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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).