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## A comparison of cumulative-germination response of cheatgrass (*Bromus tectorum* L.) and five perennial bunchgrass species to simulated field-temperature regimes

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*Poa secunda*

### ABSTRACT

Cheatgrass (*Bromus tectorum* L.) has come to dominate millions of hectares of rangeland in the Intermountain western United States. Previous studies have hypothesized that one mechanism conferring a competitive advantage to this species is the ability to germinate rapidly at low temperatures in the fall, winter and spring and, therefore, initiate growth and establishment more rapidly than more desirable perennial bunchgrass species. In this experiment, we developed thermal-germination-response models for multiple seedlots of cheatgrass and five perennial grass species. We conducted sensitivity analysis on potential-cumulative-germination response to a 38-year simulation of field-variable conditions of seedbed temperature and moisture. Cheatgrass uniformly germinated at a higher rate, and required significantly less time to complete germination than any of the perennial species for all but the slowest seed subpopulations. A germination-rate-sum index was used to integrate relative response characteristics over time. This index showed that germination rate of the most rapidly germinating subpopulations of cheatgrass was 2–5 times higher than for the other species tested. Model simulations of this type provide a more ecologically relevant basis for seedlot evaluation as they allow comparisons across a wide range of potential conditions that may be experienced in the field.

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### 1. Introduction

Cheatgrass (*Bromus tectorum* L.) now dominates millions of hectares of sagebrush-bunchgrass rangeland in the Intermountain region of the western United States (Mack, 1981; Young et al., 1987; D'Antonio and Vitousek, 1992; Knapp, 1996; DiTomaso, 2000). It has been suggested that rapid germination, particularly at low temperatures in the late fall, winter and early spring, may contribute to the competitive success of this species (Hull, 1964; Harris, 1967, 1977; Harris and Wilson, 1970; Wilson et al., 1974; Thill et al., 1979; Hardegee, 1994a,b; Beckstead et al., 1996; Goodwin et al., 1996; Hardegee et al., 2003). Young and Evans (1982) evaluated thermal response of a large number of seedlots of cheatgrass and other species, under a wide variety of thermal conditions, but only reported temperature effects on

total germination percentage. Several previous studies have evaluated thermal or hydrothermal-germination response of cheatgrass and other rangeland grasses, but limited analysis to comparison of model indices, or focused on seed-dormancy processes (Wester, 1991; Jordan and Haferkamp, 1989; Hardegee, 1994a,b; Romo and Eddleman, 1995; Allen et al., 2000; Meyer et al., 2000). Hardegee and Van Vactor (2000) and Hardegee et al. (2003) proposed that model estimates of cumulative-germination response to potential field-variable temperature and moisture regimes might provide a more ecologically relevant index for species and seedlot comparisons. Hardegee et al. (2008) evaluated thermal-germination response of 41 accessions of bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey] and big squirreltail [*Elymus multisetus* (J.G. Smith) Burt-Davy] using this methodology, and Roundy et al. (2007) used a similar approach to evaluate potential-germination response of 18 cheatgrass seedlots over a four-year period at nine big sagebrush (*Artemisia tridentata* Nutt.) sites in Nevada and Utah. Historical simulation of potential-germination response can be used to rank seedlots, but also provides sensitivity analysis on

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the effects of annual and seasonal variability in temperature and water availability that may be experienced in the field (Hardegee, 2006b).

The purpose of the current study was to expand upon previous analyses of Hardegee et al. (2003), Roundy et al. (2007) and Hardegee et al. (2008) to include multiple accessions of cheatgrass, big and bottlebrush squirreltail, bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], basin wildrye [*Leymus cinereus* (Scribn. and Merr.) A. Löve] and Sandberg bluegrass [*Poa secunda* Vasey]. Specific objectives were to compare simulated germination rate of cheatgrass and perennial bunchgrass species under historical field-temperature regimes; and to evaluate potential variability in cumulative-germination response as a function of seasonal and annual variability in seedbed temperature and moisture.

## 2. Materials and methods

Thermal-germination-response data for 14 seedlots of bottlebrush squirreltail (ssp. *brevifolius*, Group A), 20 seedlots of big squirreltail, eight seedlots of cheatgrass, three seedlots of bluebunch wheatgrass, and one seedlot of Sandberg bluegrass, were derived from several previous studies as described by Hardegee et al. (2003, 2008), Hardegee (2006a), and Roundy et al. (2007).

Five additional seedlots of bluebunch wheatgrass; five seedlots of basin wildrye, three seedlots of bottlebrush squirreltail and one seedlot of big squirreltail were harvested from nursery-grown plants at the Utah State University, Evans Farm, Millville, UT in 1996 for germination testing in 1997. The cultural practices for seed production followed similar procedures described by Jones et al. (2003) for big and bottlebrush squirreltail. The five seedlots of basin wildrye originated from two released varieties (Trailhead and Magnar) and three wildland collections (Benson, UT; Soda Springs, ID; Delcio, NV). The additional seedlots of bluebunch wheatgrass also originated from two released varieties (Whitmar and Goldar) and three wildland collections (Ainsworth, BC; Connell, WA; Meeker, CO). The three additional accessions of bottlebrush squirreltail and one accession of big squirreltail were derived from wildland collections (*E. elymoides* ssp. *brevifolius* from Buford, CO, Pueblo, CO and Los Lunas, NM; *E. multisetus* from Sand Hollow, ID). The three *E. elymoides* ssp. *brevifolius* accessions belonged to Group A as identified by Jones et al. (2003) and Hardegee et al. (2008). The Ainsworth, BC collection of bluebunch wheatgrass, and Sand Hollow, ID collection of bottlebrush squirreltail, were the same as two previous accessions included from the previous study by Hardegee et al. (2003).

One additional seedlot of Sandberg bluegrass was obtained from a commercial seed company and evaluated for thermal-germination response in 2007 using the same general experimental design described by Roundy et al. (2007) for cheatgrass seedlots, except that germination vials were replicated 4 times within each chamber.

Twenty-one constant-temperature regimes between 3 °C and 38 °C were tested for the 15 additional seedlots using a similar experimental design as described by Hardegee (2006a). Germination vials, containing 30 seeds each, were replicated 5 times within each environmental chamber but individual temperature regimes were not replicated. Seeds were monitored every day, for up to 52 days in some of the colder temperature treatments, and were counted and removed when they exhibited radicle extension of  $\geq 2$  mm.

The statistical-gridding (SG) procedure developed by Hardegee and Winstral (2006) and tested by Hardegee (2006b) was used to model germination rate ( $\text{day}^{-1}$ ) for each seedlot as a function of temperature and seed-subpopulation. Germination rates

as a function of temperature for all subpopulations (5–95% in 5% increments) of each seedlot were estimated for each hour of a 255-day period between 6 October and 18 June of a given hydrologic year for a 38-year seedbed-microclimatic simulation as previously described by Hardegee et al. (2003). This process was repeated for all hours of the test period regardless of simulated soil-water potential (Flerchinger and Hardegee, 2004) as described by Hardegee et al. (2008). Under a second scenario, germination rates were estimated only for hours in which water potential was determined to be less negative than  $-1.0$  MPa (Hardegee et al., 2003; Roundy et al., 2007).

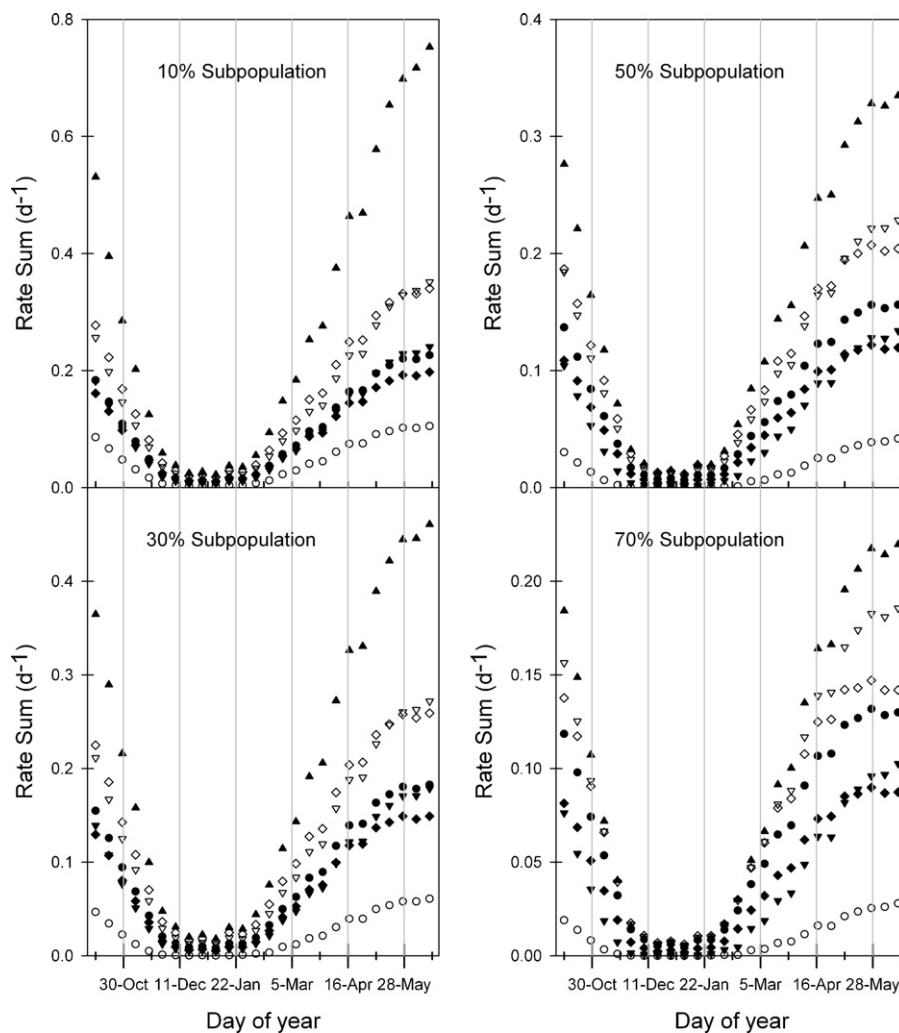
Hourly-rate estimates reflect the percentage progress toward germination of a given subpopulation during each hour. The summation of hourly-rate values over a 24-hour period represents the percentage progress toward germination for a given day, therefore, germination time can be estimated as the time it takes for the cumulative-germination-rate sum to become equal to 1 (Roundy and Biedenbender, 1996; Phelps and Finch-Savage, 1997; Hardegee et al., 1999).

Germination-rate sums were calculated for each combination of species, accession, seedlot-collection year, and subpopulation for every day of the 255-day simulation period for each year. Germination time was also calculated for every subpopulation for 12 simulated planting dates in each year starting on 6 October and every 21-days thereafter until 28 May. The last 8 simulated planting dates in this study were identical to those described by Hardegee et al. (2008) for 41 squirreltail seedlots. Rate-sums and germination times were averaged across seedlot accessions that were collected in different years, and then averaged across all years of the test period by Julian date. Mean rate sums for a given Julian date and seedlot accession were then averaged by species. The 5 seedlots of basin wildrye exhibited two distinct groupings based on relative population response and were divided into two categories: released varieties (LeciR; Trailhead and Magnar) and wildland collections (LeciW; Benson, UT; Soda Springs, ID; Delcio, NV).

Species were compared for relative germination response using mixed-model Analysis of Variance (ANOVA) for: comparison of daily-rate sums on the 12 simulated planting dates; comparison of annual rate-sums accumulated over the entire 255-day evaluation period; and comparison of germination time as a function of simulated planting date for model simulations using all hourly temperatures; and for model simulations in which thermal accumulation was only calculated when simulated soil-water potential was less negative than  $-1.0$  MPa. Daily-rate sums and germination-time values were only evaluated for select subpopulations (10%, 30%, 50% and 70%). The Fisher's protected least-square-difference test was used for multiple comparisons of significant main-treatment effects.

## 3. Results

The seasonal distribution of daily-germination rate-sums, as affected by temperature only, is shown in Fig. 1. Species response was roughly ranked based on maximum-daily rate-sum of the 50% subpopulation in the following order of relative germination rate (high to low): cheatgrass > bluebunch wheatgrass, big squirreltail > bottlebrush squirreltail > Sandberg bluegrass, basin wildrye (wildland collections) > basin wildrye (released varieties). Daily-germination rate-sum estimates were reduced by approximately 70% when thermal accumulation was limited to periods when water potential was estimated to be less negative than  $-1.0$  MPa (Fig. 2), but relative seedlot response and differences among seedlots were similar. The results of multiple-comparison tests for significant differences among species are shown in Table 1 for selected subpopulations and planting dates. Significant differ-



**Fig. 1.** Seasonal variability in mean daily-rate-sum as a function of seed subpopulation and species for *Bromus tectorum* (▲), *Elymus multisetus* (◇), *Pseudoroegneria spicata* (▽), *Elymus elymoides* ssp. *brevifolius* (●), *Leymus cinereus* wildland collections (▼), *Poa secunda* (◆), and *Leymus cinereus* released varieties (○). Daily-rate-sum means were derived by first averaging by seedlot across all years, and then across seedlots within a given species. Rate-sum means in this figure were calculated for all hours regardless of water-potential estimate.

ences in daily-rate sums were dependent upon both planting date and subpopulation (Table 1).

Data for subpopulation variability in daily thermal-rate summation show a consistent and expected pattern of seasonal variability across all species. Regardless of subpopulation, estimated values for daily-germination rate are lowest during winter and higher in late fall and spring (Fig. 1). Daily-rate summations limited to water potentials less negative than  $-1.0$  MPa were reduced in the fall as this season is relatively dry in southwestern Idaho.

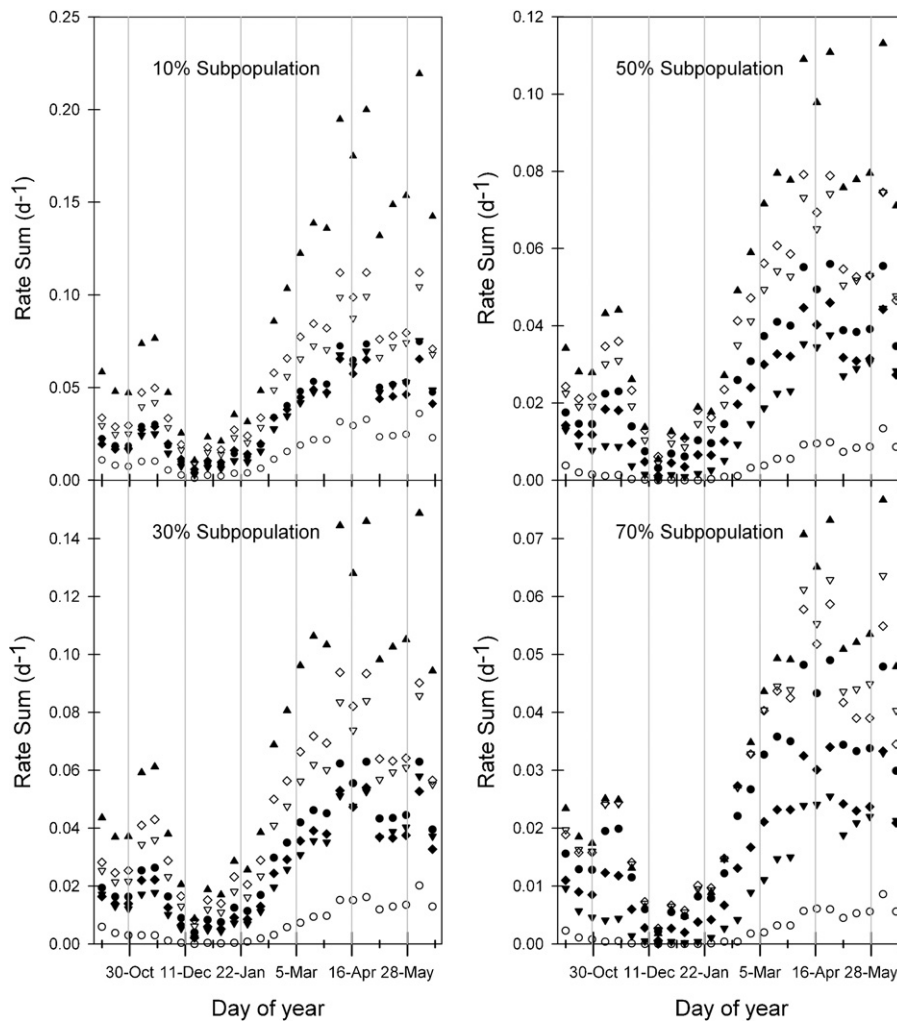
Patterns of predicted-cumulative germination matched the daily-rate-sum data but the absolute magnitude of differences among species was highly dependent on planting date (Fig. 3 and Table 2). Simulated germination times for the 50%-seed subpopulation ranged from about 50 to 100 days for most species for simulated planting dates in early December, to only 3 to 10 days in late May (Fig. 3a). Simulated germination times were greatly delayed when thermal accumulation was restricted to periods of relative water availability (Fig. 3b). This delay was relatively greater during warmer planting periods when the seeds were more likely to experience water stress.

The mean cumulative-annual-rate-sum as a function of seed subpopulation during the 255-day test period is shown for all species in Fig. 4. The cumulative-annual-rate-sum integrates the data in Fig. 1 to provide a more concise index for comparison of

species and seedlot differences. As with the daily-rate-sum data, significance of species and seedlot differences were subpopulation-dependant (Table 3). In general, cheatgrass germination rates were 2–5 times higher than for the other species for the most rapidly germinating subpopulations, but less so for slower-germinating seed subpopulations (Figs. 1, 2, and 4). An alternative way to interpret the data in Fig. 4 is to consider that the numerical value of the cumulative-rate-sum is equivalent to the number of times a given subpopulation would be expected to germinate if seeds with the same germination-rate response were planted on the first day of the simulation, and replanted immediately after germination occurred from the previous planting event. The data in Fig. 4 overestimate the number of periods in which germination would be expected to occur in the field as they do not take into account water-potential effects. Cumulative-annual-rate-sum estimates for water potentials less negative than  $-1.0$  MPa were approximately 70% lower than those shown in Fig. 4, but relative species differences were very similar (data not shown).

#### 4. Discussion

Wester (1991) summarized the results of many previous studies investigating temperature and water-stress effects on rangeland-plant germination. The majority of these studies evaluated only



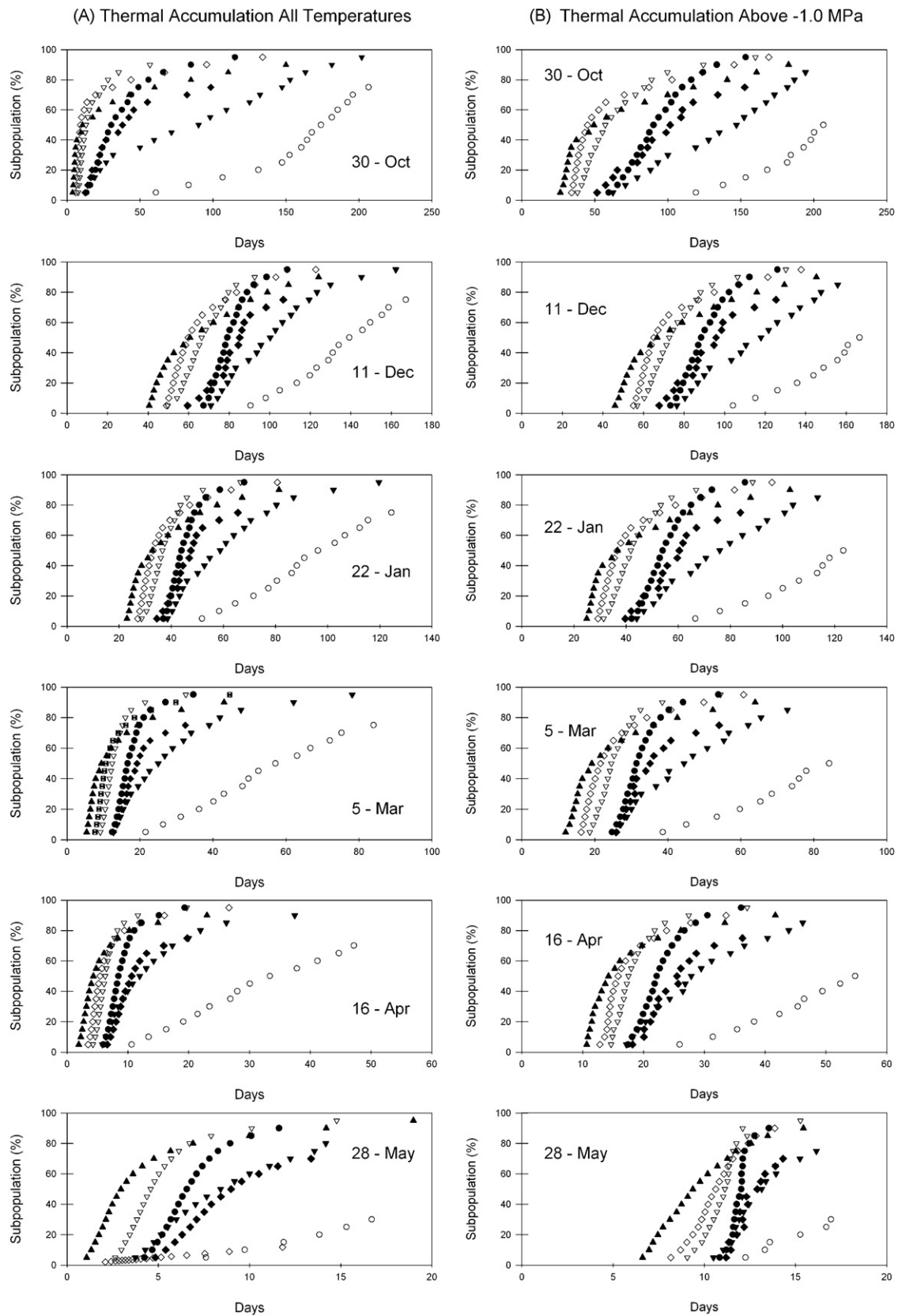
**Fig. 2.** Seasonal variability in mean daily-rate-sum as a function of seed subpopulation and species for *Bromus tectorum* (▲), *Elymus multisetus* (◇), *Pseudoroegneria spicata* (▽), *Elymus elymoides* ssp. *brevifolius* (●), *Leymus cinereus* wildland collections (▼), *Poa secunda* (◆), and *Leymus cinereus* released varieties (○). Daily-rate-sum means were derived by first averaging by seedlot across all years, and then across seedlots within a given species. Rate-sum means in this figure were calculated only for hours where the water potential was estimated to be less negative than  $-1.0$  MPa.

a limited number of static treatment effects, and did not address species-level variability in germination response. Young and Evans (1981, 1982), Evans and Young (1983), Evans et al. (1977), and Young et al. (1981, 2003) measured germination response of a large number of rangeland grass species to a wide range of constant and alternating-temperature regimes, but reported only total germination response. Young and Evans (1977) and Kitchen and Monsen (1994) reported thermal effects on rate as well as total germination percentage of squirreltail and bluebunch wheatgrass, respectively, but used a rate index that is confounded by differences in germination percentage (Scott et al., 1984; Brown and Mayer, 1988). Thermal and hydrothermal models have been used to generate rate indices integrating potential response over a wide range of environmental conditions but most previous comparisons for rangeland species have been limited to simple ranking of thermal or hydrothermal coefficients (Jordan and Haferkamp, 1989; Allen et al., 2000; Meyer et al., 2000). Hardegee and Van Vactor (2000) and Hardegee et al. (2003) suggested that thermal- and hydrothermal-germination models could be used in conjunction with measured or simulated microclimatic data to develop a more ecologically relevant basis for seedlot and species comparisons. Hardegee et al. (2003) and Hardegee (2006b) used this approach to simulate germination response to historical conditions of seedbed moisture and

temperature, but only for one or two seedlots of a given species. Roundy et al. (2007) evaluated potential-germination response to field-variable microclimatic conditions but limited analysis to evaluation of single species. Hardegee et al. (2008) is the only study of this type that has compared more than two seedlots of different species (big and bottlebrush squirreltail). The current study included re-analysis of these previous studies (Hardegee et al., 2003, 2008; Hardegee, 2006b; Roundy et al., 2007) but expanded the comparison to include a wider range of simulated planting dates, and new data for additional species and seedlots. The current study also considered a water-potential threshold for thermal accumulation as discussed by Hardegee et al. (2003) and Roundy et al. (2007).

The results in this study confirm previous assertions that cheatgrass exhibits superior germination response to many perennial grass species, especially under conditions of low temperature in the late fall, winter and early spring (Hull, 1964; Harris, 1967, 1977; Harris and Wilson, 1970; Wilson et al., 1974; Thill et al., 1979; Hardegee, 1994a,b; Beckstead et al., 1996; Goodwin et al., 1996; Hardegee et al., 2003). Our model simulations predicted relatively similar germination rates among species during the coolest part of the year (Figs. 1 and 2). Small germination-rate differences, however, were magnified when the inverse of rate was





**Fig. 3.** Mean-predicted cumulative-germination response as a function of selected planting dates using all temperature data (A) and temperature data only for hours where the water potential was estimated to be less negative than  $-1.0$  MPa (B) for *Bromus tectorum* (▲), *Elymus multisetus* (◇), *Pseudoroegneria spicata* (▽), *Elymus elymoides* ssp. *brevifolius* (●), *Leymus cinereus* wildland collections (▼), *Poa secunda* (◆), and *Leymus cinereus* released varieties (○).

**Table 1**

Significance matrix for individual comparisons of selected mean-daily-germination-rate sums from Figs. 1 and 2. Significant (S) and non-significant (N) treatment comparisons were determined using the Fisher's protected least-square-difference test for significant main-treatment effects. A single indicator was used when the significance was identical for both figures. If significance differed for the two figures, significance indicators are separated by a slash. Planting-dates: 2 (30 October), 4 (11 December), 6 (22 January), 8 (5 March), 10 (16 April), and 12 (28 May). Brte (*Bromus tectorum*), Pssp (*Pseudoroegneria spicata*), Elmu (*Elymus multisetus*), Elel (*Elymus elymoides* ssp. *brevifolius*), LeciW (*Leymus cinereus* wildland collections), Pose (*Poa secunda*), LeciR (*Leymus cinereus* released varieties).

| Species-pair | 10% Subpopulation |   |     |   |    |     |   |   |     |     |    |    | 30% Subpopulation |   |   |   | 50% Subpopulation |     |   |     | 70% Subpopulation |   |     |     |
|--------------|-------------------|---|-----|---|----|-----|---|---|-----|-----|----|----|-------------------|---|---|---|-------------------|-----|---|-----|-------------------|---|-----|-----|
|              | Planting Date     |   |     |   |    |     |   |   |     |     |    |    |                   |   |   |   |                   |     |   |     |                   |   |     |     |
|              | 2                 | 4 | 6   | 8 | 10 | 12  | 2 | 4 | 6   | 8   | 10 | 12 | 2                 | 4 | 6 | 8 | 10                | 12  | 2 | 4   | 6                 | 8 | 10  | 12  |
| Brte         | Pssp              | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S/N               | N | S | S | S                 | N   | N | N   | N                 | N | S/N | N/S |
| Brte         | Elmu              | S | S   | S | S  | S   | S | S | S   | S/N | S  | S  | S                 | N | S | S | S                 | S/N | N | N   | N                 | N | S   | S   |
| Brte         | Elel              | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | N | N   | S                 | S | S   | S   |
| Brte         | LeciW             | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | N | N   | S                 | S | S   | S   |
| Brte         | Pose              | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | N | N   | S                 | S | S   | S   |
| Brte         | LeciR             | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | S | S/N | S                 | S | S   | S   |
| Pssp         | Elmu              | S | S/N | N | S  | N   | N | S | S   | S   | N  | N  | N                 | N | N | N | N                 | N   | N | N   | N                 | N | N   | S/N |
| Pssp         | Elel              | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S                 | N | S | S | S                 | S   | N | N   | S/N               | S | S   | S   |
| Pssp         | LeciW             | S | S   | S | S  | N   | N | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | S | S/N | S                 | S | S   | S   |
| Pssp         | Pose              | S | N   | N | S  | N/S | N | S | S   | S   | S  | S  | S                 | N | S | S | S                 | S   | N | N   | S                 | S | S   | S   |
| Pssp         | LeciR             | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | S | S   | S                 | S | S   | S   |
| Elmu         | Elel              | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | N | N   | S                 | S | S   | N   |
| Elmu         | LeciW             | S | S   | S | S  | N/S | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | S | S   | S                 | S | S   | N/S |
| Elmu         | Pose              | S | S   | S | S  | N/S | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | N | N   | S                 | S | S   | S   |
| Elmu         | LeciR             | S | S   | S | S  | S   | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | S | S   | S                 | S | S   | S   |
| Elel         | LeciW             | N | N   | N | N  | N   | N | N | N   | N   | N  | N  | S                 | S | S | N | N                 | S   | N | S   | S                 | S | S   | N   |
| Elel         | Pose              | N | N   | N | N  | N   | N | N | N   | N   | N  | N  | N                 | N | N | N | N                 | N   | N | N   | N                 | N | N   | N   |
| Elel         | LeciR             | S | S   | S | S  | N/S | S | S | S   | S   | S  | S  | S                 | S | S | S | S                 | S   | S | S   | S                 | S | S   | S   |
| LeciW        | Pose              | N | N   | N | N  | N   | N | N | N   | N   | N  | N  | N                 | N | N | N | N                 | N   | N | N   | N                 | N | N   | N   |
| LeciW        | LeciR             | S | N   | N | S  | N   | N | S | S/N | N   | S  | S  | S                 | N | N | N | S                 | N   | N | N   | N                 | N | N   | S   |
| Pose         | LeciR             | S | S   | S | S  | N   | N | S | S   | N   | S  | S  | N/S               | S | N | N | S                 | N   | N | N   | S                 | S | S   | N/S |

calculated to estimate actual germination time (Fig. 3), which is a more relevant basis for comparison of potential field performance (Arnold, 1959).

Several assumptions were made in this analysis that could affect interpretation of the simulated germination response. Assumptions inherent in thermal-germination models *per se* are thoroughly discussed by Hardegee et al. (1999). These assumptions were minimized for the statistical-gridding model used in the current experiment as developed and tested by Hardegee (2006a,b)

and Hardegee and Winstral (2006). Additional assumptions were made in the application of the water-potential threshold concept first applied in a modeling context by Roundy et al. (2007). Hardegee et al. (2003) assessed the relative importance of different water-potential thresholds, however, and Roundy et al. (2007) confirmed that a threshold of -1.0 MPa would be expected to explain the majority of periods during which wet-thermal accumulation toward germination would be expected to occur. Additional studies should be conducted to confirm this methodology with other

**Table 2**

Significance matrix for selected individual comparisons of mean-germination times from Fig. 3A and B. Significant (S) and non-significant (N) treatment comparisons were determined using the Fisher's protected least-square-difference test for significant main-treatment effects. A single indicator was used when the significance was identical for both figures. If significance differed for the two figures, significance indicators are separated by a slash. Dashes indicate treatments for which germination was not predicted to occur. Planting-dates: 2 (30 October), 4 (11 December), 6 (22 January), 8 (5 March), 10 (16 April), and 12 (28 May). Brte (*Bromus tectorum*), Pssp (*Pseudoroegneria spicata*), Elmu (*Elymus multisetus*), Elel (*Elymus elymoides* ssp. *brevifolius*), LeciW (*Leymus cinereus* wildland collections), Pose (*Poa secunda*), LeciR (*Leymus cinereus* released varieties).

| Species-pair | 10% Subpopulation |     |   |     |    |     |     |     |     |     |     |    | 30% Subpopulation |     |     |   | 50% Subpopulation |     |     |     | 70% Subpopulation |     |     |     |
|--------------|-------------------|-----|---|-----|----|-----|-----|-----|-----|-----|-----|----|-------------------|-----|-----|---|-------------------|-----|-----|-----|-------------------|-----|-----|-----|
|              | Planting Date     |     |   |     |    |     |     |     |     |     |     |    |                   |     |     |   |                   |     |     |     |                   |     |     |     |
|              | 2                 | 4   | 6 | 8   | 10 | 12  | 2   | 4   | 6   | 8   | 10  | 12 | 2                 | 4   | 6   | 8 | 10                | 12  | 2   | 4   | 6                 | 8   | 10  | 12  |
| Brte         | Pssp              | N   | S | S   | S  | S   | N/S | S   | S   | S   | S   | N  | N                 | N   | N/S | S | S                 | N   | N   | N   | N                 | N   | N   | N   |
| Brte         | Elmu              | N   | S | S/N | S  | S   | N   | S/N | S/N | S   | S   | N  | N                 | N   | N   | N | N                 | N   | N   | N   | N                 | N   | N   | N   |
| Brte         | Elel              | S   | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | N   | N   | N   | N                 | S   | S   | S   |
| Brte         | LeciW             | N/S | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | S   | S   | S   | S                 | S   | S   | S   |
| Brte         | Pose              | N/S | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | S/N | N   | S   | S                 | S   | S   | S   |
| Brte         | LeciR             | S   | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | -/- | S/- | S/- | S/-               | S/- | S/- | -/- |
| Pssp         | Elmu              | N   | N | N   | N  | N   | N/S | N   | S/N | S/N | N/S | N  | N                 | N   | N   | N | N                 | N   | N   | N   | N                 | N   | N   | N   |
| Pssp         | Elel              | N/S | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | -/- | S/- | N/- | S/-               | S/- | N/- | -/- |
| Pssp         | LeciW             | N/S | S | S   | S  | N/S | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | S   | S   | S   | S                 | S   | S   | S   |
| Pssp         | Pose              | N   | N | N   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | S   | S   | S   | S                 | S   | S   | S   |
| Pssp         | LeciR             | S   | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | -/- | S/- | S/- | S/-               | S/- | S/- | -/- |
| Elmu         | Elel              | S   | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | S   | S   | S   | S                 | S   | S   | N   |
| Elmu         | LeciW             | N/S | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | S   | S   | S   | S                 | S   | S   | S   |
| Elmu         | Pose              | N/S | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | S   | S   | S   | S                 | S   | S   | -/S |
| Elmu         | LeciR             | S   | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | -/- | S/- | S/- | S/-               | S/- | S/- | -/- |
| Elel         | LeciW             | N   | N | N   | N  | N   | N   | N   | N   | N   | N   | N  | N                 | N   | N   | N | N                 | N/S | S   | S   | S                 | S   | S   | S   |
| Elel         | Pose              | N   | N | N   | N  | N   | N   | N   | N   | N   | N   | N  | N                 | N   | N   | N | N                 | S/N | N   | N   | N                 | S   | S   | S   |
| Elel         | LeciR             | S   | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | -/- | S/- | S/- | S/-               | S/- | S/- | -/- |
| LeciW        | Pose              | N   | N | N   | N  | N   | N   | N   | N   | N   | N   | N  | N                 | N/S | N   | N | N                 | N   | N   | S/N | N                 | N   | N   | N   |
| LeciW        | LeciR             | S   | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | -/- | S/- | S/- | S/-               | S/- | S/- | -/- |
| Pose         | LeciR             | S   | S | S   | S  | S   | S   | S   | S   | S   | S   | S  | S                 | S   | S   | S | S                 | -/- | S/- | S/- | S/-               | S/- | S/- | -/- |



**Table 3**  
Significance matrix for individual comparisons of cumulative-annual-rate sums, from Fig. 4, as a function of species-pair and subpopulation. Significant (S) and non-significant (N) treatment comparisons were determined using the Fisher's protected least-square-difference test for significant main-treatment effects. Brte (*Bromus tectorum*), Pssp (*Pseudoroegneria spicata*), Elmu (*Elymus multisetus*), Elel (*Elymus elymoides* ssp. *brevifolius*), LeciW (*Leymus cinereus* wildland collections), Pose (*Poa secunda*), LeciR (*Leymus cinereus* released varieties).

| Species-pair |       | Subpopulation (%) |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
|--------------|-------|-------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
|              |       | 5                 | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 | 65 | 70 | 75 | 80 |
| Brte         | Pssp  | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | N  | N  | N  |
| Brte         | Elmu  | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | N  |
| Brte         | Elel  | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | N  |
| Brte         | LeciW | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Brte         | Pose  | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Brte         | LeciR | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Pssp         | Elmu  | N                 | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | S  |
| Pssp         | Elel  | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Pssp         | LeciW | N                 | N  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Pssp         | Pose  | N                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Pssp         | LeciR | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Elmu         | Elel  | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | N  | N  | N  |
| Elmu         | LeciW | N                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Elmu         | Pose  | N                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Elmu         | LeciR | S                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| Elel         | LeciW | N                 | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | S  |
| Elel         | Pose  | N                 | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | S  |
| Elel         | LeciR | N                 | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  |
| LeciW        | Pose  | N                 | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  | N  |
| LeciW        | LeciR | N                 | N  | S  | S  | S  | S  | S  | S  | S  | S  | S  | N  | N  | N  | N  | N  |
| Pose         | LeciR | N                 | N  | N  | S  | S  | S  | S  | S  | S  | S  | S  | S  | S  | N  | N  | N  |

species and seedlots using hydrothermal-germination-response data.

Many important biotic and abiotic factors that affect germination response and subsequent emergence, growth and establishment in the field were also ignored in this analysis (Hegarty, 1973; Egli and TeKrony, 1996; Weaich et al., 1996; Beckstead et al., 2007). More rapid germination of cheatgrass is also only one component of a competitive syndrome that includes rapid root and shoot growth (Hull, 1963; Harris, 1967, 1977; Link et al., 1990; Svejcar, 1990; Aguirre and Johnson, 1991; Nasri and Doescher, 1995; Arredondo and Johnson, 1998; Arredondo et al., 1998), high seed production (Young et al., 1969; Humphrey and

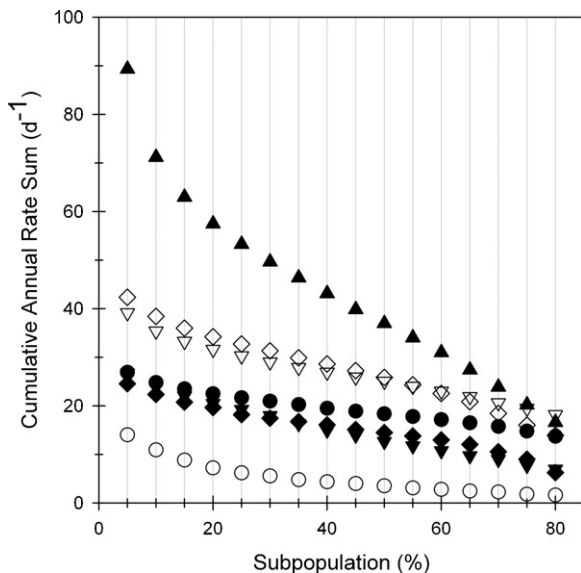
Schupp, 2001; Hempy-Mayer and Pyke, 2008), resource exclusion through efficient water utilization, especially in the upper soil layers (Evans et al., 1970; Cline et al., 1977; Melgoza et al., 1990; Booth et al., 2003a; Humphrey and Schupp, 2004), alteration of the fire cycle (Whisenant, 1990; Knapp, 1996), and changes in nitrogen dynamics (Evans et al., 2001; Booth et al., 2003b; Rimer and Evans, 2006). We believe, however, that this modeling approach yields a much higher level of ecologically relevant information than previous methods, and that this information could be used to identify and distinguish germination syndromes (Angevine and Chabot, 1979; Humphrey and Schupp, 1999) rather than merely ranking relative species response.

## 5. Conclusions

Methodologies discussed in this study provide a more ecologically relevant basis for comparison of thermal and water-potential effects on seed-germination response than previous approaches. Assessment of potential-germination response to a wide range of potential field conditions expands the comparison of species and seedlots to also consider the effect of highly stochastic weather and climate variability as moderated by the seedbed. Future utilization of these techniques could lead to classification of hydrothermal-germination syndromes, and a system for ranking sites and years based on relative favorability of seedbed microclimate. This type of tool would greatly assist in the interpretation of alternative seeding treatments and in quantification of climatic influences on establishment success. Methodology for evaluating weather and climate impacts on establishment success may also provide a basis for interpreting potential climate-change impacts on the stability of current plant communities.

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**Fig. 4.** Cumulative-annual-rate sums for the 255-day test period as a function of seed subpopulation and species for *Bromus tectorum* (▲), *Elymus multisetus* (◇), *Pseudoroegneria spicata* (▽), *Elymus elymoides* ssp. *brevifolius* (●), *Leymus cinereus* wildland collections (▼), *Poa secunda* (◆), and *Leymus cinereus* released varieties (○). Vertical lines indicate the subpopulations used in the ANOVA and multiple-comparison procedures.

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