



RESEARCH ARTICLE



# Management and environmental factors associated with simulated restoration seeding barriers in sagebrush steppe

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Adverse weather conditions, particularly freezing or drought, are often associated with poor seedling establishment following restoration seeding in drylands like the Great Basin sagebrush steppe (U.S.A.). Management decisions such as planting date or seed source could improve restoration outcomes by reducing seedling exposure to weather barriers. We simulated the effects of management and environmental factors on seedling exposure to post-germination barriers for bottlebrush squirreltail (*Elymus elymoides*), Sandberg bluegrass (*Poa secunda*), and bluebunch wheatgrass (*Pseudoroegneria spicata*). We combined germination timing models with daily soil moisture and temperature estimates to calculate yearly germination favorability and post-germination freezing and drought barriers for three planting dates (15 October, 15 November, and 15 March) and three seed sources or cultivars per species for 5,000 sites in each of 40 years (water years 1980–2019). We tested the effects of site environmental variables (elevation, mean annual precipitation, heat load, and clay content) and management choices (seed source and planting date) on germination favorability and barrier occurrence (mean and variability (coefficient of variation)). Seedling exposure to barriers was strongly linked to management decisions in addition to site mean precipitation and elevation. Later fall plantings and seed sources with slower germination (lower mean germination favorability) were less likely to encounter freezing and drought barriers. These results suggest that management actions can play a role comparable to site environmental variables in reducing exposure of vulnerable seedlings to adverse weather conditions and subsequent effects on restoration outcomes.

**Key words:** drought, freeze, Great Basin, perennial grass, weather

## Implications for Practice

- Dryland restoration seeding success is affected by weather impacts on seedling survival, but the general impacts are hard to quantify with limited sites and/or years in experiments and observational studies. However, a simulation approach can describe the range of seedling mortality patterns associated with management decisions, macroclimate, and soils.
- Our results suggest that the effects of management decisions, like seed sources and planting date, on Great Basin seeding outcomes are comparable to the effects of site abiotic variables, because these decisions affect germination timing relative to seedling exposure to adverse weather.
- ASI Jointly considering germination behavior, seeding timing, and other management decisions on weather-induced seedling mortality could reduce variability and enhance success in dryland restoration seedings.

## Introduction

Post-fire seeding is a primary restoration method for preventing conversion of native-dominated perennial shrub steppe to non-native annual grassland in the Great Basin, a cold desert in the

western United States (Svejcar et al. 2017; Mahood & Balch 2019). Successful establishment of perennial grasses is particularly important in this system due to their ability to compete with invasive annual grasses (Davies et al. 2012; Bansal & Sheley 2016). However, poor outcomes with restoration seeding in the region are common (Knutson et al. 2014; Shriver et al. 2019) and are associated with variable and adverse weather conditions, such as extreme dry or cold periods that

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affect small seedlings post-germination but prior to seedling emergence (James et al. 2011; James et al. 2019; Larson et al. 2021). The prevalence and variability of weather-related barriers to seedling establishment are not well characterized in the Great Basin, despite their likely influence on long-term restoration outcomes (Bradford et al. 2018; Hagger et al. 2018; Hardegee et al. 2018a). Describing the distribution of restoration barriers across space and time is a key step in selecting, developing, and improving restoration practices at large spatial scales (Madsen et al. 2016; Havrilla et al. 2020; Shaw et al. 2020).

High spatiotemporal variability in environmental conditions and associated restoration outcomes is typical of the Great Basin and similar dryland regions. Weather during the early establishment phase is strongly linked to long-term restoration outcomes in many systems (Copeland et al. 2019; Groves et al. 2020; Werner et al. 2020). In the Great Basin, dry or freezing conditions in upper soil layers can cause high mortality for seedlings between germination and emergence (Boyd & Lemos 2013; Gornish et al. 2015; James et al. 2019). However, the effects of weather conditions on mortality can be highly complex, dynamic, and sensitive to the length and severity of dry or freezing periods (Boyd & Lemos 2013; Roundy & Madsen 2016; Pyle et al. 2021). In contrast to weather, the general macroclimate and the effects of the site environment have a more consistent influence on restoration outcomes. For example, restoration success varies with elevation (Knutson et al. 2014; Germino et al. 2018), topography (e.g. slope and aspect, Boehm et al. 2021), and soil properties (Barnard et al. 2019; Davidson et al. 2019).

Restoration outcomes are also strongly influenced by management decisions in addition to weather and site environmental variables. For example, seeding methods and timing (Shaw et al. 2020) can determine whether or not seedlings encounter adverse or favorable weather conditions during vulnerable early life stages (Boyd & James 2013; Boyd & Lemos 2015; Hardegee et al. 2020). The selection of species as well as seed source or cultivar within species (Larson et al. 2015; Baughman et al. 2019; Leger et al. 2019) is another key management decision that can influence restoration outcomes across environmental conditions. In particular, seed sources vary in performance traits such as germination response, growth rate, and drought or freezing tolerance (Baughman et al. 2019; Leger et al. 2019) and these differences can alter the impact of exposure to post-seeding establishment barriers.

Describing the risk of seedling exposure to adverse weather and associated restoration barriers as a function of historical weather variability across the Great Basin could suggest better practices for increasing restoration success in particular sites. However, little is known regarding the variability of restoration barriers across this region and their sensitivity to major management decisions regarding planting date, species, and source population or cultivar. For instance, slower germinating seed sources or later fall or winter planting dates could decrease exposure of small seedlings to freezing, and potential mortality, associated with fluctuating temperature and moisture conditions in the fall and early winter (Hardegee et al. 2020). Annual and seasonal variability in restoration barriers are also poorly described relative to spatial variation in abiotic factors like soils and microclimate. Here, we address this gap by simulating the spatiotemporal variability in germination favorability, an index

based on the accumulation of favorable seedbed conditions for germination, and characterizing freezing and drought barriers that occur during the vulnerable post-germination period. We examine the potential for altering this variability with management choices of planting date, species, and cultivars within a species to improve restoration outcomes. Finally, we describe the effects of average precipitation, elevation, soil texture, topographic heat load, and clay content on exposure and variability of potential restoration outcomes.

## Methods

### Locations

We randomly selected 5,000 locations per species within the Great Basin to predict germination rates with the following steps (Fig. 1). First, we identified the potential range for each species at a 500-m scale based on distribution models (Barga et al. unpublished data, methods in Barga et al. 2018). We defined presence locations (binary) from continuous predictions of occurrence probability maps using a threshold appropriate for distribution models based on presence-only data, the maximum sum of sensitivity and specificity (Max SSS, Liu et al. 2013; Liu et al. 2015). We constrained our sampling to the Great Basin region based on the Columbia Plateau, Snake River Plain, Western and Eastern Great Basin zones from LANDFIRE as well as shrubland and grassland potential vegetation types, to avoid riparian, woodland, urbanized, or cultivated agriculture areas (30 m resolution, LANDFIRE Environmental Site Potential layer, version 1.4.0, Wildland Fire Science 2016). We chose the LANDFIRE data as they have complete coverage across our large area. Selected locations were mostly in Inter-Mountain Basins Big Sagebrush Shrubland or Sagebrush Steppe vegetation types (Wildland Fire Science 2016). We also limited areas for point selection to less than 2,500 m in altitude, to avoid including high elevation areas (mountain tops) with distinct environmental characteristics and higher resilience to disturbance than lower elevation sagebrush steppe (Chambers et al. 2014). To match site locations with input weather data used in subsequent soil microclimate modeling, we randomly selected centroids from the weather data cells (1/24° resolution, gridMET, Abatzoglou 2013) within our previously screened areas.

### Soil Moisture and Temperature

We simulated daily soil moisture and temperature at 0–2 and 2–5 cm depths with SOILWAT2, an ecosystem water balance model, at each of the 15,000 study locations. SOILWAT2 is a process-based daily simulation model that represents the soil profile with multiple layers and includes surface cover and topography (R package rSOILWAT2 v4.0.0, Schlaepfer & Andrews 2019; Schlaepfer & Murphy 2019). The model represents evaporative demand with processes across soil layers including temperature, percolation and hydraulic redistribution, evaporation, transpiration, deep drainage, and snow dynamics (further details, Supplement S1). We used SOILWAT2 simulations to represent conditions at each study location following restoration seeding in bare soil.

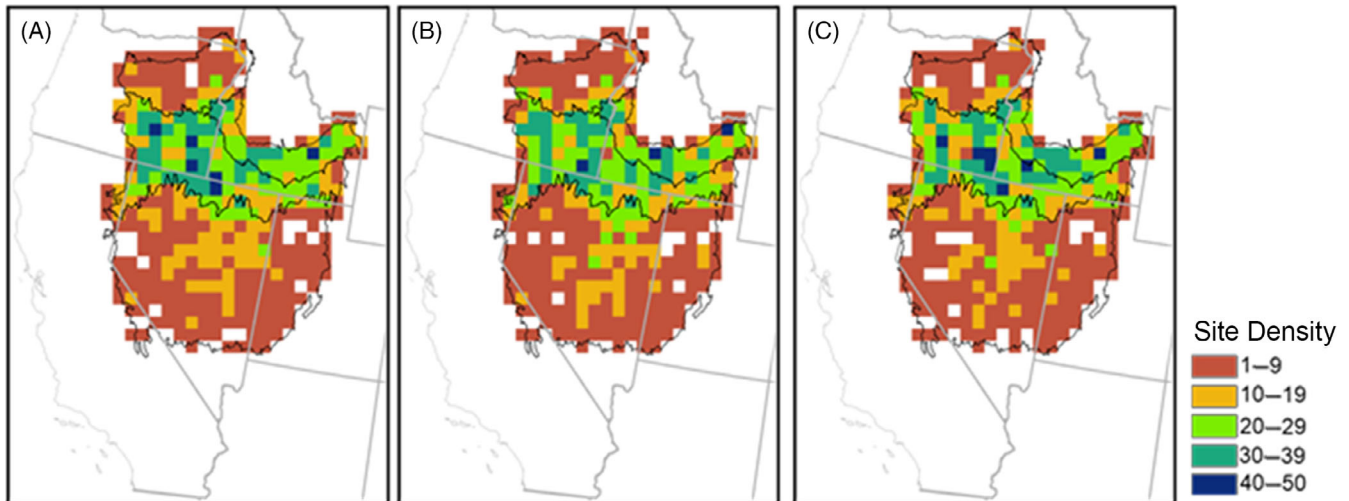


Figure 1. The density of sites (5,000 per species) per 1,600 km<sup>2</sup> (400 km grid) for each of the three species: (A) *Pseudoroegneria spicata*, (B) *Poa secunda*, and (C) *Elymus elymoides*. Outlined areas show the ecoregions that constrained the randomized points.

Simulations were based on bulk density and soil texture at 0–5, 5–15, 15–30, 30–60, 60–100, and 100–200 cm depths (30 m, POLARIS, Chaney et al. 2019) and daily precipitation and minimum and maximum air temperature (approximately 4 km, 1/24° resolution, gridMET, 1979–2019, Abatzoglou 2013). Soil properties at 2–5 and 5–10 cm depths were linearly interpolated from the above soil depth categories prior to simulation runs.

#### Species and Seed Sources

We simulated germination response of three native perennial bunchgrasses commonly seeded in large-scale restoration projects for this study: bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) Á. Löve, hereafter, “PSSP”; Sandberg bluegrass, *Poa secunda* J. Presl, hereafter, “POSE”; and bottlebrush squirreltail, *Elymus elymoides* (Raf.) Swezey, hereafter “ELEL”. We used both cultivars and wild-collected sources with previously documented hydrothermal germination responses (see Supplement S2 for details, Hardegee et al. 2003; Jones et al. 2003; Hardegee et al. 2008; Hardegee et al. 2010; Larson et al. 2015; Larson et al. 2016). Cultivars and/or source populations were, for PSSP: “Anatone,” “T1561,” and “Whitmar”; for POSE: “Mountain Home,” “Opportunity,” and “Sherman”; and for ELEL: “Antelope Creek,” “Fish Creek,” and “Rattlesnake” (Supplement S2).

#### Wet-Thermal Germination Models

We predicted germination rates and timing using daily estimates of soil temperature and water potential and previously developed wet-thermal germination-response models (Hardegee et al. 2008; Hardegee et al. 2010; Larson et al. 2015; Larson et al. 2016; Hardegee et al. 2018b). Germination response to constant temperature was evaluated in programmable environmental chambers (described in Hardegee & Burgess 1995). Thirty-five seeds of each seedlot were germinated on cellulose dialysis membranes in germination cells (described in

Hardegee & Emmerich 1992). The cellulose membranes separated the seeds from an osmotic solution of polyethylene glycol (8000) with a concentration determined to yield a water potential of  $-0.033$  MPa (Hardegee & Emmerich 1990). Germination was defined as radicle extension of  $\geq 2$  mm. Germination evaluation occurred in the same germination environment, but the procedure varied slightly among seed source and species. Species/sources were evaluated with two replicate vials in each of three replicated thermal environments at 8, 12, and 18°C (Larson et al. 2015; Larson et al. 2016), except for the PSSP “Whitmar” cultivar (Hardegee et al. 2010), which was evaluated for three or four germination vials of each seedlot replicated in three different thermal chambers at 3° increments between 3 and 21°C.

Germination response models typically divide each seed population into subpopulations based on relative germination rate (Covell et al. 1986). The 25% subpopulation characterizes potential germination response of the more robust and faster-germinating seeds, whereas 50% is typically used to characterize median population response (Hardegee et al. 2013). Approximately 95% of the variation in the germination response of these species can be described by linear thermal response between base temperature and optimal temperature for germination, when above a threshold water potential of  $-1.5$  MPa (Hardegee et al. 2017; Hardegee et al. 2018b). As such, germination rate was estimated to be zero below the base temperature (where germination rate = 0), below a water potential of  $-1.5$  MPa, and for soil temperatures above 22.5°C (at 2–5 cm depth). Germination rate estimates from the linear models for each day after planting and before 1 June were added together to calculate cumulative rate sum, hereafter, “rate sum,” which represents daily progress toward germination (rate sum = 1) for that given subpopulation (based on relative germination rate) of seeds. For example, when the rate sum for the 25% subpopulation is estimated to equal 1, it means that the fastest 25% of the seed cohort will have germinated. The day on which germination was expected to occur is when the rate sum = 1 (Roundy & Biedenbender 1996). A rate

sum greater than 1 does not have direct biological meaning, as this would only occur after this subpopulation of seeds have germinated. However, rate sum values greater than 1 can be considered a general index of seedbed favorability for germination during any given time period (Hardegee et al. 2003; Hardegee et al. 2013; Hardegee et al. 2020).

### Germination and Potential Restoration Barriers

Soil moisture and temperature predictions were combined with germination models to predict germination favorability and potential post-germination restoration freezing and drought barriers separately for each site, species cultivar or source, and planting date (15 October, 15 November, 15 March) for each year (planting date—1 June) from 1979 to 2019. We estimated potential restoration barriers with timing from germination models for the 50% subpopulations (the median response, as opposed to the faster 25% subpopulations used for the rate sum calculation) for each species and source to target barriers most likely to impact a large proportion of germinating seeds. Barrier occurrence was evaluated after each discrete period where germination was predicted (rate sum = 1) within the same water year (planting date through 1 June). This allowed for multiple periods of simulated germination and subsequent barriers within each water year for a given planting date. Freezing barriers were defined as periods of  $\geq 1$  day with either less than  $0^{\circ}\text{C}$  or less than  $-5^{\circ}\text{C}$  soil temperatures at 2–5 cm depth for mild and severe categories, respectively. Drought barriers were defined as periods of  $\geq 7$  days at less than  $-1.5$  MPa soil water potential at 2–5 or 5–10 cm depths for mild and severe categories, respectively (see example in Fig. S1).

These freezing and drought barrier definitions are only representations of potential mortality conditions, as little information is available on the exact temperature and moisture values related to seedling mortality for these species and seed sources. However, one experiment showed that freezing periods of 2 days strongly decreased emergence of recently germinated PSSP, whereas older seedlings were more resistant to freezing stress (Boyd & Lemos 2013). Another study with PSSP showed that 4-day dry periods strongly limited recruitment in field conditions (Pyle et al. 2021). Our drought barriers assume that a prolonged period of less than  $-1.5$  MPa (wilting point) could lead to substantial mortality due to shallow rooting depths of young seedlings, as opposed to a pattern of gradual drying; however, the simulation does not account for the potential for older seedlings to resist drought with root depths into deeper soil layers (Hanslin et al. 2019).

We estimated how species and seed source affected the relative risk of encountering barriers, for the same plant date and site, with standardized anomalies. Standardized anomalies describe extremes relative to average conditions and their variability, in this calculation, the risk of encountering a barrier. Standardized anomalies were calculated by site, plant date, and germination barrier: year value for barrier – long-term (40-year) barrier mean/standard deviation (40 years) of barrier. Higher relative risk for encountering a particular barrier was defined as the proportion of years with standardized

anomalies greater than 1 and low risk as the proportion of years with standardized anomalies less than  $-1$ .

### Site Environmental Variables

We gathered elevation, solar radiation (heat load), precipitation, and soils data for each location to describe site environmental conditions. Elevation was based on a 30-m DEM (Digital Elevation Model, LANDFIRE 2020). We calculated topographic microclimate with heat load index (HLI), an estimate of solar radiation as a function of latitude, slope, aspect, and landscape position (“hli” function, R package spatialEco, McCune 2007; Evans 2020). We used the 30-year average annual precipitation to approximate the precipitation regime for each site (1981–2010, 800-m resolution, PRISM 2020). We described site near-surface soil texture with percent clay in the 0–5 cm soil layer (30-m resolution, POLARIS, Chaney et al. 2019).

### Analysis

For each site, plant date, species, and seed source (cultivars or collections), we calculated mean and CV (coefficient of variation) in germination favorability (rate sum), number of freezing barriers, and number of drought barriers. For each site, we also quantified five environmental variables: elevation, HLI, clay content, and 30-year average annual precipitation as well an interaction term between elevation and 30-year average annual precipitation. We assessed the relationship between environmental variables and mean and variability (CV) in germination favorability (rate sum) and barrier occurrence with a Bayesian estimation approach using generalized linear models (R package “rstanarm,” Goodrich et al. 2020). We checked environmental variables for collinearity prior to constructing models (Table S1). Because we were primarily interested in the general direction of the effects of the variables, as well as a similar suite of variables across all the models, we developed the full model and did not attempt to fit the best model among the variables (Tables S2 & S3; for model fit see Figs. S2–S4). Mean and CV across sites were regressed against environmental variables. In addition, we included source population and planting date as categorical, independent variables. As part of the rstanarm model fitting, all variables are internally centered prior to coefficient estimation but the posterior mean estimates are unscaled (Goodrich et al. 2020). For each model run, we specified a Gaussian distribution. We used four Markov chain Monte Carlo chains, each with 2,000 iterations, with the first 1,000 as the warmup period and used the default weakly informed priors (Muth et al. 2018). We omitted the March planting date in analyses for the severe freezing barrier because the freezing barrier did not occur after this planting date in any simulations. Additional variable combinations also resulted in zero barriers, and these combinations were removed from variability (CV) calculations. Posterior mean coefficients were z-scaled for each model to aid in interpretation across variables. Even though both response variables, CV and mean barriers, are continuous data, we repeated the analysis with a censored model (Supplement S3) because we expected some zero-inflation as the original data are (left-censored) count data. However, we decided



to present here results from the Bayesian generalized model and results from the censored model in the [Supplement](#) because the censored model confirmed our findings and did not perform better than the chosen method (Tables S4–S7; Figs. S5–S10). All analyses were conducted in R version 4.0.3 (R Core Team 2020).

## Results

A small number of sites for each species were generally unfavorable for germination according to our simulations, based on having more than half (20) of years with no germination (rate sum <1) for most planting dates, despite meeting our initial site selection criteria. We removed those sites from all analyses (ELEL, seven sites; POSE, five sites; PSSP, three sites). Similarly, we removed all variable combinations (site, year, species, source, planting date) for analysis of barriers where no germination was predicted (rate sum <1).

### Environmental and Management Variables and Germination Favorability

Mean and variability (CV) in germination favorability (rate sum) were linked to both major abiotic variables, particularly precipitation and elevation, and management factors, both seed source within species and planting date. Specifically, mean germination favorability was higher in warmer, wet sites (lower elevation, higher precipitation, higher heat load index [non-significant for POSE]), with precipitation and elevation interacting such that

increases in precipitation had greater positive effects at low, than high elevations (Table S4, similar relative coefficients for censored models, Table S5; Figs. S11–S13). The opposite trends were observed for the effects of elevation, precipitation, and their interaction on germination favorability CV, with higher variability in cool, dry sites (higher elevations, lower precipitation, lower heat load index) and greater differences due to precipitation at lower elevations (Table S6, similar relative coefficients for censored models, Table S7; Figs. S14–S16). The soil texture variable, clay content, was positively associated with lower means and higher variability for germination favorability for PSSP and ELEL, but not significantly associated for either means or CV for POSE (Tables S4 & S6). Seed source strongly influenced means and weakly related to variability in favorability (rate sum) for all species (Tables S4 & S6; Fig. 2). November and March seeding dates were associated with higher variability and lower means in favorability for all species, the latter a simple consequence of fewer days included in sums (Tables S4 & S6; Fig. 2).

Some environmental and management variables had similar effects on post-germination barrier risk (mean occurrence) and variability (CV), while others diverged by species or by mild versus severe barrier types for freezing or drought. Freezing barrier risk was significantly associated with interactions between precipitation and elevation across species and severity categories; however, the direction of these effects varied by both severity category and species (Table S4). Within the range of elevations and precipitation of the sites, mild freezing risk was elevated with increased precipitation at low elevations, with the opposite trend at higher elevations

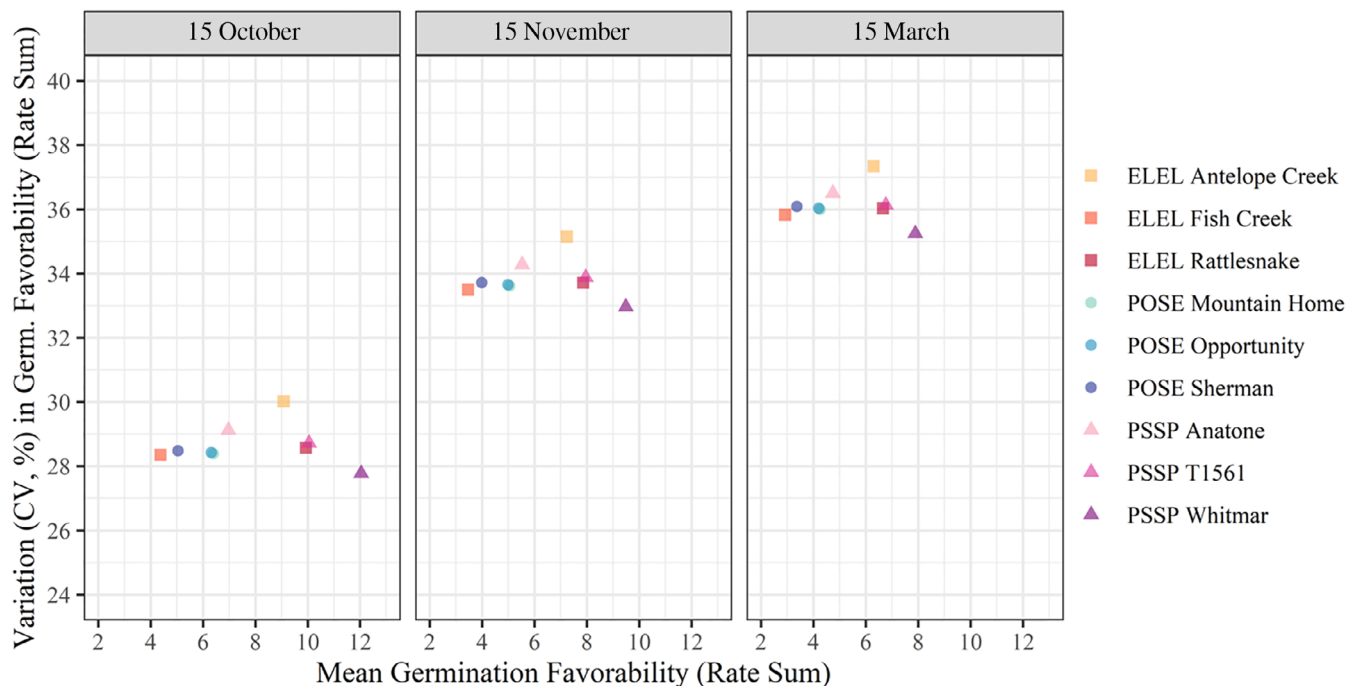


Figure 2. Variation (CV, %) and mean for germination favorability (rate sum, values = 1 indicate predicted germination) by plant date and seed source for each species (species codes and symbols: squares, ELEL, *Elymus elymoides*, light orange-red for sources; circles, POSE, *Poa secunda*, light-dark blue for sources; triangles, PSSP, *Pseudoroegneria spicata*, light pink-purple for sources, see text for seed source details). Consistently favorable seedbed conditions are indicated by higher mean and lower variation in germination favorability.

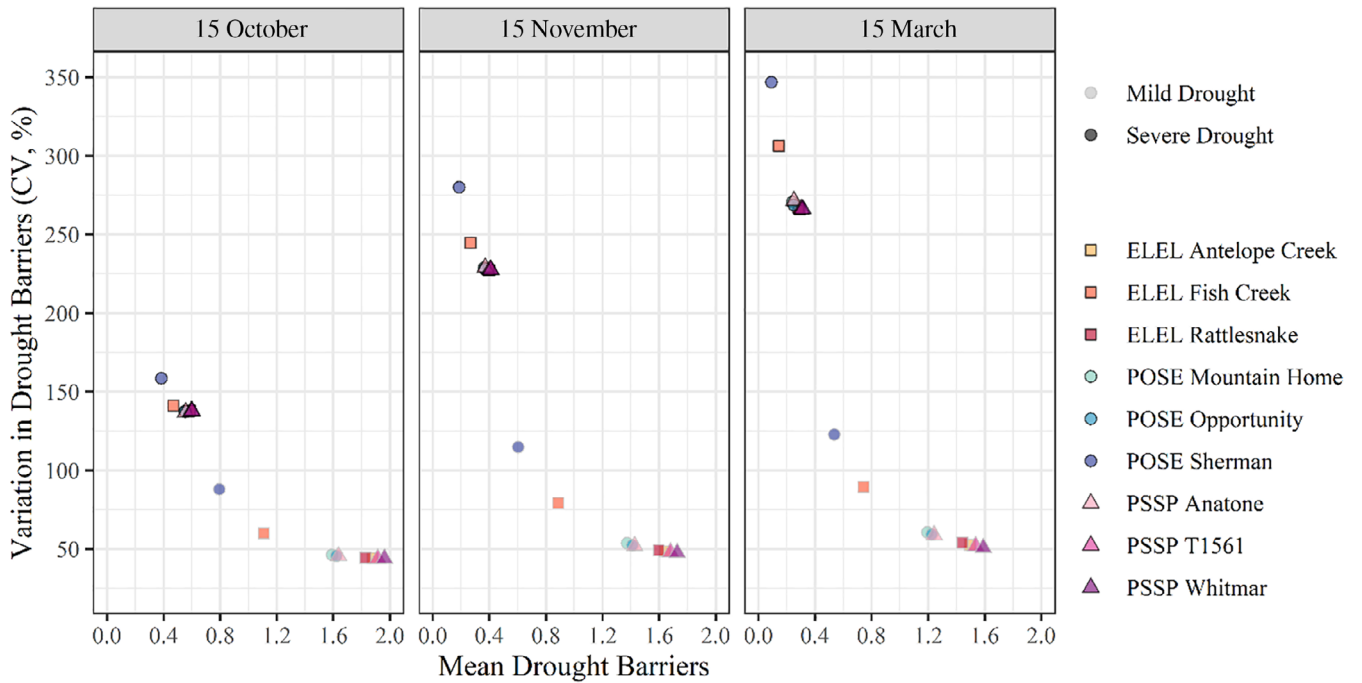


Figure 3. Drought barrier variation (CV, %) and risk of occurrence (mean) by severity (mild and severe), plant date, and seed source for each species (species codes and symbols: squares, ELEM, *Elymus elymoides*, light orange-red for sources; circles, POSE, *Poa secunda*, light-dark blue for sources; triangles, PSSP, *Pseudoroegneria spicata*, light pink-purple for sources, darker symbols are for severe drought; lighter symbols are for mild drought, see text for seed source details). Consistently lower risk of encountering drought barriers is indicated by lower means and variability.

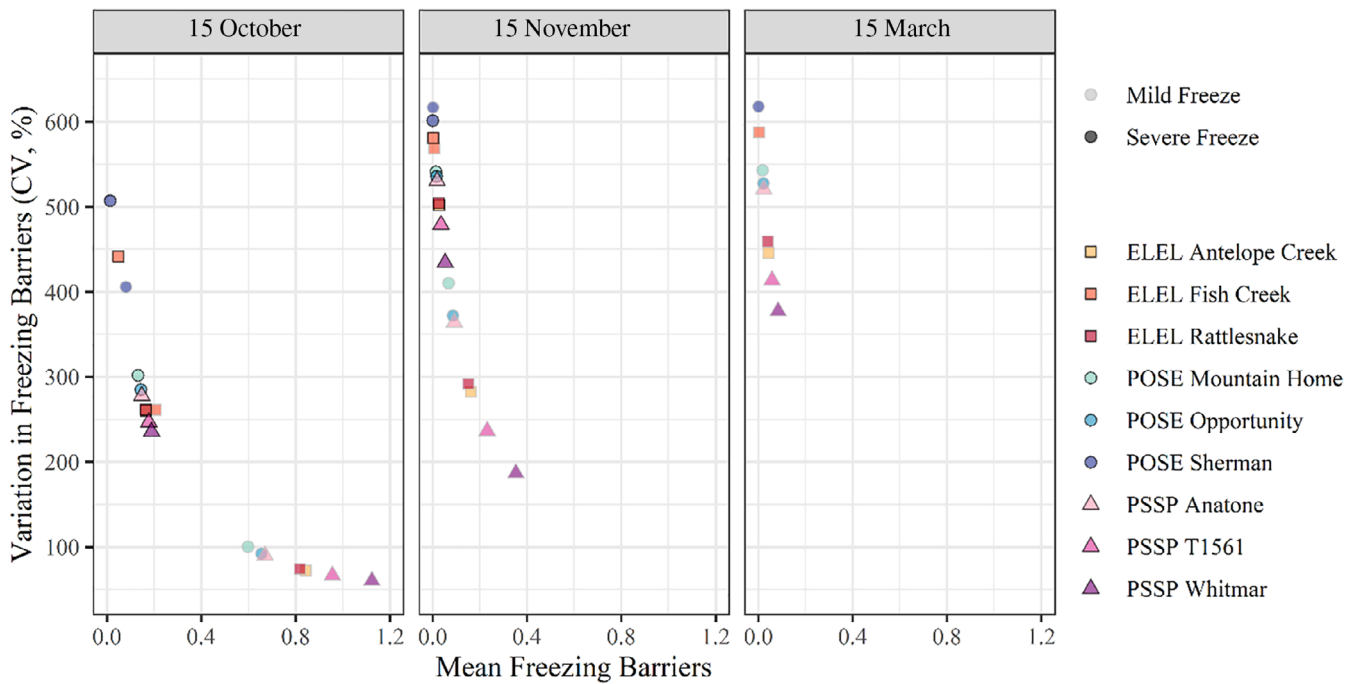


Figure 4. Freezing barrier variation (CV, %) and risk of occurrence (mean) by severity (mild and severe), plant date, and seed source for each species (species codes and symbols: squares, ELEM, *Elymus elymoides*, light orange-red for sources; circles, POSE, *Poa secunda*, light-dark blue for sources; triangles, PSSP, *Pseudoroegneria spicata*, light pink-purple for sources, darker symbols are for severe drought, lighter symbols are for mild drought, see text for seed source details). Consistently lower risk of encountering freezing barriers is indicated by lower means and variability. The severe freezing barrier did not occur in March planting date simulations.

(Table S4; Figs. S11–S13). However, risk of mild freezing also generally declined at higher elevations for POSE (Fig. S12) and not for ELEL or PSSP (Figs. S11 & S13). In contrast, higher precipitation was associated with lower risk of severe freezing across the elevation range in the study for all species (Table S4; Figs. S11–S13). Freezing barrier risk also generally increased across categories and in sites in cooler topographic microclimates (lower heat load index) and with lower clay content (Table S4).

Variability in freezing barriers was also affected by interactions between elevation and precipitation, except for mild barriers for POSE (Table S6). The effects of precipitation and elevation on variability in mild freezing barriers varied by species, though variability was generally higher with higher precipitation across most of the elevation range (Figs. S14–S16). Higher precipitation and elevations were associated with higher variability in severe freezing risk for all species, with less difference associated with precipitation at lower elevations (Figs. S14–S16). Freezing barrier variability, in both mild and severe categories, was higher in warmer topographic microclimate (higher heat load index) sites with higher clay content (Table S6).

Risk of both mild and severe drought was associated with interactive effects of precipitation and elevation. Drought risk for all categories and species was generally higher in warmer, drier sites (lower elevation and precipitation, higher heat load index, Table S4; Figs. S11–S13). Higher clay content was associated with increased mild drought risk and reduced risk of severe drought (Table S4). Variability in drought risk was generally higher at cooler, wetter sites (higher elevation and precipitation, lower heat load index) across severity categories and species, though interactive effects of precipitation and elevation varied (Table S6; Figs. S11–S13). Higher clay content was associated with lower variability, particularly for severe drought (Table S6). Management decisions related to seed source (within species) and planting date significantly affected both freezing and drought risk and variability in most cases. Seed sources significantly diverged in risk of exposure to drought and freezing for all species and severity categories, except for models for variability in severe drought (Tables S4 & S6; Figs. 3 & 4). In some cases, the effects of seed source were consistent across freezing and drought barriers and severity categories. For instance, for PSSP, “Whitmar” was associated with

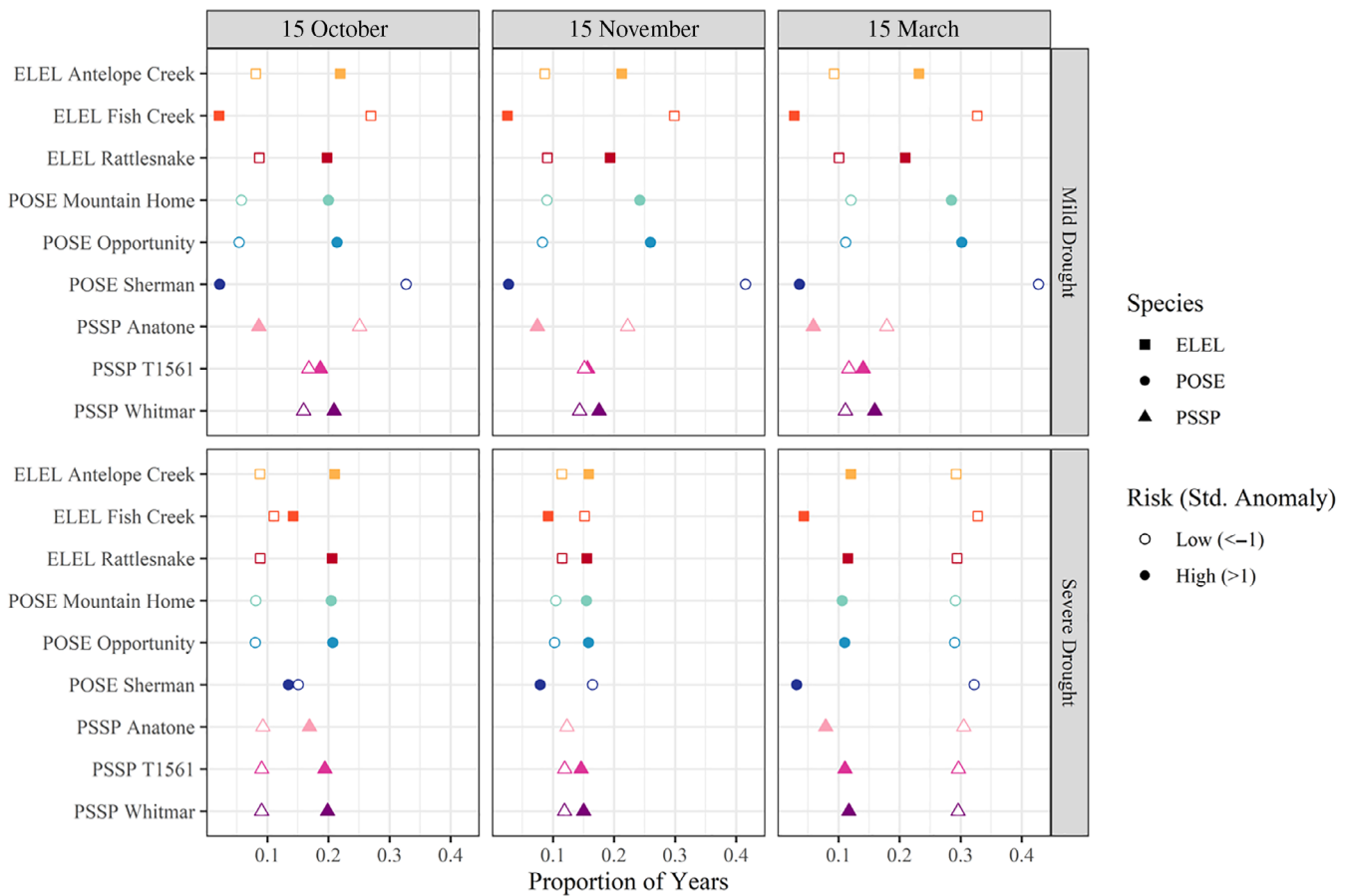


Figure 5. Proportion of years with relatively high or low risk for drought barriers based on the standardized anomaly for the site and planting date (value – mean/standard deviation, high risk, > 1, low risk, < –1) by barrier severity, plant date, and species and seed source (species codes and symbols: squares, ELEL, *Elymus elymoides*, light orange-red for sources; circles, POSE, *Poa secunda*, light-dark blue for sources; triangles, PSSP, *Pseudoroegneria spicata*, light pink-purple for sources, see text for seed source details).

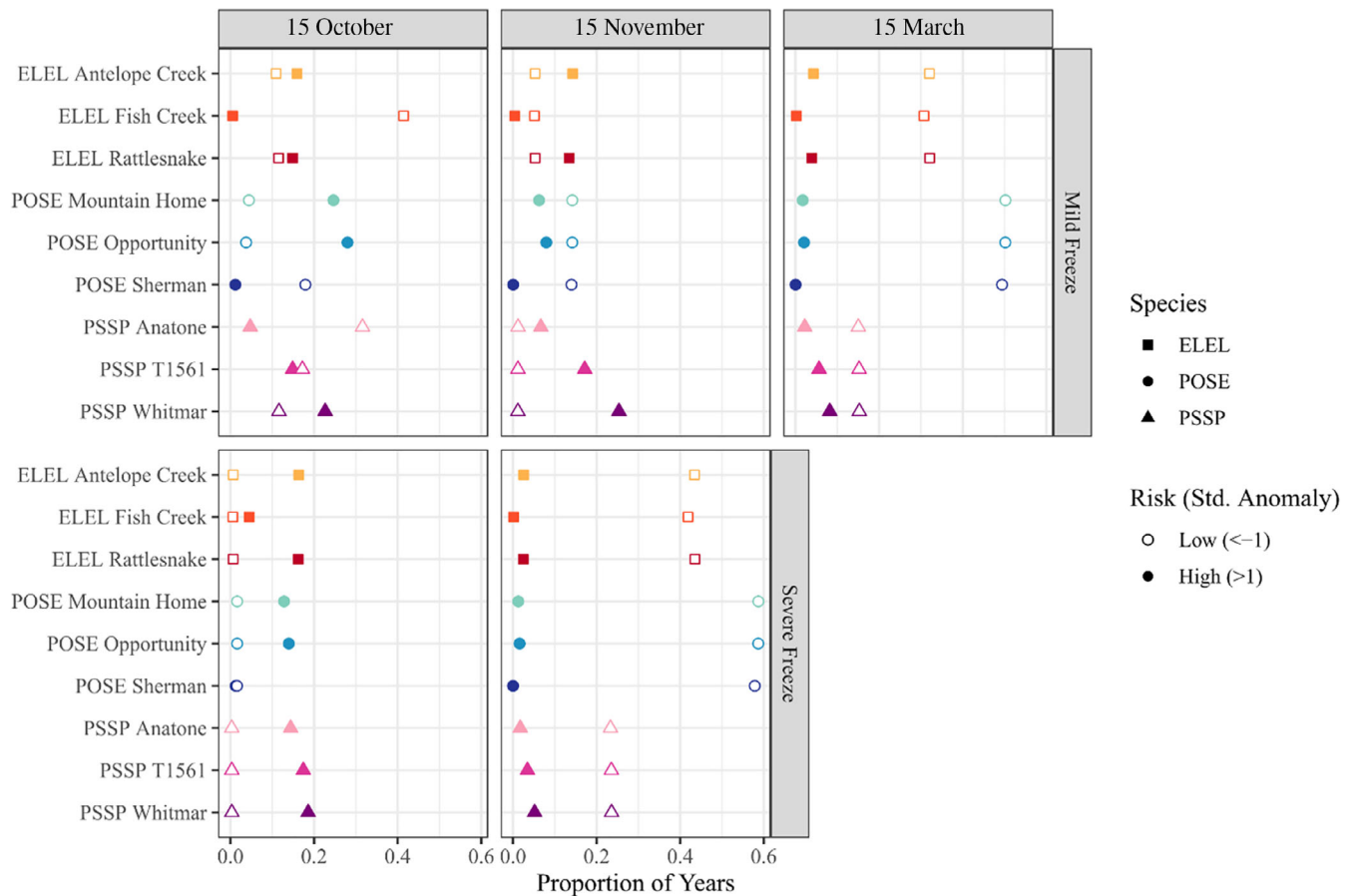


Figure 6. Proportion of years with relatively high or low risk for freezing barriers based on the standardized anomaly for the site and planting date (value – mean)/standard deviation, high risk, >1, low risk, <-1) by barrier severity, plant date, and species and seed source (species codes and symbols: squares, ELEM, *Elymus elymoides*, light orange-red for sources; circles, POSE, *Poa secunda*, light-dark blue for sources; triangles, PSSP, *Pseudoroegneria spicata*, light pink-purple for sources, see text for seed source details). The severe freezing barrier did not occur in March planting date simulations.

higher risk and variability, and “Anatone” with lower risk and variability for encountering barriers across mild and severe categories for both freezing and drought barriers (Tables S4 & S5). In contrast, in ELEM models, “Fish Creek” was consistently associated with lower risk and variability for drought and freezing barriers, both for severe and mild categories, but whereas “Rattlesnake” and “Antelope” appeared relatively similar, and differences in risk and variability associated with these sources were less consistent across barrier types and severity categories (Tables S4 & S5). Similar to the effects on germination favorability, lower mean barrier occurrence and higher variability in barriers were associated with later planting dates, November and March compared to October, for all types of barriers (Tables S4 & S6; Figs. 3 & 4).

Germination behavior across species and seed sources led to differences in exposure to post-germination barriers that altered the proportion of high-risk versus low-risk years for a given planting date and site (Figs. 5 & 6). Specifically, the ELEM source Fish Creek and the POSE cultivar “Sherman” had higher variability and lower means for drought and freezing barriers than other species and sources (Figs. 3 & 4); this was also

fundamentally associated with lower rate sums, or germination favorability (Fig. 2). Therefore, the less-frequent exposure to high risk (high proportion of low-risk years) for these species and seed sources (Figs. 5 & 6) is likely also related to lower average germination favorability (Fig. 2). Differences in relative risk across species and seed sources were also much greater for particular seeding dates and barrier types (i.e. mild drought, March vs. severe drought, November, Fig. 5).

### Discussion

Our results demonstrate that management decisions, like planting date and seed source, can be highly influential in controlling risk of poor and variable restoration outcomes associated with early seedling life stages, between germination and emergence, in the Great Basin. These management factors were comparable to the effects of major environmental variables, namely elevation and precipitation, that have recognized influence over regional regeneration and post-fire seeding outcomes (Chambers et al. 2014; Knutson et al. 2014). In general, planting date interacted with germination behavior, a function of species



and seed source, leading to divergent exposure to adverse weather even for the small set of seed sources considered in this study.

Seed source and planting date are major decisions in management planning. For instance, seedling establishment could be enhanced by tailoring planting date to weather conditions (with short-term climate forecast predictions) at a particular site and thereby reducing the likelihood of exposure of small, post-germination seedling to drought or freezing conditions. Planting date has relatively well documented relationships with germination timing and restoration outcomes in sagebrush steppe (Wainwright et al. 2012; Boyd & James 2013; Boyd & Lemos 2015). However, heterogeneity in germination behavior related to seed source is less understood and not necessarily included in management planning. In our simulations, germination behavior and associated exposure to restoration barriers was highly variable within and across the common species despite the small set of seed sources that we used in this analysis. This suggests careful selection of seed source based on germination behavior, particularly in concert with planting date, might be a useful strategy for avoiding post-germination early seedling drought and freezing barriers. For instance, our results showed that *Pseudoroegneria spicata* “Whitmar,” a species/seed source with relatively high exposure to mild freeze barriers, might experience about a threefold likelihood of encountering freezing barriers on average if seeded on 15 October compared to 15 November. In contrast, fall planting dates had much less of an effect on exposure to freezing for the slower germinating species/source *P. secunda* “Sherman”. Though our results demonstrate the potential impacts of one specific trait, relative germination rate, on restoration outcomes, many other germination and seedling traits known to vary by seed source are likely to influence establishment of seeded species across environmental gradients (Larson et al. 2015; Baughman et al. 2019; Leger et al. 2019).

Higher germination favorability and barrier occurrence for fall versus spring plantings is partially due to our simulation approach, as germination favorability and barriers continuously accumulated until early summer. This approach may overestimate both favorability and barrier impacts, because in field conditions, multiple post-germination seed mortality events would diminish the quantity of remaining viable seeds, likely leading to a negative or neutral relationship between barriers and seedling numbers for fall planting dates. In contrast, sequential barriers are less likely to affect outcomes with spring planting dates due to the shorter favorable germination window during this period truncated by dry summer conditions. On the other hand, spring seeding dates have a limited window for encountering favorable environmental conditions for germination and seedling growth prior to summer drought. While this simulation approach does have limitations, it also recognizes the trade-offs relevant to management in the region, where winter snow and early spring mud often limit large-scale seeding operations to either late-fall and mid-spring periods.

Our simulations are generally only weak representations of early seedling mortality or even germination behavior in field conditions. Numerous environmental variables omitted from our simulation influence seedling mortality, from pathogens to soil crusting, and some of these may also interact with other environmental and

management factors (e.g. fungal pathogens and freezing, Gornish et al. 2015). Germination behavior with respect to moisture and temperature may diverge between field soil conditions and the laboratory environment, mostly due to the highly dynamic nature of soil microclimate. In addition, seedling mortality with drought and freezing is linked to a complex set of physiological responses to sequences of environmental conditions, rather than the more simplistic temperature or soil moisture scenarios included here. Thresholds or interactions for environmental factors directly tied to mortality are not well characterized for our focal species or other herbaceous species broadly used in restoration in the Great Basin, despite field observations supporting their importance (e.g. Boyd & Lemos 2013; James et al. 2019). Though our simulation approach may not holistically represent field outcomes, it allows for relative comparisons of the effects of management decisions and environmental conditions across broad spatiotemporal scales.

Our barrier simulations were designed to target barriers likely to affect early life stages for seedlings. However, sparse data are available to describe the exact environmental conditions likely to cause mortality for our target species (or sources within species) and the effects of these conditions are also likely to vary with physiological processes associated with antecedent weather and seedling size. For example, grass seedlings are able to withstand extreme drought, when slow drying allows for root growth (Hanslin et al. 2019). Similarly, freezing tolerance can be affected by previous acclimation to cold, and this acclimation also varies by cultivar (Eagles 1989). Despite this lack of biological information related to mortality, our results are broadly consistent with observations of weather effects on mortality, and subsequent restoration outcomes in the Great Basin for common grass species (James et al. 2019; Pyle et al. 2021) and big sagebrush (*Artemisia tridentata* L.), a widely seeded and studied species (O'Connor et al. 2020).

Environmental factors like precipitation and temperature are often linked to natural regeneration and restoration success and variability across broad scales in the Great Basin (Chambers et al. 2014; Knutson et al. 2014). Our results demonstrate that conditions favoring germination in certain critical periods may also increase the potential for risk of adverse weather conditions for seedlings. For example, freezing barriers are more likely to occur, on average, in relatively warmer, wetter sites (low elevation, high precipitation, warmer topographic position) in this cold desert region because fall germination is more likely in these locations than in higher elevation and/or drier locations. This simulation approach was also able to demonstrate significant, though generally weaker, effects of soil texture and microclimate relative to macroclimate factors like average precipitation and elevation, as well as differences in their effects across species models. However, these effects were not necessarily consistent across barrier types and/or species. For example, clay content strongly increased risk and variability of severe drought for PSSP and ELEL, but only weakly for POSE, underscoring how germination behavior, a function of species and seed source in this analysis, may influence exposure to seedling exposure to adverse weather conditions.

However, beyond the effects of environmental variables, this study demonstrates how seeding date and differences in germination

behavior, associated even with seed source for one species, can have consequential outcomes with respect to amplifying or dampening both variability and overall exposure to adverse conditions likely to lead to seedling mortality. Efforts to increase restoration success may benefit from additional research focused on specific weather-related barriers causing seedling mortality (Bradford et al. 2018; Hardegree et al. 2018a; O'Connor et al. 2020), particularly techniques that directly address these barriers. For example, seed coatings and other methods can be used to manipulate germinate timing and increase the likelihood seeds will encounter favorable conditions (Pedrini et al. 2020) or seeding methods (depth, mulch) can be applied to improve the soil microclimate conditions encountered by early-stage seedlings (Shaw et al. 2020).

Ecosystem function in sagebrush steppe is threatened by multiple, interacting change drivers including non-native species invasion, increasing wildfire, and climate change (Abatzoglou & Kolden 2011; Bradford et al. 2020). These concurrent pressures are likely to increase restoration needs. Harnessing the interplay between management practices, site environment, and weather to maximize plant survival during early life stages could be an avenue for reducing the rate of seed-based restoration failure in this semi-arid region.

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## Supporting Information

The following information may be found in the online version of this article:

- Supplement S1.** SOILWAT2 soil water and temperature modeling details.
- Supplement S2.** Species source and cultivar details.
- Supplement S3.** Comparison of Bayesian Regression and left censored regression (Tobit).
- Figure S1.** Example of cumulative germination interrupted by potential barriers for one site, one year, and one species source.
- Figure S2.** Comparison of the observed and simulated posterior predictive distributions ( $N = 200$ ) for *Pseudoroegneria spicata* mean and coefficient of variation (CV) using the “pp\_check” function in “rstanarm” package.
- Figure S3.** Comparison of the observed and simulated posterior predictive distributions ( $N = 200$ ) for *Poa secunda* mean and coefficient of variation (CV) using the “pp\_check” function in “rstanarm” package.

**Figure S4.** Comparison of the observed and simulated posterior predictive distributions ( $N = 200$ ) for *Elymus elymoides* mean and coefficient of variation (CV) using the “pp\_check” function in “rstanarm” package.

**Figure S5.** Comparison of the sampled residuals against the theoretical residuals for Bayesian glm and tobit regression for the mean responses for PSSP.

**Figure S6.** Comparison of the sampled residuals against the theoretical residuals for Bayesian glm and tobit regression for the CV responses for PSSP.

**Figure S7.** Comparison of the sampled residuals against the theoretical residuals for Bayesian glm and tobit regression for the mean responses for ELEL.

**Figure S8.** Comparison of the sampled residuals against the theoretical residuals for Bayesian glm and tobit regression for the CV responses for ELEL.

**Figure S9.** Comparison of the sampled residuals against the theoretical residuals for Bayesian glm and tobit regression for the mean responses for POSE.

**Figure S10.** Comparison of the sampled residuals against the theoretical residuals for Bayesian glm and tobit regression for the CV responses for POSE.

**Figure S11.** Marginal effects of elevation based on three levels of 30-year mean precipitation on mean barrier occurrence and germination favorability for *Pseudoroegneria spicata* based on the predictive posterior distribution from the rstanarm analysis.

**Figure S12.** Marginal effects of elevation based on three levels of 30-year mean precipitation on mean barrier occurrence and germination favorability for *Poa secunda* based on the predictive posterior distribution from the rstanarm analysis.

**Figure S13.** Marginal effects of elevation based on three levels of 30-year mean precipitation on mean barrier occurrence and germination favorability for *Elymus elymoides* based on the predictive posterior distribution from the rstanarm analysis.

**Figure S14.** Marginal effects of elevation based on three levels of 30-year mean precipitation on coefficient of variation (CV) of barrier occurrence and germination favorability for *Pseudoroegneria spicata* based on the predictive posterior distribution from the rstanarm analysis.

**Figure S15.** Marginal effects of elevation based on three levels of 30-year mean precipitation on coefficient of variation (CV) of barrier occurrence and germination favorability for *Poa secunda* based on the predictive posterior distribution from the rstanarm analysis.

**Figure S16.** Marginal effects of elevation based on three levels of 30-year mean precipitation on coefficient of variation (CV) of barrier occurrence and germination favorability for *Elymus elymoides* based on the predictive posterior distribution from the rstanarm analysis.

**Table S1.** Pairwise correlations for the four environmental variables (elevation, precipitation, heat load index [HLI], and clay content) used in models for means and coefficients of variation.

**Table S2.** Rhat (a measure of convergence, values greater than 1.01 suggest convergence issues) for GLM models with Bayesian priors for mean response variables by species.

**Table S3.** Rhat (a measure of convergence, values greater than 1.01 suggest convergence issues) for GLM models with Bayesian priors for coefficient of variation response variables by species.

**Table S4.** Standardized coefficients for GLM models with Bayesian priors for means by species.

**Table S5.** Standardized coefficients for Tobit models for means by species.

**Table S6.** Standardized coefficients for GLM models with Bayesian priors for CV by species.

**Table S7.** Standardized coefficients for Tobit models for CV by species.

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