, Dencker, & Chambers, 2015) as wetter conditions should reduce drought stress during the spring growing season and also reduce drought stress during the dry season (Hardegree, Jones, et al., 2016). We also hypothesized that seedling emergence and establishment would be greater in locations with finer textured soils and lower cheatgrass densities because of greater soil water retention and reduced competition for soil water (Brabec et al., 2017; Melgoza, Nowak, & Tausch, 1990).

2 | MATERIALS AND METHODS

2.1 | Study sites and species

To examine how plant life stage transitions are influenced by a suite of environmental conditions, we established a distributed network of 16 sites seeded in multiple years over an approximately 160,000 km^2 area of the Great Basin (Figure 1; Table S1). All sites historically supported Wyoming big sagebrush plant communities with diverse mixtures of native perennial grasses, forbs and shrubs, but wildfires fuelled by the invasive annual grass *B. tectorum* have eliminated most of the native plant community (Figure S1). These conditions represent a typical restoration situation in the Great Basin. Sites were stratified along gradients of mean annual precipitation (162–316 mm), elevation (826–1,451 m) and soil texture (Tables S1 and S2).

2.2 | Experimental approach

Fifteen sites were sown in 2012 and 2013 while one site (Riley, Table S1), which served as a pilot for this experimental approach,

was sown in 2006, 2007, 2008. Collectively, this distributed network of sites and years provided 33 seeding experiments. At all sites except Riley, we established 32 10 × 10-m plots separated by 4-m buffers. Plots were randomly assigned to one of four species and one of two seeding years (2012 or 2013) in a completely randomized design and each treatment was replicated four times (4 species × 2 seedings years × 4 replications = 32 plots per site). The four perennial grass species were the native perennial bunchgrasses *Elymus elymoides* (Raf.) Swezey var. Toe Jam Creek, *Poa secunda* J. Presl var. Mountain Home, *Pseudoroegneria spicata* (Pursh) A. Löve, var. Anatone and the non-native perennial bunchgrass, *Agropyron desertorum* (Fisch. ex Link) Schult var. Hycrest. The spring prior to seeding, we sprayed glyphosate to reduce *B. tectorum* abundance, and in late September plots were tilled. Between 21 October and 28 November, plots were broadcast seeded (600 pure live seed/m^2 mixed with rice hulls) and packed with a roller to improve soil–seed contact. The aim of this approach was to create an optimal planting depth and uniform seedbed, so we could examine direct effects of the environment on recruitment independent of variation in seedbed preparation or planting depth. Seedling establishment with this planting method is comparable to establishment achieved with commonly used seed drills (James & Svejcar, 2010). At Riley, we used the same seeding approach, but did not include *P. secunda* and plots were smaller (0.5 × 2 m).

2.3 | Weather and climate predictors

At each site, weather stations (Onset, Bourne, USA) and soil water and temperature probes (three per site at 5 cm soil depth) were used to quantify precipitation, soil temperature and soil moisture. We used daily soil moisture and temperature data to model accumulation of hydrothermal time (Hardegree et al., 2013; Hardegree, Sheley, et al., 2016), allowing us to determine when germination was
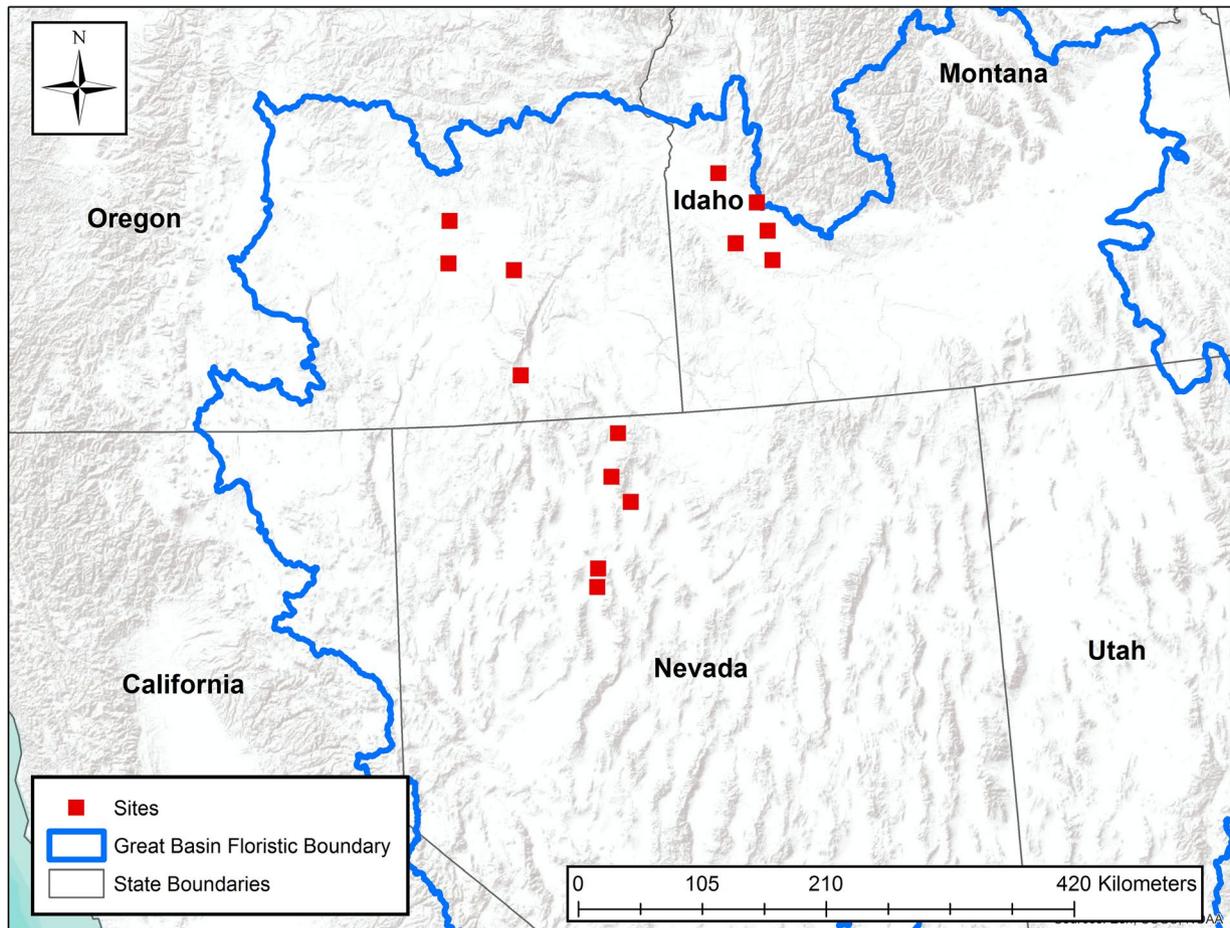
FIGURE 1 Location of study sites. Table S1 provides coordinates and site characteristics

likely to occur at each site and year. Cumulative CWD for each site and water year (1 October to 30 September) was calculated using the Climatic Water Deficit Toolbox for ArcGIS (Dilts et al., 2015). Gridded environmental data for CWD calculations were derived from PRISM data (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 8 Oct 2018). While monthly PRISM precipitation data correlated with monthly precipitation we measured on site (R^2 = .76, see supplementary material), PRISM data is derived at a coarser scale, thus the measures of CWD should be considered a relative index of drought stress at a site. Soils data were derived from the United States Department of Agriculture SSURGO soils database (https://websoilsurvey.nrcs.usda.gov, created 8 Oct 2018).

2.4 | Seed and seedling sampling

We quantified four key demographic transitions that drive variation in plant recruitment in seed-based restoration efforts in these and other dryland systems (James et al., 2011; Lewandrowski, Erickson, Dixon, & Stevens, 2017). These transitions were germination (transition between a sown seed and a seed with a radical), seedling emergence (transition between a seed with a radical and emergence of the coleoptile from the soil surface), seedling establishment (transition

between an emerged seedling and a seedling that persists through the end of the first growing season) and survival of juvenile seedlings (in this system, we considered this to include the transition between an established seedling at the end of the first growing season to a seedling that survives to the end of the second growing season).

We estimated germination by placing 50 viable seeds mixed with field soil in nylon meshed bags (15 × 10 cm) and burying the bags in the 0–5 cm soil layer adjacent to each plot for each species at each site (Abbott & Roundy, 2003). Bags were buried the same day plots were seeded, and germinated, dead and dormant seeds were counted the following spring. To make these determinations, we followed the methods used in James et al. (2011). Briefly, seed bags were transported to a lab where seeds were separated from soil using a fine mesh screen and water. Seeds were visually inspected under a dissecting microscope and scored as either germinated or not germinated. Seeds that were not germinated seeds were plated on petri dishes with wet filtered paper and incubated at 20°C for 21 days. During this period, seeds that germinated were counted and removed and scored as dormant. We performed a cut test on seeds that did not germinate and used a dissecting microscope to inspect the endosperm to confirm if remaining seeds were dead.

Emergence probability was determined by counting the number of plants that emerged in the seeded plots between February

and June of the first seeding year. To do this, we placed a 0.5 × 2-m permanent transect in each plot and censused these plots every 3 weeks, marking newly emerged plants with a toothpick and relocating previously marked plants to determine if the previously emerged seedlings were alive or dead. Previous work where we sampled plots on a weekly basis (James et al., 2011) showed that in many cases even when seedlings die, their stems can persist for several weeks before desiccating and blowing off the plots, giving us opportunity to observe seedling emergence and mortality over a coarser time-scale. However, it is possible that some seedlings emerged then died very quickly (shorter than our sample return interval) meaning that we may under count the number of seedlings that emerged. For the Riley site, the entire plot was sampled. Seedlings that survived until June were considered established. Plants were recounted the end of the second growing season to determine the number of juvenile plants. *Bromus tectorum* density was quantified at the end of the first seeding year by counting individuals within the transects.

2.5 | Statistical approach

We used a Bayesian probit model to estimate conditional probabilities of germination, emergence, seedling establishment and juvenile survival (Albert & Chib, 1993). Each model included fixed effects for species, seeding year and seeding year × species and random effects for site, site × seeding year, site × seeding year × species and plot. Priors on fixed effect parameters were uniform with support on the whole real line, and priors on random effects parameters were normal with mean 0, standard deviation τ. The prior on each τ was uniform over the positive real line.

Additional fixed effects were included for environmental predictors (Table 1). We used posterior predictive p-values to identify significant ($p < .05$) predictors (Gelman et al., 2014). These p-values were

defined as $\min \left(\Pr \left(\text{cor} \left(x, y^* \right) \leq \text{cor} \left(x, y \right) \right), \Pr \left(\text{cor} \left(x, y^* \right) \geq \text{cor} \left(x, y \right) \right) \right)$ where $\min$ and cor are minimum and correlation functions, x is a candidate predictor, y is the observed plant counts and $y^{*,s}$ is one of $s = 1, \ldots, S$ vectors of posterior predictive plant counts simulated from the posterior distribution. The $y^{*,s}$ was simulated with all environmental predictors excluded from the model. The p-values test the null hypothesis of zero correlation between predictors and plant counts, and predictors were included in the model when this hypothesis was rejected. To test for species by environmental predictor interactions, significant environmental predictor main effects were included in the model and the same p-value formula was used, except a multiple comparisons adjustment was implemented to maintain an overall p-value of .05 for each species. The MCMC algorithm needed to fit the models was constructed in Fortran (Intel Corporation, 2013).

The above analysis focused on a limited number of covariates that our ecological knowledge of dryland systems led us to believe would be important for seedling establishment. When this approach fails to reveal strong climate effects, it is logical to ask if a more exhaustive model selection process would identify climate correlates of survival. To address this question, when our initial approach based on a priori hypotheses failed to find significant covariates, we also searched for relationships between survival and two additional climate correlates (daily precipitation and daily soil water content in the top 5 cm of soils) using the 'climwin' R package (Bailey & van de Pol, 2016). The climwin approach aggregates a selected climate covariate over all possible 'climate windows' and then uses AIC to select the best model. Additional description of this method is included in the supplementary information. Because of the multiple comparisons contained in this exhaustive model selection process, this second analysis is best viewed as a hypothesis-generating exercise, rather than a test of an a priori hypothesis.

FIGURE 2 Point estimates (points) and 95% confidence intervals (bars) estimating life stage transition probabilities averaged across species at 16 study sites in two seeding years (white points, 2012; black points, 2013). An exception is Riley (RI), which was seeded 2006 (white points), 2007 (black points) and 2008 (grey points). Dashed lines represent mean values. The emergence panel shows probabilities germinated seed emerged, the establishment panel shows probabilities emerged seedlings established the first growing season and the juvenile panel shows probabilities established seedlings survived through the second growing season
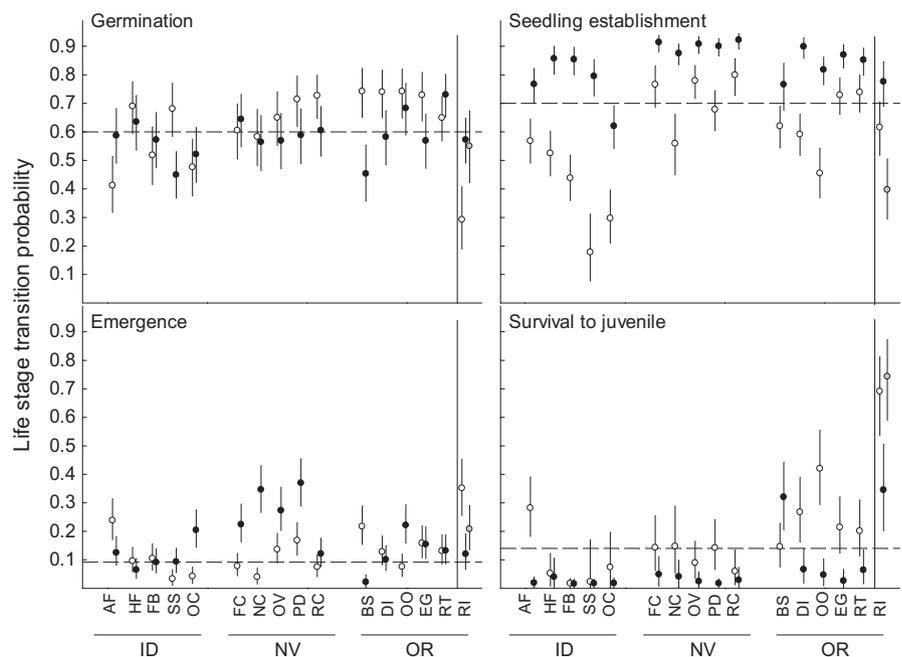
3 | RESULTS

3.1 | Experiment-wide life stage transition probabilities

Averaged across species, transition probabilities varied widely among the four life stages (Figure 2). In general, the probability that seeds germinated was relatively high (0.6 ± 0.1, mean ± SD), but the probability that germinated seeds emerged was low (0.15 ± 0.09). Once emerged, seedlings had a relatively high probability of surviving to establishment the first growing season (0.70 ± 0.17), but established seedlings had a low probability of surviving to the juvenile stage the second growing season (0.14 ± 0.18).

While the four study species showed relatively similar patterns of survival across the four life stages (Figure 3), the introduced grass *A. desertorum* had higher probabilities of germination, emergence and juvenile survival than the three native grasses. Consequently, 2 years after seeding, *A. desertorum* density averaged 9.0 ± 10.3 plants/m² while native plant density averaged 3.4 ± 3.2 plants/m² (mean ± SD; Table S3). Overall, there were only modest differences in survival across the three native species, but *E. elymoides* had a lower germination probability than the other two native species.

3.2 | Variation in environmental conditions

Environmental predictors varied widely among sites and years (Table 1). Overall, the study years occurred during periods of below average to average precipitation. Growing season (October to June) precipitation following seeding ranged from 106 to 322 mm across experiments (48%–117% of the long-term average, Table S2) and included large differences in precipitation timing (Figure 4a) with spring precipitation ranging from 28 to 190 mm (Figure S2). Soil
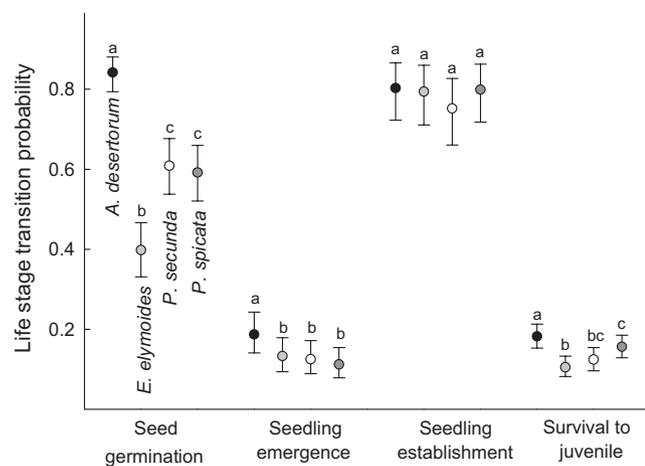
temperatures the first 30 days following predicted germination also varied widely (Figure 4b), ranging from −0.98 to 6.8°C across experiments (Figure S2, histogram distribution of temperatures). Variation in drought stress was substantial, ranging from CWD of 359 mm in higher elevation sites in eastern Oregon to 989 mm in lower elevation sites in southwestern Idaho. Cheatgrass density the first growing season following seeding ranged from 5 to 409 plants/m² (Table S3).

3.3 | Environmental predictors of survival

Environmental predictors were correlated with germination, emergence and juvenile survival probabilities, but not seedling establishment probability (Figure 5). The effects of these predictors did not
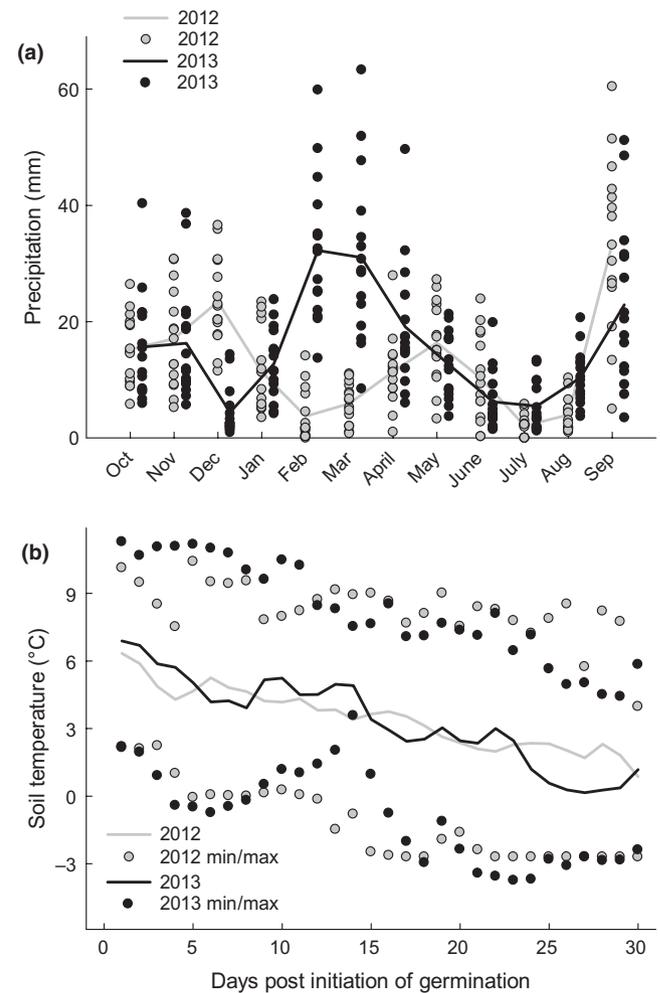
FIGURE 4 Environmental data from sites of seeding experiments. (a) Lines depict monthly precipitation averaged across 15 sites sown in 2012 and 2013. Individual symbols depict monthly values for individual sites and years. (b) Lines depict average soil temperatures across the 15 sites at the 5-cm soil depth for the first 30 days post initiation of germination. Points show minimum and maximum values for each combination of sites and seeding year. For clarity, we do not show values for the Riley site which was sown in different years, but Riley site values fell within the range of values shown here
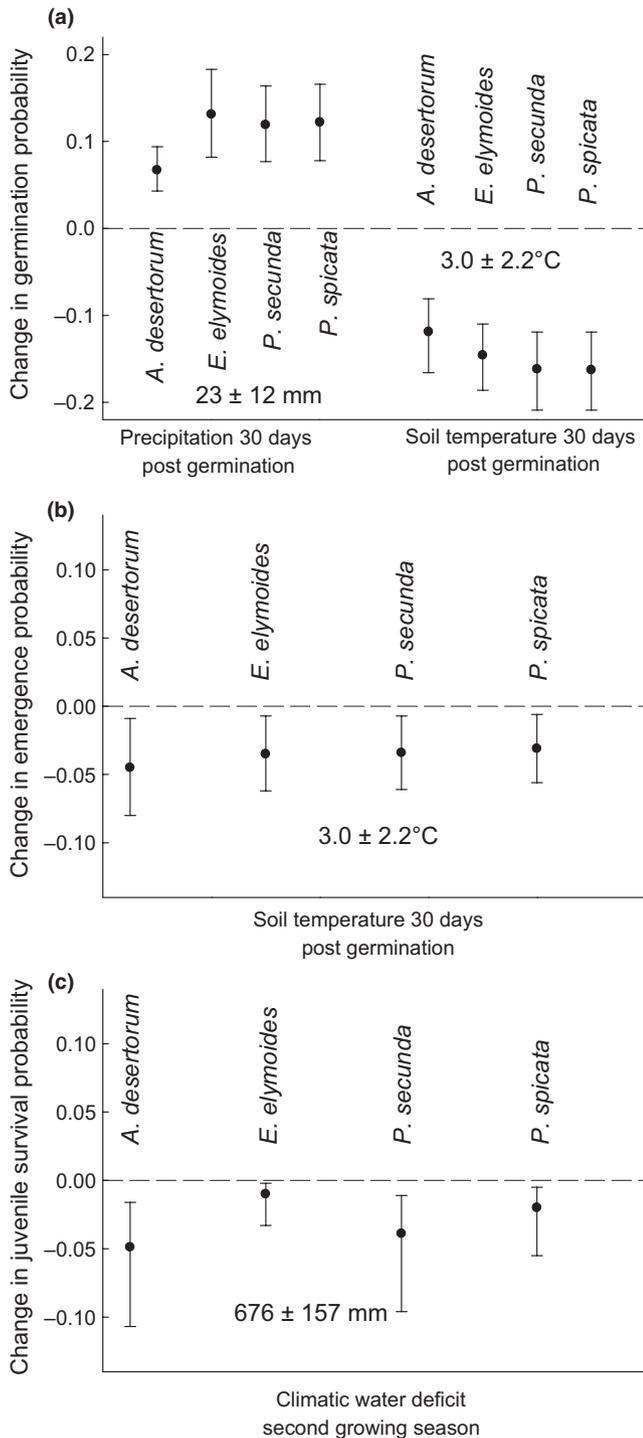
FIGURE 3 Point estimates (points) and 95% confidence intervals (bars) estimating probabilities that planted seeds germinated, probabilities germinated seed emerged, probabilities emerged seedlings established and probabilities established seedlings survived through the second growing season. The estimates are averaged over sites and seeding years, and values with different letters within each life stage are significantly different (*p* < .05)

FIGURE 5 Point estimates (points) and 95% confidence intervals (bars) estimating (a) probabilities seeds germinated, (b) probabilities germinated seeds emerged (c) and probabilities established seedlings survived to become juvenile plants. The x-axis shows the predictor that significantly influenced survival at each life stage. The y-axis shows the effects of elevating the predictors from their mean value to one standard deviation above their mean value. Points greater than zero indicate that increasing the predictor one standard deviation increased survival while points less than zero indicate increasing the predictor one standard deviation decreased survival

differ across species ($p > .05$). Germination probabilities increased when precipitation was relatively high the first 30 days after germination was predicted to begin, but germination probabilities decreased as soil temperature increased over this time period ($p < .01$, Figure 5a). High soil temperature during this period also was associated with reduced emergence probabilities of germinated seeds ($p < .001$, Figure 5b). Establishment probabilities of emerged seedlings were not significantly affected by our a priori environmental predictors (CWD during the water year ($p = .07$); spring precipitation ($p = .36$); sand ($p = .29$); cheatgrass density ($p = .24$)). High CWD the second water year was associated with reduced survival of established seedlings to the juvenile stage ($p<.001$, Figure 5c).

Because our a priori approach failed to detect a relationship between environmental predictors and seedling survival the first growing season, we used climwin to search for other environmental windows that might influence seedling survival over this time period (see supplementary material). Our search for relationships between seedling establishment probabilities and climate correlates using climwin produced different results depending on the baseline model used. If we did not account for the non-independence of observations from the same year, climwin identified a strong positive relationship between mean soil water and precipitation between 20 and 5 weeks before the 1-year survival census was measured. However, if we accounted for the non-independence of observations from the same year these relationships became weaker and were consistent with the results of our a priori analysis suggesting influence of climate on first-year survival is weak and hard to detect.

The environmental predictors accounted for a considerable amount of observed variation in germination and emergence but little of the observed variation in juvenile survival (Figure 6a–c). No predictors were associated with variation in seedling establishment. Collectively, the environmental predictors that were significantly associated with variation in different demographic transitions explained little of the variation in cumulative survival 2 years following seeding ($R^2 = .01$, $p = .496$, Figure 6d).

4 | DISCUSSION

Identifying the factors that limit plant establishment across multiple life-history stages is an important step towards understating how restoration resources can be deployed efficiently and where the development of new tools and strategies could produce the largest improvements in restoration outcomes. By using a common experimental design across a distributed network of restoration sites, we observed that variation in precipitation and soil temperature at time-scales of weeks was associated with large variation in germination and emergence probabilities across the four most widely seeded grass species in our system. As hypothesized, higher precipitation following seeding was associated with higher germination (Figure 5). Contrary to our hypothesis, however, higher soil temperatures in the weeks following seeding were associated with lower germination and emergence and accounted
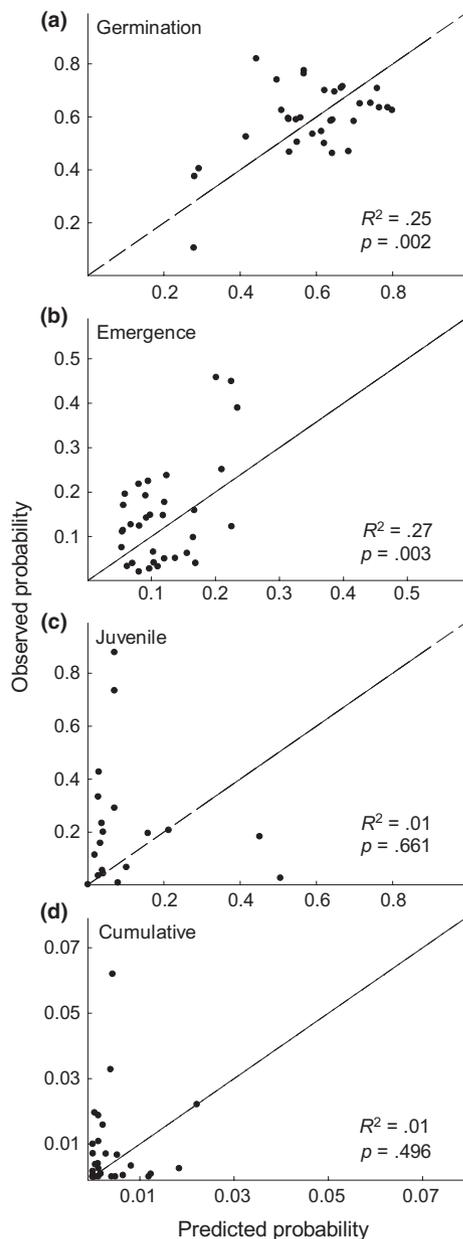
FIGURE 6 Predicted and observed (a) probabilities seeds germinated, (b) probabilities germinated seed emerged, (c) probabilities established seedlings survived through the second growing season and (d) probabilities seeds became plants and survived through the second growing season. Only *Pseudoroegneria spicata* plots are presented, because plots of other species reveal similar prediction accuracy. Within a panel, each point represents a combination of site and seeding year

for a substantial portion of the variation in germination and emergence probabilities that we observed across our 33 site-years (Figure 6). More specifically, a one standard deviation increase in temperature (2.2°C, Table 1) was associated with a 30% reduction in emergence probability (Figure 5). To our knowledge, this is the first time that variation in temperature within such a short timeframe (i.e. 30 days) has been linked to grass seedling survival in cold desert systems. The influence of small changes in soil temperatures on restoration outcomes has clear implications for

understanding how climate warming may affect perennial grass recruitment in these cold desert systems.

While seedling recruitment in dryland systems is logically assumed to be limited by precipitation (e.g. Schwinning & Kelly, 2013), within the range of precipitation variation observed in this study, and contrary to our hypotheses, we were unable to detect a significant relationship between seedling survival the first growing season and either cumulative precipitation, growing season precipitation or CWD in the first year following seeding. This was surprising since seedling survival the first growing season showed the highest average survival probability and this transition also had the highest variation in survival (seedling establishment transition, Figure 2). The climwin analysis that compared two baseline models (one with year as a random effect and the other that did not include this effect) suggested that because weather conditions at our many sites were strongly correlated within years, we had little statistical power to detect environment–demography relationships. This kind of data-driven approach would require a substantially greater number of independent observations (i.e. years; Teller, Adler, Edwards, Hooker, & Ellner, 2016). Despite these correlations among weather conditions at sites, we were able to detect a relationship between water limitations and seedling survival over the second growing season, with juvenile survival decreasing as CWD during the second growing season increased (Figure 6). While the relationship between water limitations and seedling survival was surprisingly weak, our experimental approach did allow us to identify an important role of temperature in limiting seedling recruitment. In fact, temperature appeared to have a direct effect on seed germination and emergence as well as an indirect effect on seedling survival by increasing evaporative demand of water and imposing greater soil water limitations on seedlings during the second growing season.

The importance of temperature in driving plant community dynamics in cold desert systems is becoming increasingly recognized. For example, the cover of sagebrush (*Artemisia tridentata*), the dominant shrub in these systems, is substantially more sensitive to changes in temperature than changes in precipitation (Renwick et al., 2018). Another recent study found that the probability of sagebrush occurrence following seeding was negatively associated with temperature: cooler temperatures lead to more precipitation delivered as snow, lower rates of evapotranspiration in spring and a higher probability of sagebrush occurrence (Shriver et al., 2018). While warmer soil temperatures in winter have often been viewed as favouring seedling growth by allowing seedling development during periods when water is available (Aguirre & Johnson, 1991) and the potential for freezing of germinated seeds and seedings is minimal (Brabec et al., 2017), our results suggest that warm soil temperatures in winter reduce seedling recruitment. It is possible that early germination in fall poses a risk to plants if germination is followed by long periods of dry or freezing conditions. Previous work manipulating snowpack showed that grass survival during the germination stage is negatively impacted by freezing (Gornish et al., 2015). Given the high mortality that occurs following germination, future work that mechanistically examines how fluctuations in soil moisture and

temperature over this short time period affect survival would be a productive next step.

Our hypothesis that fine-textured soils and low cheatgrass densities would increase survival was not supported, as these predictors were never significant for any life stage transition. There may be several reasons for these findings. Even though our seeding experiments included a wide and representative range in soil texture, we may not have enough seeding years to detect how precipitation timing and amount and soil texture influence soil water availability and survival. For cheatgrass, it could be that the effects of cheatgrass density on survival are relatively unimportant compared to abiotic factors in driving variation in seedling survival (Mangla, Sheley, James, & Radosevich, 2011). Alternatively, cheatgrass competitive effects could scale with biomass and not density. Additionally, sites that supported greater cheatgrass density may also have provided conditions more favourable for perennial grass establishment, making it difficult to detect the negative effects of cheatgrass on native seedling survival. A logical next step would be to evaluate these factors under controlled conditions in the glasshouse by growing seedlings at different combinations of soil temperatures and soil texture combinations that represent the conditions observed across our sites.

Taken together, the variation in the predictors that were significantly associated with variation in life stage transition probabilities (Figure 5, precipitation 30 days post germination, soil temperature 30 days post germination, CWD second growing season) accounted for little of the variation observed in cumulative survival of seedlings 2 years following seeding (Figure 6d). Given the many of combinations of predictor values likely associated with survival variation, including abiotic variables such as frost heaving or biotic variables such as animal predation that were not measured in this study, it is not surprising that a single predictor or subset of predictors would explain only a small portion of variation in cumulative seedling survival (Young et al., 2019). While our results suggest that we have far to go in predicting restoration outcomes, and that variation in these outcomes are unlikely to be associated with simple aggregate measures of environmental variation, we can use results from this and similar studies to inform the type of research framework necessary to move restoration towards a predictive science. Namely, our results suggest a need for an integrative research approach that combines field experiments conducted in multiple years, process-based models and measurements of phenological, physiological and morphological traits that drive variation in seedling survival (e.g. Schlaepfer, Lauenroth, & Bradford, 2014). The statistical models used here and in previous studies are useful for narrowing the scope of integrative approaches and deciding how to allocate effort. For example, results from our study show grass seed germination was uniformly high across almost all sites, years and species while emergence was uniformly low and significantly affected by temperature. This suggests future work should spend less effort modelling and measuring germination and more effort determining how daily sequences of temperature and soil moisture the weeks following germination influence seedling

emergence. Similarly, we were unsuccessful at predicting survival between the first and second growing season, which identifies this as an important area of future work. While such a detailed approach will require substantial investment, it is likely the next necessary step towards developing accurate predictions of restoration outcomes.

5 | CONCLUSIONS

Previous research in these cold desert systems has found a positive relationship between annual precipitation and grass establishment when mean annual precipitation ranges between 200 and 400 mm (Knutson et al., 2014), and some work indicates perennial grass seedlings often fail to persist at sites with less than 310 mm of annual precipitation (Robins et al., 2013). Management recommendations derived from this work suggest restoration resources are best allocated to high elevation/precipitation sites and years with extremely favourable rainfall. While these recommendations are logical, in many situations managers are faced with seeding into suboptimal conditions for several reasons, including the urgent need to increase biodiversity in low elevation systems, uncertainty in planting year weather, or because funding for restoration is only available for a certain time period (Hardegree, Jones, et al., 2016). Our study shows that there is substantial variation in seedling survival under the stressful warm/dry conditions managers routinely face (Duniway et al., 2015). Namely, in our study, annual precipitation did not exceed 300 mm per year in any of our experiments, and 20 of the 33 site-years received less than 200 mm. Despite these dry conditions, more than 2 years following seeding, 40% of our sites maintained five native plants/m^2 or more, a common density benchmark used to gauge restoration success (Boyd & Davies, 2012). This is an encouraging sign there are viable pathways to restoring biodiversity at more xeric sites, though future work will be needed to identify the conditions that allow establishment.

Finally, we found that warmer temperatures can negatively affect grass seedling recruitment. This new insight should be immediately useful for management in two critical ways. First, the ability to accurately predict weather conditions in the range of weeks to months is rapidly increasing, particularly for temperature (Hardegree et al., 2018). While this forecasting may become more challenging with climate change, managers may be able to use these forecasts to make decisions about timing of seeding. Second, climate change models predict increased temperature in the Great Basin around 2°C over the next several decades, particularly in winter (Snyder et al., 2019), which is when we observed warmer temperatures having a negative effect on seedling germination and emergence. Our model suggests that a 2°C temperature increase will reduce germination and emergence about 30% and negatively affect seedling survival by increasing CWD. While multiple factors will influence how temperature increases associated with climate change will affect restoration, the relatively high sensitivity that these recruitment processes show that temperature deserves to be considered in current and future

planning, including the timing and location of seeding efforts, functional trait variation among seed source populations and the use of seed coating technologies that could diversify germination timing within seeded populations.

AUTHORS' CONTRIBUTIONS

J.J.J., E.A.L., P.B.A., R.L.S. and S.P.H. conceived the ideas and secured research funding; J.J.J., E.S.G., P.B.A., R.L.S. and S.P.H. designed the methodology and implemented the field experiment and collected data; M.J.R. and P.B.A. analysed the data and advanced the conceptual framework of the study and interpretation of results. J.J.J. led the writing of the manuscript and all authors contributed critically to the development of ideas, writing of the manuscript and gave approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.fb01pj3 (James et al., 2019).

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