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Temporal Variability in Microclimatic Conditions for Grass Germination and Emergence in the Sagebrush Steppe☆

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ABSTRACT

Sagebrush steppe ecosystems in the western United States are characterized by harsh environmental conditions with high annual and seasonal variability in both precipitation and temperature. Environmental variability contributes to widespread failure in establishing stands of desired species on degraded and invaded landscapes. To characterize seasonal microclimatic patterns and planting date effects on restoration outcomes, we evaluated long-term simulations of seed germination response of cheatgrass (*Bromus tectorum* L.), bottlebrush squirreltail (*Elymus elymoides* [Raf] Swezey), and Idaho fescue (*Festuca idahoensis* Elmer) to annual patterns of soil temperature and moisture. Extremely high annual variability in both the conditions favorable for germination and patterns of post-germination drought and thermal stress make it difficult to justify general inferences about seedbed treatment and planting date effects from individual, short-term field studies. We discuss the interpretation of individual-year and seasonal plant establishment factors and offer a mechanistic model for interpreting planting date and year effects on initial seedling establishment. Historical ranking and mechanistic descriptions of individual-year seedbed conditions may allow for expanded inferences through meta-analysis of limited-term field experiments.

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Introduction

Throughout the western United States, lower-elevation Basin and Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata* and *A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) rangelands have undergone large-scale conversion from diverse, healthy, perennial plant—dominated communities to near monocultures of invasive annual grasses (Chambers and Wisdom, 2009). Cheatgrass (*Bromus tectorum* L.) and other annual grasses currently dominate millions of hectares of sagebrush steppe rangeland and are expected to continue range expansion under anticipated future conditions of wildfire and climate change (Abatzoglou and Kolden, 2011; Bradley, 2010; Knapp, 1996). The need for restoration of degraded sagebrush steppe is substantial, but establishment of perennial grasses, forbs, and shrubs from seed is prone to failure in these harsh environments that receive, on average, less than 250 mm of annual precipitation (Anderson et al., 1957; Arkle et al., 2014; Hemstrom et al., 2002; Jordan, 1981; Knutson et al., 2014; Pyke et al., 2013; Reisner et al., 2013; Wisdom et al., 2005). A major problem constraining our ability to advance restoration science in these systems is the short-term nature of most research results that limits general inferences and, therefore, management applicability. Because of the difficulty in publishing negative results, existing literature also tends to be biased toward years with above-average precipitation (Hardegree et al., 2011).

Numerous authors have hypothesized that rapid germination in the fall, winter, and early spring may contribute to the success of cheatgrass relative to native perennial grasses (Beckstead et al., 1996; Harris, 1967, 1977; Roundy et al., 2007). Hardegree et al. (2010, 2013) confirmed the rapid germination rate of cheatgrass relative to native perennial species over a broad range of temperature and water potential conditions, but germination rate is not necessarily a limiting factor for nondormant seedlots of any of these species (Hardegree and Van Vactor, 2000; Roundy et al., 2007). Germination response of rangeland grasses, however, is typically much higher than seedling emergence in the field (Boyd and Lemos, 2013; Hardegree and Van Vactor, 2000; James et al., 2011). Newly germinated plants are particularly vulnerable to abiotic

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soil conditions, and postgermination/pre-emergent mortality from thermal and drought stress may be a principal bottleneck during the early stages of seedling recruitment (Boyd and Lemos, 2013; James et al., 2011).

Annual variability in both the amount and timing of precipitation are extremely high on sagebrush steppe rangelands (Rajagopalan and Lall, 1998). Previous use of weather information in restoration planning has generally been limited to selection of suitable plant materials as a function of long-term average precipitation (Jensen et al., 2001; Lambert, 2005; Ogle et al., 2008). Mature perennial grass species can be highly competitive with introduced annual weeds, and their presence confers significant resistance to annual weed invasion (Chambers et al., 2007, 2014a, 2014b). Microclimatic requirements for early plant establishment, however, are much more restrictive than those necessary for the persistence of mature plants, and transition pathways between undesirable and desirable vegetation states may require a specific and perhaps infrequently occurring weather pattern (Call and Roundy, 1991; Hardegree et al., 2011; Peters, 2000; Westoby et al., 1989). Unfortunately, a single-year seeding event in the year immediately after wildfire remains the predominant management treatment for restoration of disturbed rangelands in the Great Basin (Eiswerth and Shonkwiler, 2006; Eiswerth et al., 2009; Kulpa et al., 2012). Establishment success needs to be more explicitly linked to probabilities associated with both favorable and unfavorable conditions for seed germination, emergence, and establishment (Bakker et al., 2003; Hardegree et al., 2011, 2013; James et al., 2011). The bulk of the historical rangeland seeding literature, however, reports only gross seasonal weather information such as annual or seasonal precipitation and mean temperature (Hardegree et al., 2011).

Hardegree et al. (2013) evaluated the seasonality of seedbed favorability for germination at a field test site in southeastern Idaho. The purpose of this study is to expand upon the analysis of Hardegree et al. (2013) to further assess both the seasonal and annual variability in seedbed conditions for germination, as well as the probability of postgermination mortality events from temperature and water stress. Additional objectives are to suggest methodology for placing short-term field studies into the context of longer-term site variability and discuss the ramifications of this variability on the interpretation of seedbed treatment and planting date effects from rangeland seeding studies.

Methods

Hardegree et al. (2013, 2015) have previously described the soil-microclimate and hydrothermal-germination models used in this analysis. The Simultaneous Heat and Water (SHAW) model was previously calibrated for estimating seedbed microclimatic conditions at seeding depth for a sandy-loam soil (Flerchinger et al., 2012) using weather data from the Boise Airport to yield hourly soil temperature and water potential estimates at a 2-cm soil depth for every hour between October 1, 1961 and September 30, 2005. SHAW is a process-based model that estimates a time series of volumetric soil water content, water potential and temperature throughout the soil profile as a function of soil texture, bulk density, surface conditions (including snow accumulation), and vegetation in response to meteorological inputs of precipitation (rain and snow), solar radiation, wind speed, humidity, and air temperature (Flerchinger and Saxton, 1989a, 1989b). This soil-type and weather scenario is representative of the 300 mm/yr precipitation zone characterizing Wyoming big sagebrush habitat in the Snake River Plain in southeastern Idaho.

Hydrothermal germination models derived by Hardegree et al. (2013, 2015) for cheatgrass (Kuna, Idaho collection), bottlebrush squirreltail (*Elymus elymoides* [Raf] Swezey) (GV accession), and Idaho fescue (*Festuca idahoensis* Elmer) were used in this study. These 3 seedlots were selected from the 13 seedlots of 7 species evaluated by Hardegree et al. (2013, 2015) to represent the full range of relative germination rate among the seedlots previously tested. The cheatgrass accession was previously shown to have a germination rate response approximately twice that of GV squirreltail, which was among the most rapidly germinating native perennial seedlots tested by Hardegree et al. (2013, 2015). This Idaho fescue seedlot was chosen as one of the slowest germinating seedlots among the native perennial species previously tested.

Hydrothermal germination rate was estimated separately for every subpopulation of every seedlot in 5% increments between 5% and 95% germination for every hour of the 44-year simulation as described by Hardegree et al. (2013). Hourly rate estimates were aggregated to obtain daily rate-sums for the entire study period. Per-day germination rate-sums represent the fractional progress toward germination for a given subpopulation during a given day (Hardegree, 2006; Hardegree et al., 2015). Postplanting germination date for a given subpopulation can, therefore, be estimated to occur when the sum of daily rate-sum estimates become equal to 1 (Roundy and Biedenbender, 1996). Cumulative rate-sums for a fixed time period can also be used as a quantitative index of seedbed favorability for comparison of alternative time periods or seedbed treatments (Hardegree et al., 2013). We estimated daily, monthly, and seasonal rate-sum values for every year of the simulation as an index of favorability for germination during a given time interval as described by Hardegree et al. (2013). We also simulated post-planting cumulative germination curves for all seedlots for 21 planting dates between October 1 and July 8 for each year following the general procedure described by Hardegree et al. (2010, 2015).

Soil microclimatic conditions at seeding depth were evaluated to identify all hours spent at temperatures below 0 °C and at water potentials more negative than −1.5 MPa as an indicator of conditions that could result in postgermination/pre-emergence mortality. These temperature and water potential thresholds may only reflect general conditions that contribute to postgermination seedling mortality as exact threshold values may be species or seedlot specific, probably have a temporal component that may be longer than 1 hour, and likely exhibit within-population variability in mortality effects (Boyd and Lemos, 2013). Hourly microclimatic estimates at seeding depth were used to identify days within the simulation period that experienced at least 1 hour below these temperature and water potential thresholds. For any day with at least 1 hour below a given threshold, the number of hours below the threshold was also determined.

Results

Annual variability in air temperature was relatively low from year to year compared with precipitation, but mean air temperature fell below 0 °C in both December and January (Fig. 1). Modeled average-daily soil temperatures tended to be higher than air temperature throughout the year by approximately 0.9 °C (±0.2 SE) in the coldest months of December to January, 2.6 °C (±0.1 SE) in the March to May spring period, and 4.6 °C (±0.05 SE) during the June to August summer period. Precipitation occurred primarily in the late fall through early spring at the test location but was highly variable from year to year.

May and October-to-May precipitation were only weakly correlated ($r^2 = 0.12$), and there was a high probability (54%) of having lower than average precipitation in May during an otherwise above average precipitation year (Fig. 2).

Hardegree et al. (2013) used daily rate-sum values as an index of general favorability for germination on a given day. Rate-sum values represent the relative predicted progress of a given seed subpopulation toward germination during a given time period (Hardegree et al., 2003, 2013). Fig. 3 shows the previously described seasonality in seedbed favorability for germination but also extremely high variability in favorability from year to year as the mean daily rate-sum and standard deviation of the mean daily rate-sum are of the same magnitude for a given time period. Relative rate-sum differences are proportional to relative germination rates of cheatgrass (fast), bottlebrush squirreltail (intermediate), and Idaho fescue (slow).

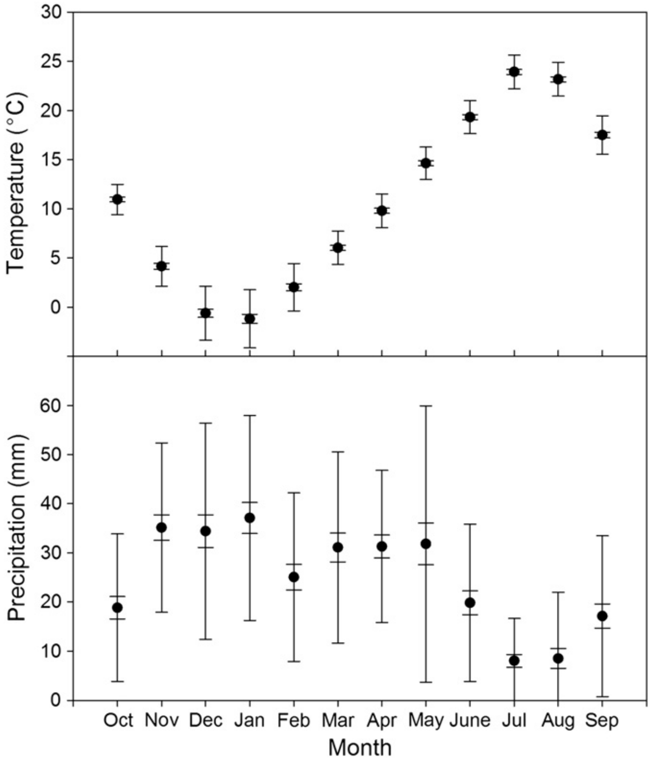

Fig. 1. Monthly mean air temperature and precipitation for the 44-year simulation period. Outer error bars represent ± 1 standard deviation. Inner error bars represent ± 1 standard error of the mean. Error bars that extend below the lower axis are symmetrical with upper error bars.

The 1965 and 1968 hydrologic years had similar and approximately average total cumulative rate-sums for the October-to-May period but very different predicted cumulative germination as a function of planting date (Fig. 4). The 1965 hydrologic year had a relatively uniform distribution of favorable germination periods through the course of the year, but 1968 had highly unfavorable periods of germination in both the winter and spring.

Potential postgermination mortality events from low temperature and drought also have a well-defined seasonal distribution (Fig. 5). The temperature and water potential thresholds used in this study may not represent actual species-specific mortality thresholds, but Fig. 5 generally reflects the seasonal pattern of relative freezing and drought stress. Starting in late October, the probability of having days with at least 1 hour below 0 °C at seeding depth increases from near zero to about 85% in January and then drops back to zero in mid to late April. The risk of postgermination mortality from water stress peaks in July and August but is also relatively high during midwinter (see Fig. 5) when freezing temperatures convert liquid water to ice and effectively lower soil water availability (Flerchinger et al., 2006).

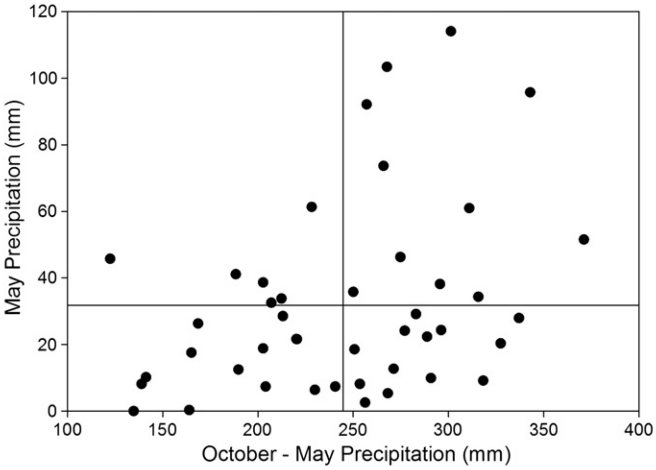

Fig. 2. Establishment-season precipitation (October to May) versus May precipitation for all years of the simulation. Vertical and horizontal lines represent mean values. For years with above-average precipitation during October to May, 54% had below-average precipitation in May.

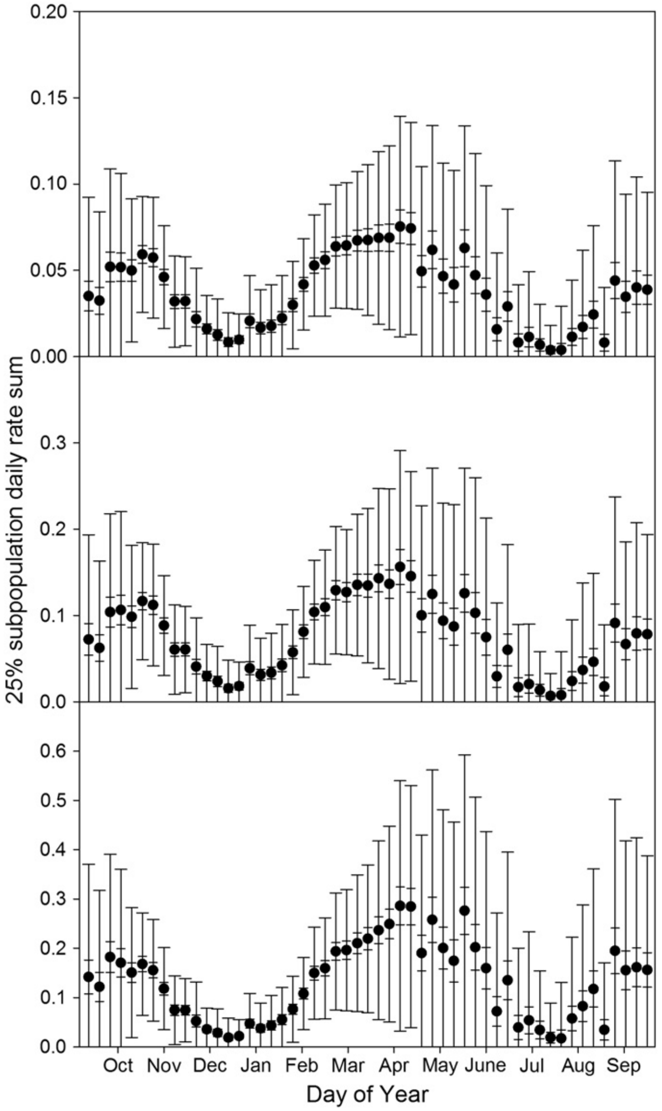

Fig. 3. Seasonal patterns of daily rate-sum values for the 25% subpopulation of Idaho fescue (upper), bottlebrush squirreltail (middle), and cheatgrass (lower). Outer error bars represent ± 1 standard deviation. Inner error bars represent ± 1 standard error of the mean. Error bars that extend below the lower axis are symmetrical with upper error bars. Only every seventh day is shown for clarity.

It is unlikely that a single hour below these water potential and temperature thresholds is sufficient time for significant postgermination mortality to occur. Fig. 6 shows the mean and variability in the number of hours per day below drought and water stress thresholds for any day that had at least 1 hour below 0 °C or −1.5 MPa. Drought in the summer and freezing events in the winter tend to persist over a significant portion of any day in which they occur, indicating a higher likelihood of actual mortality occurring on any given day.

Discussion

Annual variability in both the amount and timing of precipitation is extremely high on sagebrush-steppe rangelands (Rajagopalan and Lall,

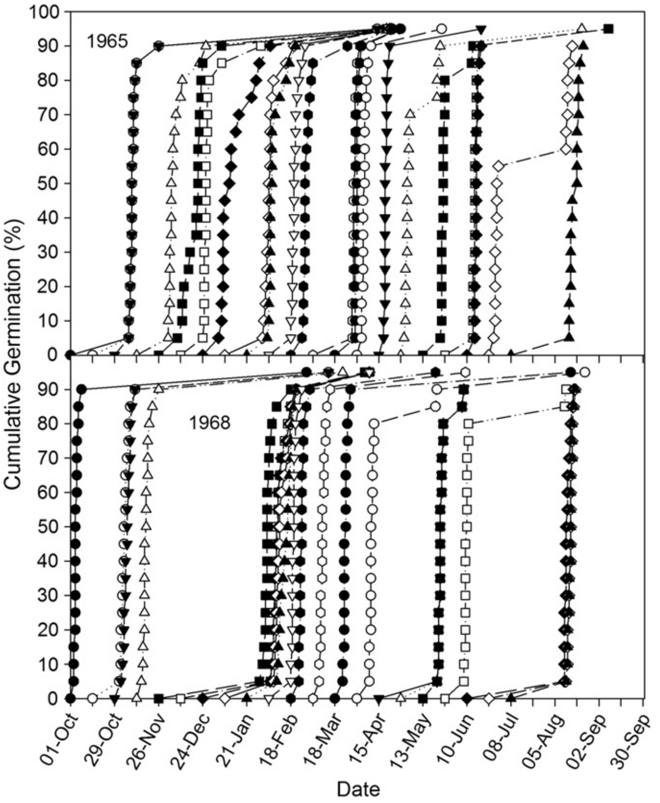

Fig. 4. Modeled cumulative germination of bottlebrush squirreltail for 21 simulated planting dates in the 1965 and 1968 hydrologic years. These years were chosen for comparison because both had average general favorability for germination during the October-to-May establishment period but a different seasonal pattern of favorability; 1968 had a relatively sustained low-temperature period in November and December, relatively higher temperature and precipitation in February and March, and relatively dry conditions in April and May. Symbols were included solely to facilitate tracking of cumulative curves from different planting dates.

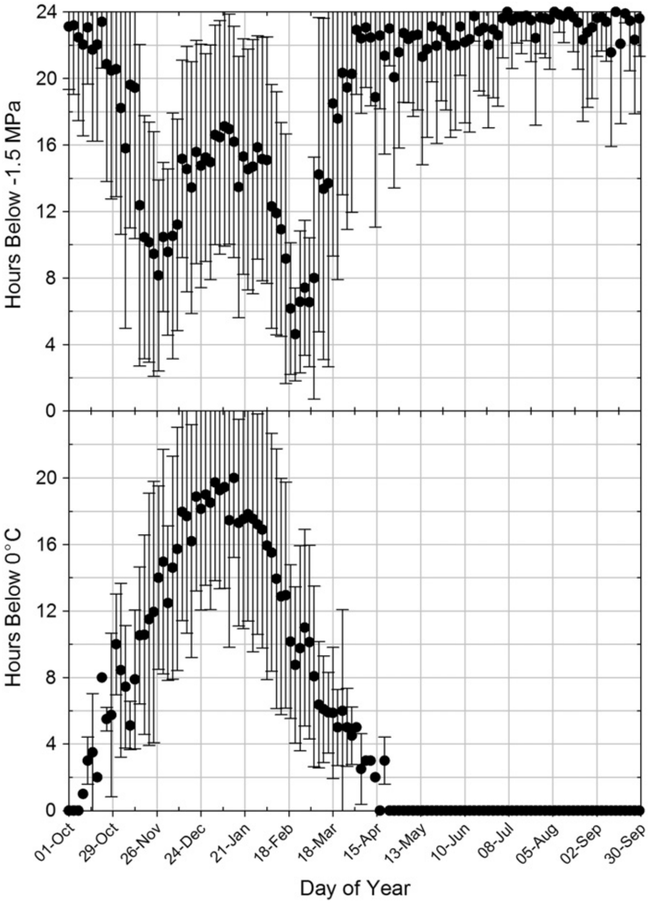

Fig. 6. Seasonal pattern of average number of hours per day of soil temperature below 0 °C or soil water potential below − 1.5 MPa at seeding depth for days with at least 1 hour below temperature and water potential thresholds. Error bars represent ± 1 standard deviation. Error bars that extend beyond the upper or lower axes are symmetrical with respect to the mean. Only every third daily data point is shown for clarity.

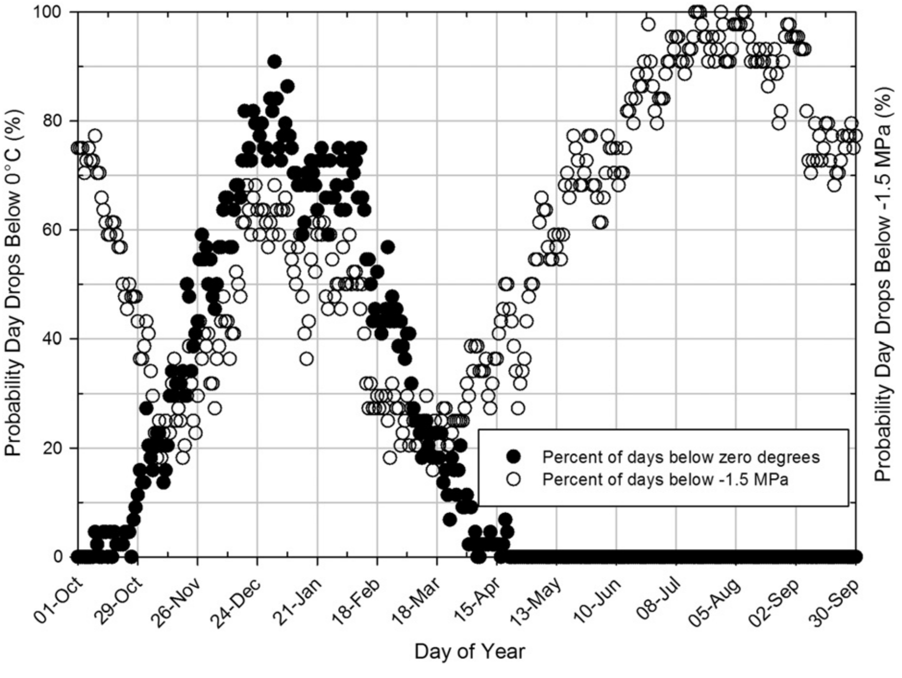

Fig. 5. Seasonality of days with at least 1 hour of soil temperature below 0 °C or soil water potential below − 1.5 MPa at seeding depth for the 44-year modeling period.

1998; see Fig. 1). Although the values for the standard error of the mean are sufficient to establish the statistical significance of seasonal differences, the relatively large standard deviation values demonstrate the high probability of sustained drought in any given month. High variability in both total-annual and seasonal-distribution of precipitation imposes severe limitations to inferences made from typical rangeland seeding studies, which are generally of insufficient length to survey the full range of variability that could occur at a given site (Hardegree et al., 2011). Fig. 1 shows high annual variability in precipitation but obscures somewhat the high variability in the seasonal pattern of precipitation. Years with above-average precipitation can still have episodes of extreme drought during critical establishment months in the spring when temperatures are otherwise high enough to support rapid growth and establishment. Fig. 2 shows a relatively high probability of low precipitation during the critical May establishment month, even in years with above-average total precipitation (Hardegree et al., 2003).

Variability in air temperature is much lower than the relative variability in precipitation, but mean air temperature notably drops below 0 °C for 2 months of the year (see Fig. 1). Below-zero conditions may cause significant mortality in newly germinated seeds or pre-emergent seedlings that are not sufficiently developed to withstand these temperatures (Boyd and Lemos, 2013). Fortunately, the soil and potential snow cover mitigate low-temperature extremes of air temperature in the winter (Gornish et al., 2015), but soil heat absorption during the summer may exacerbate evaporative demand during the seedling phase of plant establishment.

The seasonal patterns of rainfall and temperature shown in Fig. 1 are typical for many low-elevation sagebrush steppe ecosystems in the Great Basin. The majority of precipitation occurs in late fall through early spring followed by high temperatures and relative drought through summer and early fall. General sources of guidance for rangeland restoration and fire rehabilitation applications in this region recommend fall seeding of desirable species to take advantage of any favorable periods for establishment during the subsequent winter and spring (Monsen and Stevens, 2004; Plummer et al., 1968; Roundy and Call, 1988). Frequently, however, the timing of planting on sagebrush-steppe rangelands is determined by logistical concerns and equipment limitations (Douglas et al., 1960; Hart and Dean, 1986; McGinnies, 1973; Stewart, 1950). Eisworth and Shonkwiler (2006) confirmed the relative benefits of fall/winter seeding using meta-analysis of Bureau of Land Management (BLM) postfire seeding trials in Nevada, but there are relatively few experimental studies of planting-date effects in the region that have been replicated in more than 1 or 2 consecutive years (Hardegree et al., 2011). Hardegree et al. (2011) surveyed almost 60 years of rangeland seeding literature and found that fall planting was determined to be superior to spring planting in 73% of sagebrush-steppe studies where planting season was evaluated. Hardegree et al. (2011) also found, however, that published studies on the subject were biased toward years with above-average precipitation, and that the majority of reported seeding success was generally for fewer species than represented in the full seed mix planted.

Hardegree et al. (2013) found that only 54% of annual variability in seedbed favorability for germination could be explained by total annual precipitation and suggested that a cumulative rate-sum of potential germination progress may yield a more ecologically relevant index of seedbed favorability for germination. Fig. 3 reproduces a graph previously described by Hardegree et al. (2013) to describe average seasonal favorability for germination but also shows the standard deviation of the rate-sum favorability index, which is more representative of annual variability than the standard error. As with precipitation, the mean and standard deviation of seedbed favorability over time obscures the relatively high variability in the timing of favorable germination conditions within any given year. In Fig. 4, we estimated cumulative germination curves for bottlebrush squirreltail for 21 simulated planting dates in 2 years that had similar, as well as average, germination rate-sum indices for the October-to-May establishment period. However, 1968 differed from 1965 in that it had a relatively sustained low-temperature period in November and December, relatively higher temperature and precipitation in February and March, and relatively dry conditions in April and May.

Various studies have shown that germination is generally not limiting over the course of a planting season, but field experiments often show large discrepancies between predicted germination and measured emergence (Boyd and Lemos, 2013; Hardegree and Van Vactor, 2000; James et al., 2011; Roundy et al., 2007). Pre-emergent mortality has been variously associated with resistance to emergence from soil physical factors or soil crusts, seed predation, and seed/seedling pathogens (Belnap, 2003; Lehrsch et al., 2005; Mao et al., 1997; Neher et al., 1987). We focus here on potential pre-emergence seeding mortality from desiccation and thermal stress as seeds are relatively impervious to low temperature and water stress before germination. Given the seasonal probability of occurrence and duration of freezing and drought (Figs. 5 and 6), the relative timing of germination demonstrated in Fig. 4 may be particularly important in determining rates of survival to emergence. Slow germination and high within-population variability in germination rate may prove to be successful strategies for mortality avoidance for some species on some sites in some years.

Further analysis of these data may yield additional insights into the role of germination timing in avoidance of postgermination mortality; identification of seed germination syndromes based on relative germination rate and within-population variability in rate; practical guidance for the interpretation of planting date effects in such a highly variable field environment; site-characterization guidelines to facilitate meta-analysis of diverse field studies; a mechanistic framework to assist in the interpretation of seedbed preparation and planting treatment effects on seedling establishment; and potential guidance on the degree of annual-planting-date replication that may be necessary to adequately survey natural variability in field conditions. It is possible, however, that the high cost of field trials will always be a limiting factor to annual replication in the field, and a microclimatic modeling approach may be the only cost-effective way of addressing potential annual variability. If this is the case, then more attention may need to be paid to the validation and calibration of the type of models that can be used for this type of simulation.

Striking differences in the relative timing of annual weed and native perennial grass germination may yield additional insights into the optimal timing of weed control measures, which are also subject to high uncertainty due to variable site and weather conditions. This modeling approach could also be used to evaluate temperature and water relations deeper in the soil profile and perhaps directly address the issue of resource allocation relative to ecological resilience and resistance to weed invasion as a function of rooting depth (Chambers et al., 2014a, 2014b). Finally, a more weather-centric and probabilistic understanding of establishment success, partial success, and failure may lead to more effective, long-term strategies for adaptive management and contingency planning for restoration of arid and semiarid rangelands (Hardegree et al., 2012). Probabilistic descriptions of field conditions would also be useful in conjunction with emerging improvements in seasonal weather forecasting for natural resource management applications (Garbrecht and Schneider, 2007; Hardegree et al., 2011).

Management Implications

Most recent field studies of rangeland seeding treatments report on-site measurements of precipitation and other meteorological variables, but the majority of older studies only report precipitation totals during the year of treatment or long-term climatological averages rather than study-specific weather information. Field studies can also be considered nonpublishable if the majority of seeding trial results is negative, which may be responsible for a relative bias in the seeding literature toward treatment years with higher than average precipitation. This study only addresses temporal variability at a single location, but ranking of individual treatment years within the context of historical variability may allow for expanded inferences from relatively short-term field studies at any location. Study-specific ranking of precipitation and temperature, however, are insufficient to describe the seasonal timing of germination relative to potential mortality events from water and thermal stress. We suggest that future seeding studies include both a description of long-term variability in seasonal precipitation and temperature and associated probabilities of microclimatic drought and thermal stress. A standardized description of historical microclimatic variability may also provide a sufficient context for meta-analysis of similar seeding trials over time.

References

Abatzoglou, J.T., Kolden, C.A., 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. Rangel. Ecol. Manag. 64, 471–478.

Anderson, D., Hamilton, L.P., Reynolds, H.G., Humphrey, R.R., 1957. Reseeding desert grassland ranges in southern Arizona. Ariz. Agric. Exp. Station. Bull. 249 32 pp.

Arkle, R.S., Pilliod, D.S., Hanser, S.E., Brooks, M.L., Chambers, J.C., Grace, J.B., Knutson, K.C., Pyke, D.A., Welty, J.L., Wirth, T.A., 2014. Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin. Ecosphere 5, 31.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X.D., Ambrose, L.G., Waddington, J., 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecol. Appl. 13, 137–153.

Beckstead, J., Meyer, S.E., Allen, P.S., 1996. *Bromus tectorum* seed germination: between-population and between-year variation. Can. J. Bot. 74, 875–882.

Belnap, J., 2003. Comparative structure of physical and biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), Biological soil crusts: structure, function and management. Springer-Verlag, Berlin, Germany, pp. 177–192.

Boyd, C.S., Lemos, J.A., 2013. Freezing stress influences emergence of germinated perennial grass seeds. Rangel. Ecol. Manag. 66, 136–142.

Bradley, B.A., 2010. Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography 33, 198–208.

Call, C.A., Roundy, B.A., 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. J. Range Manag. 44, 543–549.

Chambers, J.C., Wisdom, M.J., 2009. Priority research and management issues for the imperiled Great Basin of the western United States. Restor. Ecol. 17, 707–714.

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol. Monogr. 77, 117–145.

Chambers, J.C., Bradley, B.A., Brown, C.S., D'Antonio, C., Germino, M.J., Grace, J.B., Hardegree, S.P., Miller, R.F., Pyke, D.A., 2014a. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17, 360–375.

Chambers, J.C., Miller, R.F., Board, D.I., Pyke, D.A., Roundy, B.A., Grace, J.B., Schupp, E.W., Tausch, R.J., 2014b. Resilience and resistance of sagebrush ecosystems: Implications for state and transition models and management treatments. Rangel. Ecol. Manag. 67, 440–454.

Douglas, D.S., Hafenrichter, A.L., Klages, K.H., 1960. Cultural methods and their relation to establishment of native and exotic grasses in range seedings. J. Range Manag. 13, 53–57.

Eiswerth, M.E., Shonkwiler, J.S., 2006. Examining post-wildfire reseeding on arid rangeland: a multivariate Tobit modelling approach. Ecol. Model. 192, 286–298.

Eiswerth, M.E., Krauter, K., Swanson, S.R., Zielinski, M., 2009. Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. J. Environ. Manag. 90, 1320–1325.

Flerchinger, G.N., Saxton, K.E., 1989a. Simultaneous heat and water model of a freezing snow-residue-soil system. I. Theory and development. Trans. ASAE 32, 565–571.

Flerchinger, G.N., Saxton, K.E., 1989b. Simultaneous heat and water model of a freezing snow-residue-soil system. II. Field verification. Trans. ASAE 32, 573–578.

Flerchinger, G.N., Seyfried, M.S., Hardegree, S.P., 2006. Using soil freezing characteristics to model multi-season soil water dynamics. Vadose Zone J. 5, 1143–1153.

Flerchinger, G.N., Caldwell, T.G., Cho, J., Hardegree, S.P., 2012. Simultaneous heat and water (SHAW) model: model use, calibration and validation. Trans. ASABE 55, 1395–1411.

Garbrecht, J.D., Schneider, J.M., 2007. Climate forecast and prediction product dissemination for agriculture in the United States. Aust. J. Agric. Res. 58, 966–974.

Gornish, E.S., Aanderud, Z.T., Sheley, R.L., Rinella, M.J., Svejcar, T., Englund, S.D., James, J.J., 2015. Altered snowfall and soil disturbance influence the early life stage transitions and recruitment of a native and invasive grass in a cold desert. Oecologia 177, 595–606.

Hardegree, S.P., 2006. Predicting germination response to temperature. I. Cardinal-temperature models and subpopulation-specific regression. Ann. Bot. 97, 1115–1125.

Hardegree, S.P., Van Vactor, S.S., 2000. Germination and emergence of primed grass seeds under field and simulated-field temperature regimes. Ann. Bot. 85, 379–390.

Hardegree, S.P., Flerchinger, G.N., Van Vactor, S.S., 2003. Hydrothermal germination response and the development of probabilistic germination profiles. Ecol. Model. 167, 305–322.

Hardegree, S.P., Moffet, C.A., Roundy, B.A., Jones, T.A., Novak, S.J., Clark, P.E., Pierson, F.B., Flerchinger, G.N., 2010. A comparison of cumulative-germination response of cheatgrass (*Bromus tectorum* L.) and five perennial bunchgrass species to simulated field-temperature regimes. Environ. Exp. Bot. 69, 320–327.

Hardegree, S.P., Jones, T.A., Roundy, B.A., Shaw, N.L., Monaco, T.A., 2011. Assessment of range planting as a conservation practice. In: Briske, D.D. (Ed.), Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. Allen Press, Lawrence, KS, pp. 171–212.

Hardegree, S.P., Schneider, J.M., Moffet, C.A., 2012. Weather variability and adaptive management for rangeland restoration. Rangelands 34, 53–56.

Hardegree, S.P., Moffet, C.A., Flerchinger, G.N., Cho, J., Roundy, B.A., Jones, T.A., James, J.J., Clark, P.E., Pierson, F.B., 2013. Hydrothermal assessment of temporal variability in seedbed microclimate. Rangel. Ecol. Manag. 66, 127–135.

Hardegree, S.P., Walters, C.T., Boehm, A.R., Olsoy, P.J., Clark, P.E., Pierson, F.B., 2015. Hydrothermal germination models: comparison of two data-fitting approaches with probit optimization. Crop Sci. 55, 2276–2290.

Harris, G.A., 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecol. Monogr. 37, 89–111.

Harris, G.A., 1977. Root phenology as a factor of competition among grass seedlings. J. Range Manag. 30, 172–177.

Hart, R.H., Dean, J.G., 1986. Forage establishment: Weather effects on stubble vs. fallow and fall vs. spring seeding. J. Range Manag. 39, 228–230.

Hemstrom, M.A., Wisdom, M.J., Hann, W.J., Rowland, M.M., Wales, B.C., Gravenmier, R.A., 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, USA. Conserv. Biol. 16, 1243–1255.

James, J.J., Svejcar, T.J., Rinella, M.J., 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. J. Appl. Ecol. 48, 961–969.

Jensen, K.B., Horton, W.H., Reed, R., Whitesides, R.E., 2001. Intermountain Planting Guide. Extension Publication AG510. Utah State University, Logan, Utah 104 pp.

Jordan, G.L., 1981. Range seeding and brush management on Arizona rangelands. Agricultural Experiment Station, University of Arizona College of Agriculture Bulletin T81121 Tucson, AZ, USA. 88 pp.

Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin desert—history, persistence, and influences of human activities. Glob. Environ. Chang. Hum. Policy Dimens. 6, 37–52.

Knutson, K.C., Pyke, D.A., Wirth, T.A., Arkle, R.S., Pilliod, D.S., Brooks, M.L., Chambers, J.C., Grace, J.B., 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. J. Appl. Ecol. 51, 1414–1424.

Kulpa, S.M., Leger, E.A., Espeland, E.K., Goergen, E.M., 2012. Postfire seeding and plant community recovery in the Great Basin. Rangel. Ecol. Manag. 65, 171–181.

Lambert, S., 2005. Guidebook to the Seeds of Native and Non-native Grasses, Forbs and Shrubs in the Great Basin. Technical Bulletin 2005-4. Bureau of Land Management, Boise, ID, USA 134 pp.

Lehrsch, G.A., Lentz, R.D., Kincaid, D.C., 2005. Polymer and sprinkler droplet energy effects on sugar beet emergence, soil penetration resistance, and aggregate stability. Plant Soil 273, 1–13.

Mao, W., Lewis, J.A., Hebbar, P.K., Lumsden, R.D., 1997. Seed treatment with a fungal or a bacterial antagonist for reducing corn damping-off caused by species of *Pythium* and *Fusarium*. Plant Dis. 81, 450–454.

McGinnies, W.J., 1973. Effects of date and depth of planting on the establishment of three range grasses. Agron. J. 65, 120–123.

Monsen, S.B., Stevens, R., 2004. Seedbed preparation and seeding practices. Restoring western ranges and wildlands vol. 1. USDA Forest Service, Fort Collins, CO, USA, pp. 121–154 General Technical Report RMRS-GTR-136.

Neher, D.A., Augspurger, C.K., Wilkinson, H.T., 1987. Influence of age structure of plant populations on damping off epidemics. Oecologia 74, 419–424.

Ogle, D., St. John, L., Cornwell, J., Stannard, M., Holzworth, L., 2008. Pasture and range seedings: planning-installation-evaluation-management. Technical Note, PM-TN-10. US Department of Agriculture, Natural Resources Conservation Service, Boise, ID, USA 35 pp.

Peters, D.P.C., 2000. Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semi-arid-arid-grassland ecotone. J. Veg. Sci. 11, 493–504.

Plummer, P.A., Christensen, D.R., Monsen, S.B., 1968. Restoring big-game range in Utah. Utah Division of Fish and Game, Ephraim, UT, USA Publication No. 68-3. 183 pp.

Pyke, D.A., Wirth, T.A., Byers, J.L., 2013. Does seeding after wildfires in rangelands reduce erosion or invasive species? Restor. Ecol. 21, 415–421.

Rajagopalan, B., Lall, U., 1998. Interannual variability in western US precipitation. J. Hydrol. 210, 51–67.

Reisner, M.D., Grace, J.B., Pyke, D.A., Doescher, P.S., 2013. Conditions favoring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. J. Appl. Ecol. 50, 1039–1049.

Roundy, B.A., Biedenbender, S.H., 1996. Germination of warm-season grasses under constant and dynamic temperatures. J. Range Manag. 49, 425–431.

Roundy, B.A., Call, C.A., 1988. Revegetation of arid and semi-arid rangelands. In: Tueller, P.T. (Ed.), Revegetation science applications for rangeland analysis and management. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 607–635.

Roundy, B.A., Hardegree, S.P., Chambers, J.C., Whittaker, A., 2007. Prediction of cheatgrass field germination potential using wet thermal accumulation. Rangel. Ecol. Manag. 60, 613–623.

Stewart, G., 1950. Reseeding research in the intermountain region. J. Range Manag. 3, 52–59.

Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manag. 42, 266–274.

Wisdom, M.J., Rowland, M.M., Tausch, R.J., 2005. Effective management strategies for sage-grouse and sagebrush: a question of triage? Transactions, North American Wildlife and Natural Resources Conference. 70, pp. 206–227