Rangeland Ecol Manage 66:127–135 | March 2013 | DOI: 10.2111/REM-D-11-00074.1

Hydrothermal Assessment of Temporal Variability in Seedbed Microclimate

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Abstract

The microclimatic requirements for successful seedling establishment are much more restrictive than those required for adult plant survival. The purpose of the current study was to use hydrothermal germination models and a soil energy and water flux model to evaluate intra- and interannual variability in seedbed microclimate relative to potential germination response of six perennial grasses and cheatgrass. We used a 44-yr weather record to parameterize a seedbed microclimate model for estimation of hourly temperature and moisture at seeding depth for a sandy loam soil type at the Orchard Field Test Site in southwestern Ada County, Idaho. Hydrothermal germination response was measured in the laboratory for two seed lots of cheatgrass (*Bromus tectorum* L.), four seed lots of bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Löve), three seed lots of bottlebrush squirreltail (*Elymus elymoides* [Raf] Swezey), and one seed lot each of Sandberg bluegrass (*Poa secunda* J. Presl.), big squirreltail (*Elymus multisetus* [J.G. Smith] M.E. Jones), thickspike wheatgrass (*Elymus lanceolatus* [Scribn. And J.G. Smith] Gould) and Idaho fescue (*Festuca idahoensis* Elmer). Germination response models were developed to estimate potential germination rate for 13 subpopulations of each seed lot for every hour of the 44-yr simulation. Seedbed microclimate was assessed seasonally and for each day, month, and year, and germination rate-sum estimates integrated for a numerical index of relative site favorability for germination for each time period. The rate-sum favorability index showed a consistent pattern among seed lots for different years, and provides a relatively sensitive indicator of annual and seasonal variability in seedbed microclimate. This index could be used with field data to define minimum weather thresholds for successful establishment of alternative plant materials, in conjunction with weather forecast models for making restoration and fire-rehabilitation management decisions in the fall season, for evaluation of potential climate-change impacts on plant community trajectories, and in optimization schemes for selecting among alternative restoration/rehabilitation management scenarios.

Key Words: climate, germination, microclimate, model, seed, weather

INTRODUCTION

Millions of hectares of sagebrush/bunchgrass rangeland in the Intermountain western United States are currently dominated by nonnative annual weeds such as cheatgrass (*Bromus tectorum* L.) and medusahead wildrye (*Taeniatherum caput-medusae* [L.] Nevski) (Young 1992; Knapp 1996; Young and Longland 1996; Davies 2008; Davies and Svejcar 2008). Rangeland restoration efforts in this region are limited by the dry climate, and complicated by relatively high spatial and temporal variability in weather (Rajagopalan and Lall 1998; Hardegree et al. 2011). New tools are needed to understand weather impacts on plant establishment, and to incorporate weather knowledge into the restoration planning process (Hardegree et al. 2012).

Seeding guides for rangelands in the Intermountain West acknowledge the general importance of climate in the form of tables that list species suitability as a function of mean annual precipitation (Jordan 1981; Jensen et al. 2001; Lambert 2005; Ogle et al. 2008; Sheley et al. 2008). Unfortunately, the microclimatic requirements for germination, emergence, and seedling establishment are much more restrictive than the longer-term climatic requirements for persistence of mature plants (Grubb 1977; Call and Roundy 1991; Peters 2000; Hardegree et al. 2003). Seeding guides may also indirectly acknowledge microclimatic limitations to establishment by suggesting climatic thresholds below which active seeding practices are not recommended (Anderson et al. 1957; Jordan 1981). One might expect, however, that even sites below an average climatological threshold will have some years in which desirable plant establishment is possible, at least in the absence of annual weed competition.

Seedbed microclimate in the Intermountain western United States is highly variable in both space and time (Pierson and Wight 1991). In addition to variability in precipitation, soil moisture and temperature are affected by solar radiation, wind, air temperature, relative humidity, vegetation, soil properties,

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Research was funded in part by the Bureau of Land Management, Intermountain Greenstripping and Rehabilitation Research Project, and the USDA-ARS Ecologically Based Invasive Plant Management program.

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Manuscript received 1 May 2011; manuscript accepted 17 June 2012.

and topography (Flerchinger and Pierson 1997). Flerchinger and Saxton (1989a, 1989b) developed the simultaneous heat and water (SHAW) model to characterize soil temperature and water content under alternative atmospheric, vegetation, and soil conditions. Enhanced understanding of natural variability in seedbed microclimate, and its impact on plant establishment and growth, may facilitate development of more effective revegetation strategies on disturbed Intermountain rangelands (Call and Roundy 1991; Roundy and Biedenbender 1996; Hardegree et al. 2003, 2010; Roundy et al. 2007).

Seed germination under temperature and water stress has received a great deal of attention in the rangeland literature (Wester 1991). Most previous germination studies evaluated only a limited number of environmental conditions with subsequent analyses constrained to simple treatment comparisons of germination rate and total germination (Scott et al. 1984; Brown and Mayer 1988). Hydrothermal models are parameterized with germination-rate data under a wide range of constant temperature and water potential conditions in the laboratory, but can subsequently be used to predict germination response to variable conditions in the field (Hardegree et al. 2003). These models have been used to assess population-level germination response of many agricultural plants but the primary application for rangeland species has been to develop static indices for seed lot comparison (Jordan and Haferkamp 1989; Allen et al. 2000; Meyer et al. 2000).

Some more recent studies have suggested that estimates of cumulative germination rate could be used as a quantitative index for ranking the general favorability of seedbed microclimate at a given site as a function of year, season, soil type, location, topography, species, and planting treatment (Hardegree et al. 2003). Hardegree et al. (2003, 2008, 2010) and Roundy et al. (2007) used hydrothermal models to evaluate several range grass species and seed lots under a variety of environmental conditions, but did not assess intra- and interannual variability in relative germination response.

The purpose of the current study was to use hydrothermal germination models and a soil-energy and water-balance model, calibrated for a field site in southern Idaho, to estimate the potential temporal variability in germination rate of six perennial bunchgrasses and cheatgrass. In this study, we tested whether species and seed lot performance was consistently ranked across different time periods, whether individual years and seasons were consistently ranked for relative microsite favorability across seed lots, and the efficacy of precipitation alone as a predictive index of potential germination response.

METHODS

SHAW Model Calibration and Simulation

The SHAW model uses meteorological, soil, and vegetation inputs to simulate heat and water movement through the soil–plant–atmosphere pathway (Flerchinger and Saxton 1989a, 1989b; Flerchinger and Hardegree 2004). The SHAW model was calibrated with meteorological and soil measurements for a Tindahay sandy-loam soil (sandy, mixed mesic, Xeric Torriorthent) from the Orchard Field Site in southern Ada County, Idaho, using an optimization procedure described by Flerchinger et al. (2012). Weather input data for the simulation were obtained from the Boise Airport for the period from 15 July 1961 to 30 September 2005. Each hydrologic year (1 October through 30 September) was simulated separately with an initialization of soil conditions at minimum expected water content as of 15 July in the preceding year. Simulations were initiated 2.5 mo before the start of a given hydrologic year to reduce variability caused by unknown initial soil conditions at the beginning of each simulation. Initialization of soil water content was estimated as the average of measured soil water content as a function of depth, as of 15 July, for the Orchard field data set as described by Flerchinger and Hardegree (2004). Model output was calibrated to optimize water potential and temperature predictions at a 2-cm seeding depth (Hardegree et al. 2003; Flerchinger et al. 2012). Model output consisted of water potential and temperature estimates for every hour of the 44-yr simulation period. The 2-cm depth was chosen because it was the minimum depth for which we had measured field data for model calibration (Flerchinger and Hardegree 2004).

Hydrothermal Germination Model Development and Simulation

Hydrothermal germination data were obtained for two seed lots of cheatgrass (Kuna and Orchard accessions previously reported in Hardegree et al. 2003); four seed lots of bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Löve; MOPX and P4 accessions previously reported in Hardegree et al. 2003, and two commercial seed lots of unknown provenance); three seed lots of bottlebrush squirreltail (*Elymus elymoides* [Raf] Swezey; Grand View (GV) seed lot previously reported in Hardegree et al. 2003 and two commercial seed lots of unknown provenance); one seed lot of big squirreltail (*Elymus multisetus* [J.G. Smith] M.E. Jones; previously reported as *Elymus elymoides* seed lot SH in Hardegree et al. 2003); and one seed lot each of Sandberg bluegrass (*Poa secunda* J. Presl.), thickspike wheatgrass (*Elymus lanceolatus* [Scribn. and J.G. Smith] Gould), and Idaho fescue (*Festuca idahoensis* Elmer), all obtained commercially and with unknown provenance. Each seed lot was evaluated for germination response over the temperature range of 3°C to 36°C, and the water potential range of 0 MPa to –2.5 MPa following the procedures described by Hardegree et al. (2003). Water potential treatments for each seed lot were replicated two or four times within each thermal-control chamber, and temperature treatments were replicated in three separate chambers for each experiment. Protocols for randomization of treatment vials, detection and removal of germinated seeds, fungicide application, and data evaluation are as described by Hardegree et al. (2003).

Germination counts for treatment vials within a given environmental chamber were pooled and the chamber values used as replicate samples for hydrothermal model development. Cumulative germination percentage was calculated for each combination of seed lot, temperature, and water potential for each day of the experiment. Seed populations were partitioned into subpopulations based on relative germination rate (Garcia-Huidobro et al. 1982; Benech Arnold et al. 1990). Days required to achieve 5% to 95% germination, in 5% increments, were calculated for each treatment by interpolation from the cumulative-germination curves (Covell et al. 1986). Inverse days required to achieve a given germination percentile was considered to equal the per-day germination rate of the subpopulation represented by that percentile ranking. Daily germination rates were divided by 24 to obtain hourly germination rate estimates for a given temperature/water potential combination (Hardegree and Van Vactor 2000).

A hydrothermal germination-rate model was developed for each subpopulation of each seed lot using a modification of the statistical gridding procedure described by Hardegree and Winstral (2006) for thermal germination data. Instead of plotting germination rate as a function of subpopulation and temperature, we plotted germination rate as a function of water potential and temperature for each subpopulation of each seed lot. Hardegree (2006) and Hardegree and Winstral (2006) documented the general validity of this approach for minimizing residual model error in thermal germination rate applications.

Calculation and Interpretation of Germination Rate-Sum Data

Hydrothermal germination rate was estimated for every subpopulation of every seed lot for every hour of the 44-yr simulation of seedbed temperature and water potential. Hourly rate estimates were aggregated to obtain daily rate sums, monthly rate sums, seasonal rate sums for the period 1 March to 31 May of each year, and an annual rate sum for each hydrologic year of the simulation.

Per-hour germination rate estimates represent the fractional progress toward germination for a given subpopulation during that hour (Hardegree 2006). Germination time for a given subpopulation can be estimated to occur when the sum of hourly postplanting germination rate estimates become equal to 1 (Roundy and Biedenbender 1996). Daily, monthly, seasonal, and annual rate sums are, therefore, an index of the relative favorability of the seedbed for germination during the period of interest (Hardegree et al. 2003, 2008, 2010; Hardegree and Winstral 2006). If one considers only temperature and water potential effects on germination, a rate sum of 1 indicates that the microclimate was favorable enough for a given seed subpopulation to germinate once during a specific time period. A rate sum of 2 indicates that the same seed subpopulation would have had the opportunity to germinate twice during the same period if identical seeds were planted immediately after germination of the initial subpopulation. A rate-sum value is an "index" of seedbed favorability as it only considers temperature and water potential effects on germination but ignores other important biotic and abiotic soil factors (Hegarty 1977; Hardegree et al. 2003).

Analysis of variance was used to evaluate seed lot differences in mean annual rate sum as a function of subpopulation (5–65%). Mean comparisons of significantly different subpopulation responses were assessed using Tukey's Honestly Significant Difference test. Annual rate sum data for the 25% subpopulation of each seed lot was used to rank each year of the simulation for relative favorability in seedbed microclimate. Individual years were ranked for each species and an average rank calculated across species for each year of the simulation. Similarity of ranking of a given year was assessed by pair-wise comparisons of seed lots using Kendall's rank correlation. A coefficient of determination (R^2) was calculated to assess the correlation of average annual precipitation and annual rate sum index for the 25% subpopulation of each species.

RESULTS

Mean precipitation and temperature values for annual, seasonal, and monthly time periods are shown in Table 1. Total precipitation during the simulation period averaged 298 mm and ranged from 146 mm to 428 mm (Fig. 1; Table 1). Coefficient of variation values for precipitation show that relative variability in mean precipitation across years increases dramatically between annual and monthly time periods (Table 1). Total precipitation during the March–May spring establishment period was of intermediate variability (Table. 1). Hydrologic-year and March–May precipitation were correlated but the coefficient of determination (R^2) was only 0.32. Average seasonal precipitation in Boise is highest in late fall, winter, and spring (Table 1). Temperature variability among years and months is relatively lower than variability in precipitation (Table 1).

Figure 2 shows the annual distribution of daily rate sums for the 25% subpopulation of relatively fast (BRTE-Kuna) and slow germinating (FEID) seed lots, and a seed lot with an intermediate germination rate (ELEL-GV). The daily rate sums in this figure represent the average progress, across all simulation years, that each seed lot would be expected to make on a given day, toward a total germination percentage of 25%. The inverse of the rate sum represents the number of days that it would take each seed lot to reach 25% germination if the seeds continued to experience the same environmental conditions as on that day. From the data shown in this figure, the highest average per-day germination rates across all years were about 0.28, 0.16, and 0.08 for cheatgrass, bottlebrush squirreltail, and Idaho fescue, respectively. Under these conditions, the cheatgrass seed lot would be expected to reach 25% total germination in about 3.6 d, squirreltail in about 6.3 d, and Idaho fescue in about 12.5 d. The maximum individual daily rate sums across all years were 0.89, 0.47, and 0.19, which correspond to potential germination times of 1.1 d, 2.1 d, and 5.3 d, respectively, for the same seed lots and subpopulations. Relative germination rates across seed lots were all very low in the winter, primarily from cold temperatures commonly near or below base temperature. Higher germination rates in the spring were extremely variable from year to year due to variability in soil water.

Table 2 shows average annual rate sums across all simulation years for all seed lots and seed subpopulations between 5% and 65%. Thermal and hydrothermal model error increases significantly for slower-germinating subpopulations (> 65%) due to the steep drop in total germination percentage for relatively cold, warm, or dry treatment conditions (Hardegree 2006). Annual rate-sum indices integrate all periods during a given year when conditions are favorable for germination. Both cheatgrass seed lots showed significantly higher rate sums than the other species, especially for the more rapidly germinating seed subpopulations (Table 2).

Individual seed lots and subpopulations had significantly different rate-sum favorability indices for a given time period, but the same relative response to the full range of modeled

Table 1. Mean monthly, seasonal, and annual precipitation and temperature for the Boise Airport weather station for the period 1 October 1961 to 30 September 2005. Numbers in parentheses represent the standard error of the mean.

	Time period													
	October	November	December	January	February	March	April	May	June	July	August	September	March–May	Annual
Precipitation	19 (2.2)	35 (2.6)	34 (3.3)	37 (3.1)	25 (2.6)	31 (2.9)	31 (2.3)	31 (4.2)	20 (2.5)	8 (1.3)	9 (2.0)	17 (2.5)	94 (5.8)	298 (11.2)
CV[1] Precipitation	80	49	64	56	68	62	49	87	81	107	156	96	41	25
Temperature (°C)	11 (0.2)	4 (0.3)	−1 (0.4)	−1 (0.4)	2 (0.4)	6 (0.3)	10 (0.3)	15 (0.2)	19 (0.3)	24 (0.3)	23 (0.3)	18 (0.3)	10 (0.2)	11 (0.1)

[1] CV indicates coefficient of variation.

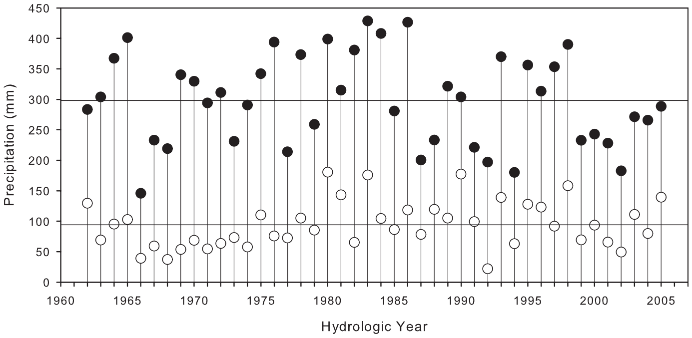

Figure 1. Annual precipitation variability in Boise, Idaho, for the period 1 October 1961 to 30 September 2005. Closed circles represent total precipitation during the hydrologic year and open circles represent total March–May precipitation. Upper and lower horizontal lines represent mean annual and March–May precipitation.

seedbed microclimate. Figure 3 shows the March–May rate-sum index for the 25% subpopulation of three seed lots ranked in descending average order across all modeled years. Kendall's rank correlation values for the seed lots shown in this figure were 0.91 for both the BRTE–ELEL and BRTE–FEID comparisons, and 0.96 for the ELEL–FEID comparison. The mean of pair-wise rank correlations across all seed lots was 0.95 and ranged from 0.84 to 0.99.

Figure 4 shows the relationship between annual precipitation and the annual rate sum of the 25% subpopulation from the same seed lots represented in Figures 2 and 3. Variability in this relationship is caused by temperature effects on germination, and by nonlinearity between precipitation and seedbed water potential. From the cheatgrass data in this figure, the average annual rate sum was 47 ± 2 SE. This rate sum, however, was achieved in years with average annual precipitation ranging from less than 215 mm to more than 370 mm (Fig. 4). Average annual precipitation in Boise is approximately 300 mm. In this general range of precipitation, annual rate-sum indices for

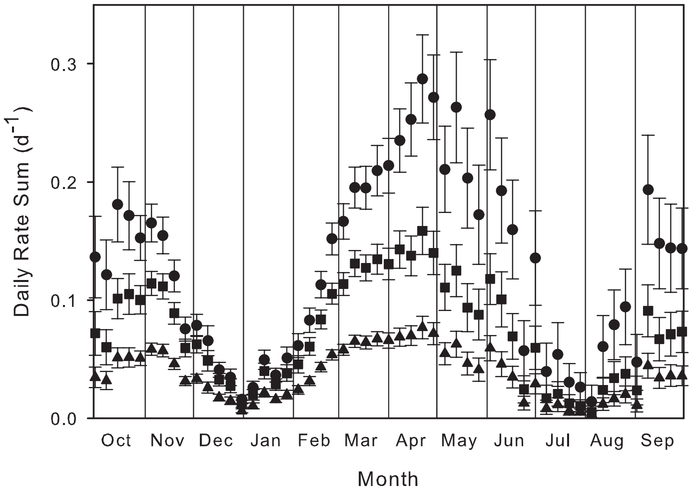

Figure 2. Average daily rate sums over the 44-yr simulation period for the 25% subpopulations of cheatgrass (BRTE-Kuna, circles), bottlebrush squirreltail (ELEL-GV, squares), and Idaho fescue (FEID, triangles). Error bars represent ± 1 standard error of the mean. Only every seventh day is shown for clarity.

Table 2. Mean annual rate sums across all years as a function of species/seed lot and subpopulation. Seed lot order is ranked highest to lowest based on the mean annual rate sum of the most rapidly germinating subpopulation (5%). Seed lot differences were analyzed by analysis of variance. Pair-wise multiple comparisons were made using Tukey's Honestly Significant Difference test. Means within columns associated with the same letter were not significantly different (α=0.05).

Species (Seed lot)[1]	Subpopulation (%)												
	5	10	15	20	25	30	35	40	45	50	55	60	65
BRTE (Orchard)	72 (2.4) a	64 (2.1) a	59 (2.0) a	55 (1.8) a	52 (1.7) a	49 (1.6) a	46 (1.5) a	43 (1.4) a	40 (1.3) a	38 (1.2) a	35 (1.1) a	32 (1.1) a	27 (0.9) a
BRTE (Kuna)	69 (2.3) a	61 (2.0) a	55 (1.8) a	50 (1.7) b	47 (1.5) b	44 (1.4) b	41 (1.3) b	38 (1.2) b	34 (1.1) b	28 (1.0) b	22 (0.8) b	15 (0.6) c	12 (0.5) cd
ELEL (GV)	35 (1.1) b	32 (1.0) b	30 (0.9) b	28 (0.9) c	27 (0.8) c	26 (0.8) c	25 (0.8) c	25 (0.8) c	24 (0.7) c	23 (0.7) c	22 (0.7) b	22 (0.7) b	21 (0.6) b
ELMU (SH)	33 (1.1) bc	29 (1.0) bc	27 (0.9) bc	25 (0.8) cd	24 (0.8) cd	23 (0.7) cd	21 (0.7) d	20 (0.6) d	18 (0.6) d	16 (0.5) d	14 (0.5) cd	11 (0.4) de	8 (0.3) fg
PSSP (MOPX)	28 (0.9) cd	25 (0.8) cd	23 (0.7) cd	22 (0.7) de	20 (0.6) de	19 (0.6) de	19 (0.6) de	18 (0.6) de	17 (0.5) de	16 (0.5) d	15 (0.5) c	15 (0.5) c	14 (0.4) c
PSSP (Comm 1)	27 (0.9) d	24 (0.8) cd	22 (0.7) cde	21 (0.7) ef	20 (0.6) ef	18 (0.6) e	17 (0.6) e	16 (0.5) e	14 (0.5) efg	13 (0.5) efg	13 (0.4) de	12 (0.4) de	11 (0.4) de
ELEL (Comm 1)	23 (0.7) de	22 (0.7) de	21 (0.7) def	20 (0.6) ef	19 (0.6) ef	18 (0.6) e	18 (0.6) de	17 (0.5) de	17 (0.5) def	16 (0.5) de	16 (0.5) c	15 (0.5) c	14 (0.5) c
PSSP (P4)	21 (0.7) ef	19 (0.6) ef	18 (0.6) efg	17 (0.6) efg	17 (0.6) efg	16 (0.5) ef	15 (0.5) ef	15 (0.5) efg	14 (0.5) fg	13 (0.5) fg	12 (0.4) de	12 (0.4) de	11 (0.4) d
PSSP (Comm 2)	20 (0.6) ef	18 (0.6) ef	18 (0.5) fg	17 (0.5) fg	16 (0.5) fg	16 (0.5) ef	15 (0.5) ef	15 (0.5) ef	14 (0.5) ef	14 (0.4) def	14 (0.4) cd	13 (0.4) cd	13 (0.4) cd
ELLA	19 (0.6) efg	17 (0.6) efg	16 (0.5) gh	15 (0.5) gh	14 (0.5) gh	13 (0.4) fg	12 (0.4) fgh	11 (0.4) gh	10 (0.3) hi	10 (0.3) hi	9 (0.3) fg	8 (0.3) fg	6 (0.2) gh
ELEL (Comm 2)	19 (0.6) efg	16 (0.5) fg	15 (0.5) gh	13 (0.5) gh	11 (0.4) h	10 (0.4) g	9 (0.3) h	7 (0.3) i	6 (0.2) j	5 (0.2) j	4 (0.2) h	3 (0.1) h	2 (0.1) i
FEID	17 (0.5) fg	16 (0.5) fg	15 (0.5) gh	14 (0.4) gh	14 (0.4) gh	13 (0.4) fg	13 (0.4) fg	12 (0.4) fgh	11 (0.3) gh	11 (0.3) gh	10 (0.3) ef	10 (0.3) ef	9 (0.3) ef
POSE	14 (0.4) g	13 (0.4) g	12 (0.4) h	11 (0.4) h	10 (0.3) h	10 (0.3) g	9 (0.3) gh	9 (0.3) hi	8 (0.3) ij	7 (0.2) ij	7 (0.2) gh	6 (0.2) g	5 (0.2) h

[1] BRTE indicates *Bromus tectorum* L.; ELEL, *Elymus elymoides* (Raf) Swezey; ELMU, *Elymus multisetus* (J.G. Smith) M.E. Jones; PSSP, *Pseudoroegneria spicata* (Pursh) Löve; ELLA, *Elymus lanceolatus* (Scribn. and J.G. Smith); FEID, *Festuca idahoensis* Elmer; POSE, *Poa secunda* J. Presl; GV, Grand View, Paradise Valley, Nevada; SH, Sand Hollow, Gem County, Idaho; MOPX, Multiple Origin Polycross seedlot P7; Comm, commercial seedlot; seedlot P4, Ainsworth, British Columbia.

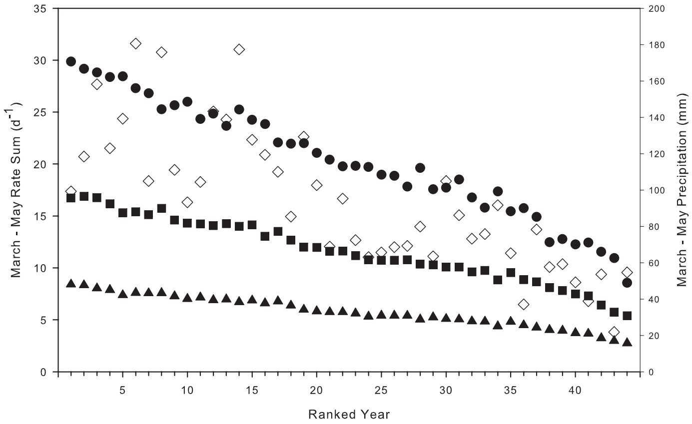

Figure 3. March–May rate-sum index for the 25% subpopulations of cheatgrass (BRTE-Kuna, circles), bottlebrush squirreltail (ELEL-GV, squares), and Idaho fescue (FEID, triangles) and March–May precipitation (diamonds) ranked in descending order of average annual rate-sum across all seed lots tested.

cheatgrass were as low as 33 and as high as 60 (Fig. 4). The coefficients of determination (R^2) for linear regression equations for the data in Figure 4 were 0.52, 0.55, and 0.54 for cheatgrass, squirreltail, and Idaho fescue, respectively.

DISCUSSION

Average climate information is currently used in rangeland restoration and rehabilitation planning for the selection of

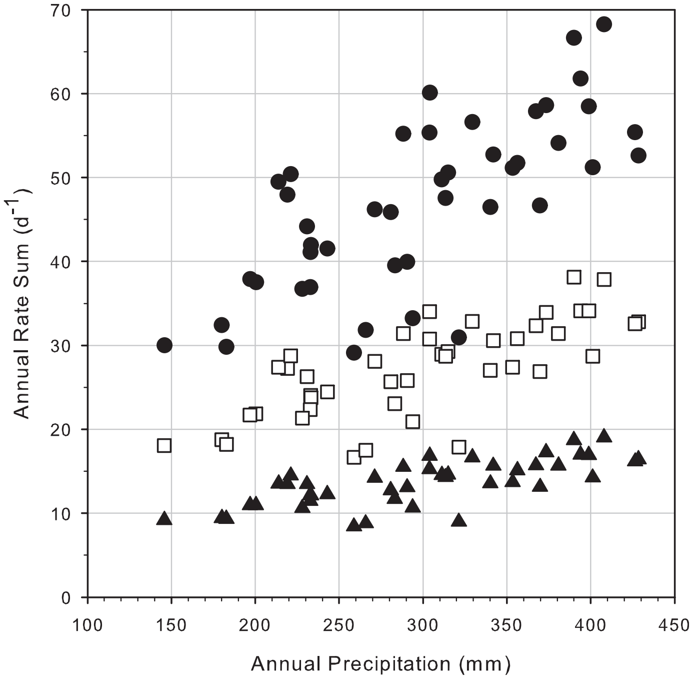

Figure 4. Annual rate sum index for the 25% subpopulations of cheatgrass (BRTE-Kuna, circles), bottlebrush squirreltail (ELEL-GV, squares), and Idaho fescue (FEID, triangles) as a function of annual precipitation. Each symbol represents the rate-sum/precipitation relationship for 1 yr of the simulation.

plant materials. The most common resource for this purpose is a table from a seeding guide that lists species as a function of mean annual precipitation, roughly adjusted for soil textural effects (Jensen et al. 2001; Lambert 2005; Ogle et al. 2008). Seasonal averages of the type shown in Table 1 are also used to justify selection of the most appropriate planting season. Fall seeding is commonly practiced in the Great Basin to take advantage of all opportunities for germination and seedling growth in the fall, winter, and spring (Plummer et al. 1968; Roundy and Call 1988; Monsen and Stevens 2004; Eiswerth and Shonkwiler 2006).

Improvement of seedbed microclimate is the principal rationale for most seedbed preparation and planting methods (Hardegree et al. 2011). These methods are designed to optimize seedbed temperature and moisture, increase the number of favorable microsites for germination and establishment, and mitigate competition for water and other resources by undesirable weedy species (Call and Roundy 1991; Krueger-Mangold et al. 2006; Sheley et al. 2006). Recommendations for site preparation and planting, however, are generally prescriptive in that they do not consider relative treatment effectiveness under alternative weather conditions. Treatment effectiveness may be less meaningful in years when water is generally available, regardless of planting methodology, or in years of consistently unfavorable microclimate when any restoration strategy would probably be unsuccessful (Wood et al. 1982; Eckert et al. 1986; Winkel and Roundy 1991; Roundy et al. 1992).

Figure 1 demonstrates the high annual variability in annual and March–May precipitation for the semiarid rangeland location modeled in this study. This variability alerts us to three issues: generic or prescriptive management is unlikely to be optimal in most years; it may be difficult to specifically identify the limiting climate factors in a given restoration year; and direct comparison of site and year effects will be problematic even for locations and treatments that receive similar total annual precipitation. Most field studies of rangeland restoration in the Great Basin do not report more than gross climatological parameters, but the majority of successful seeding studies appear to have been undertaken in years of average or above average precipitation (Hardegree et al. 2011).

Call and Roundy (1991) recommended changes to the prevailing research approach to more directly address restoration problems inherent in highly variable rangeland systems. A more general scientific understanding of targeted vegetation change may now be achievable using current conceptual models for dynamic rangeland systems (Westoby et al. 1989; Bestelmeyer et al. 2003; Sheley et al. 2006). The Natural Resources Conservation Service (NRCS) uses state-and-transition models in their ecological site descriptions (ESD), which are a primary resource for rangeland restoration planning in the Great Basin.[1] Current state-and-transition models acknowledge that there is a limited set of potential trajectories for moving between undesirable and desirable vegetation states and that many transition pathways require a specific, and perhaps infrequent, series of climatic events (Westoby et al. 1989; Batabyal and Godfrey 2002; Bestelmeyer et al. 2003; Briske et al. 2005; Bashari et al. 2008). State-and-transition models associated with NRCS ESDs, however, do not currently address the probabilities associated with transition pathways that are influenced by weather and climate variability. Site and year-specific weather data are primarily used retrospectively to qualitatively explain seeding failure. Weather data could be more effectively used by restoration planners in the Great Basin if the following steps were taken:

1) meteorological parameters were translated into microclimatic parameters that were more directly related to establishment and growth;
2) quantitative metrics, such as the rate-sum indices described here, were available to replace the qualitative criteria currently used for retrospective analysis of highly variable field, site, and treatment conditions;
3) these metrics were accessible at a spatial and temporal resolution relevant to the critical phases of plant establishment at a given location; and
4) more effective forecasting tools were available for the 3- to 12-mo planning horizon between the time of year most commonly used for seedbed preparation, weed control, and seeding (mid- to late fall) and the critical weather period for germination, seedling establishment, and initial survival (the following winter, spring and summer).

The current study addresses the first three of these issues, but also provides a microclimate-based metric that could be used in conjunction with weather forecast information for real-time management planning in the fall season.

Step one of this study was to translate meteorological variability into relevant parameters of temperature and water potential at seeding depth. Precipitation is a principal driver of soil water potential, but is not proportional to potential plant response in the winter when soil temperatures limit seed germination rates (Fig. 2). Years of average favorability in seedbed microclimate could be obtained in both above- and below-average precipitation years (Fig. 4). Indeed, only about 54% of the annual variability in relative seedbed conditions could be explained by total annual precipitation (Fig. 4). Years with relatively high total precipitation, such as 1980 and 1982, could have fundamentally different seasonal and monthly precipitation in the critical spring months (Fig. 1). A relatively favorable year or season could also have a short period of unfavorable conditions that could terminate growth before seedling establishment. The rate-sum favorability index used in this study makes it possible to interpret temporal variability in weather and seedbed microclimate with a quantitative metric directly relevant to initial seedling establishment. This metric could be further developed to evaluate both favorable periods of seedbed microclimate, and periodic mortality events that may ultimately limit relative success at different stages of seedling establishment (James et al. 2011; Boyd and James 2013 [this issue]).

It should be noted that the model simulations used in this study ignore a large number of biotic and abiotic factors that might affect predictions of actual field emergence (Hegarty 1977; Egli and TeKrony 1996; Weaich et al. 1996; Beckstead et al. 2007). Thermal models have been rigorously tested for accuracy in estimating variable temperature effects on cumulative germination response (Hardegree et al. 1999; Hardegree 2006) but it has proven difficult to simulate variable-water potential effects in the laboratory. Hardegree et al. (2003),

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[1] http://esis.sc.egov.usda.gov

however, noted that the bulk of progress toward germination in a given season is expected to occur when germination rates are relatively high during periods of low to moderate water stress, and when temperatures are only moderately suboptimal. Roundy et al. (2007) took advantage of this phenomenon to simplify the hydrothermal modeling approach for estimation of wet-thermal germination response, and Rawlins et al. (2012) subsequently obtained relatively robust predictions of actual field germination response. James et al. (2011) found that the life-stage transition between germination and emergence was more limiting to seedling establishment than germination per se. We believe, therefore, that the model simulations used in this study adequately reflect realistic patterns of potential germination in the field.

Flerchinger and Hardegree (2004) showed that seedbed model calibration could be optimized more effectively by assessing the impact of soil-model error on potential plant response. Germination-rate sums effectively integrate weather and microclimatic impacts on potential plant response and, therefore, serve as a more accurate indicator of seedbed favorability than precipitation alone. Germination indices may prove especially useful when estimating seedbed favorability as a function of topography, aspect and soil differences that may be highly variable within what is otherwise an identical weather domain.

The microclimatic ranking for a given year or time period was relatively insensitive to the species or subpopulation used to calculate the rate sum index (Fig. 3). The consistency of year rank across seed lots indicates that any seed lot or subpopulation could be used to rank relative favorability of seedbed microclimate for different years, seasons, or monthly time periods. The relative response of individual seed lots was also consistent across years, months, and seasons. These indices, therefore, could also be used to evaluate relative suitability of alternative plant materials for a given site, and perhaps yield insight into species-specific microclimatic thresholds for successful establishment.

The two cheatgrass seed lots were dramatically superior to the native plant materials in relative germination rate (Fig. 3; Table 2). The earlier germinating cheatgrass seeds had approximately twice the opportunity to germinate over the course of the year when compared to the earlier germinating seeds of the other plant species (Fig. 3; Table 2). Hardegree et al. (2003) noted that direct comparison of cheatgrass and other species may be overshadowed by the relatively high seed numbers typically produced by cheatgrass, even after wildfire (Humphrey and Schupp 2001). The two seed lots of cheatgrass used in the current study are probably insufficient for species-level inferences of relative hydrothermal response, but previous studies of thermal response showed similarly rapid germination for eight cheatgrass accessions collected in each of 2 yr from widely varying locations in Idaho, Nevada, and Washington, in the United States, and British Columbia, Canada (Roundy et al. 2007; Hardegree et al. 2010).

Germination rate-sum indices can be used to assign a quantitative value to the expected microclimatic impact of alternative management treatments under historical or predicted future weather conditions. The most promising future use of this index may require further development of accurate, relatively long-range (3–12-mo) weather forecasts for the Great Basin. Similar technology is commonly used in agriculture and for some rangeland productivity applications in other regions of the country (Jochec et al. 2001; Schneider and Garbrecht 2006; Meinke et al. 2007; Baigorria et al. 2008; O'Lenic et al. 2008). If the utility of long-term weather forecasts in the Great Basin could be established, it would be possible to construct economic models to assess the potential long-term benefits of adopting forecast/modeling technology in rangeland restoration planning (Batabyal and Godfrey 2002; Schneider and Garbrecht 2006; Bashari et al. 2008). Weather forecasts could be used to trigger contingency plans in favorable years in areas that have been previously identified for restoration, and for which premanagement logistics of equipment, personnel, and plant materials are in place (Westoby et al. 1989; Bakker et al. 2003). Even low-resolution weather forecasts could improve the cost–benefit ratio of management treatments by allowing the land manager to shift resource expenditures to years with a higher probability of success (Hardegree et al. 2003; Hardegree and Van Vactor 2004).

Microclimatic limitations in arid and semiarid systems require definition of realistic goals when establishing rehabilitation and restoration planning objectives (Call and Roundy 1991; Hobbs and Norton 1996; Ehrenfeld 2000; Jones 2003). Unpredictable weather tends to support the following pragmatic recommendations: preferential use of nonnative plant materials because their probability of establishment is higher (Asay et al. 2001) and abandonment of areas with low average precipitation (less than 25 $\mathrm{cm \cdot yr^{-1}}$) because of the high likelihood of failure even with nonnative plant materials (Anderson et al. 1957; Jordan 1981). Utilization of existing weather data and development of long-term weather forecasting tools may support expanded use of native plant materials and restoration of low-precipitation rangelands as more realistic goals.

MANAGEMENT IMPLICATIONS

Microclimatic variability in the seedbed determines the relative success of most rangeland restoration and rehabilitation projects. Precipitation variability is a principal driver of seedbed microclimate but it has been difficult to interpret precipitation effects at the temporal scale necessary to evaluate growth and mortality events during specific critical periods of seedling establishment. In this study, we developed a quantitative rate-sum index that could be used to evaluate the relative favorability of seedbed microclimate at any temporal scale. This index accounts for the moderating effects of soil on seedbed temperature and moisture, and is based on predicted response of plant materials. This index lends itself to quantitative assessment of site, year, and treatment effects on seedbed microclimate, and ranking of unique conditions relative to the whole range of conditions that could feasibly be expected to occur at a given site. Rate-sum values allow one to assign a numerical index for retrospective assessment of historical seeding success, or to project potential impacts of alternative future climate scenarios. Quantitative indices of this type might also be used to establish realistic probabilities of transition pathways between alternative vegetation states, and for economic assessment of alternative restoration management strategies.

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