Hydrothermal germination response and the development of probabilistic germination profiles

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Abstract

Millions of acres of rangeland in the western United States are now dominated by introduced annual weeds such as cheatgrass (*Bromus tectorum* L.). The ability to germinate rapidly at low temperatures has been proposed as one of many mechanisms that confer a competitive advantage to this species. Previous studies of this phenomenon, however, have been limited to relatively simple comparisons of total germinability and germination rate under selected constant-temperature treatments. In this study, we germinated seeds of cheatgrass and two native perennial bunchgrass species, bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve] and big squirreltail [*Elymus multisetus* (J.G. Smith) M.E. Jones], over the temperature range of 0–36 °C and water potential range of 0 to −2.5 MPa. A hydrothermal germination model was constructed to predict germination rate response for the 10, 25 and 50th percentile seed subpopulations. Germination rate estimates were predicted for each species, seedlot and subpopulation for every hour of a 38-year simulation of seedbed temperature and water potential. The seasonal and annual distributions of potential germination rate were integrated to assess relative seedlot response across a wide-range of microclimatic conditions. The integrated response-potential of cheatgrass was consistent with previous studies but the absolute magnitude of enhanced germination rate was relatively small compared to expected differences in seed numbers between cheatgrass and planted species in the field. Historical patterns of seedbed microclimate and predicted germination response may be useful in assessing and optimizing alternative field planting scenarios. Inclusion of weather forecasting and seedbed modeling may provide real-time management options for improving rangeland seeding success.
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Keywords: Seed; Seedbed; Microclimate; Germination; Hydrothermal; Model

1. Introduction

Millions of acres of rangeland in the western United States have been invaded by cheatgrass (*Bromus tectorum* L.), an introduced annual weed that proliferates after wildfire (Young et al., 1987; Young and Longland, 1996). Cheatgrass germinates and establishes rapidly under cool temperatures in the fall, winter and spring and competes very effectively for soil moisture (Harris and Wilson, 1970; Wilson et al., 1974). A primary consideration in restoration of disturbed rangelands is the selection of adapted plant materials that will establish and persist under weed competition (Roundy and Call, 1988; Call and Roundy, 1991).

Rangeland seeding guides typically list a variety of plant species, ranked for general adaptation under different soil types and climatic regimes (Jensen et al., 2001). Unfortunately, the microclimatic conditions necessary for plant establishment are much more

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restrictive than those required for long-term mainte-
nance of mature plant communities. Seedbed micro-
climate in the Intermountain western United States
is highly variable over space and time (Pierson and
Wight, 1991). In addition to variability in precipita-
tion, soil moisture and temperature are affected by so-
lar radiation, wind, air temperature, relative humidity,
and local vegetation and soil properties (Flerchinger
and Pierson, 1997). Flerchinger and Saxton (1989a,b)
developed the Simultaneous Heat and Water (SHAW)
model to characterize soil heat and water status un-
der alternative atmospheric, vegetation and soil con-
ditions. Enhanced understanding of natural variability
in seedbed microclimate, and its impact on plant es-
tablishment and growth, may facilitate development
of more effective revegetation strategies on disturbed
Intermountain rangelands.

Seed germination under temperature and water
stress has received a great deal of attention in the
rangeland literature (Wester, 1991). Most of these
studies evaluate only a limited number of environmen-
tal conditions with subsequent analyses constrained to
simple treatment comparisons of germination rate and
total germination indices (Scott et al., 1984; Brown
and Mayer, 1988). Since Garcia-Huidobro et al. (1982)
and Gummerson (1986), thermal and hydrothermal
modeling have become the primary methods by which
population-level germination response has been as-
sessed for agricultural plant species. These models
generate coefficients that integrate germination re-
sponse over a wide range of potential field conditions
(Garcia-Huidobro et al., 1982; Covell et al., 1986;
Hardegree et al., 1999). Model coefficients can then
be used as a basis for seedlot comparison and ranking
(Covell et al., 1986; Ellis et al., 1986; Jordan and
Haferkamp, 1989; Fidanza et al., 1996; Holshouser
et al., 1996). Thermal and hydrothermal time con-
cepts have been applied to relatively few rangeland
species, mostly to develop indices for seedlot compar-
ison (Jordan and Haferkamp, 1989; Allen et al., 2000;
Meyer et al., 2000). Hardegree and Van Vactor (2000)
and Hardegree et al. (2002) used thermal germination
models to simulate potential germination response
to 6 years of field-temperature conditions. These
simulations provided a broader picture of potential
environmental response than could be achieved by
simple treatment comparisons, or analysis of model
coefficients.

The current study expands previous analyses to
predict potential germination response to simulated-
historical conditions of seedbed temperature and
moisture. The purpose of this study was to esti-
mate hydrothermal germination response to simulated
planting conditions for every day of a 38-year test pe-
riod. Specific objectives were to quantify the impact
of microclimatic variability on potential germination
response in the field; to develop a probabilistic germi-
nation response index for comparison of cheatgrass
and two native bunchgrasses [bluebunch wheatgrass,
Pseudoroegneria spicata (Pursh) Löve and big squir-
reltail, *Elymus multisetus* (J.G. Smith) M.E. Jones];
and to provide perspective for setting establishment
goals in arid and semi-arid rangeland ecosystems that
have been invaded by annual weed species.

2. Methods

2.1. SHAW model calibration and simulation

The SHAW model uses meteorological, soil, and
vegetation inputs to simulate heat and water move-
ment through the soil–plant–atmosphere pathway
(Flerchinger and Hanson, 1989; Flerchinger and
Pierson, 1991, 1997; Hayhoe, 1994; Flerchinger et al.,
1996a,b). The SHAW model was calibrated with me-
teorological and soil measurements from the Orchard
Field Site in southern Ada County, Idaho, using pro-
cedures outlined by Flerchinger and Pierson (1991,
1997). The calibration dataset was derived from soil
temperature and water content measurements on
a Tindahay sandy-loam soil (sandy, mixed mesic,
xeric torriorthent). Three experimental plots at this
site were instrumented with thermocouples to record
hourly-average soil temperature at 1, 2, 5, 10, 20, 30,
50 and 100-cm depths. Soil water content was auto-
matically monitored every hour at these same depths,
except for 1 cm, with Time Domain Reflectometry
(TDR) probes. The Orchard site was also instru-
mented with an anemometer to measure wind run, a
pyranometer for solar radiation, a humidity sensor,
and a shielded thermocouple for air temperature.

Weather data were obtained from the National
Weather Service (NWS) for the Boise airport loca-
tion for the period 1962–1993. Subsequent NWS
data did not include all necessary weather variables

for running the SHAW model so data for the period 1993–1999 were obtained from the Orchard meteorological record. The complete weather record was evaluated, and missing hours interpolated, to compile a serially complete, hourly record, for purposes of model simulation.

The SHAW model was initialized using soil boundary assumptions of minimum residual water content during late summer (August), which is traditionally the driest month for precipitation in southern Idaho. Hourly temperature and water content were estimated at 2-cm depth for every hour between October 1, 1961 and September 30, 1999. Water content was converted to water potential using soil water retention data derived in the laboratory with soil samples from the field test site (Klute, 1986).

2.2. Germination testing

Two seedlots each of bluebunch wheatgrass, big squirreltail and cheatgrass were used in this analysis. Bluebunch (P4, Ainsworth, BC; P7, MOPX) and squirreltail (GV, Paradise Valley, NV; SH, Gem County, ID) seeds were harvested in 1997 from plants grown in a field nursery in Logan, UT. Cheatgrass seeds were collected in southern Ada County, Idaho, at the Orchard site and at Kuna Butte, south of Boise, ID, in June 1997. Seeds were stored in paper envelopes, in a refrigerator at 4 °C between collection and germination testing which began in November 1997.

Seeds were germinated under 12 constant-temperature regimes (3 °C temperature increments) between 3 and 36 °C. Each thermal regime was replicated in three separate environmental chambers of the type described by Hardegree and Burgess (1995). A computer monitoring and control system evaluated chamber temperatures every 3 min and adjusted temperature up or down whenever measured temperature deviated from programmed temperature by ≥ 0.5 °C. A datalogger monitored chamber temperature every 10 s and recorded an average temperature for every 15-min period during the experiment. Chamber lights maintained a photon irradiance of $16.0 \pm 0.4 \, \mu\text{mol m}^{-2}$ for 12 h day^{-1}.

Water potential control was achieved using germination vials of the type described by Hardegree and Emmerich (1992a). These vials utilize a cellulose membrane to separate the seeds from an osmotic solution of polyethylene glycol 8000 (PEG). The membrane has a molecular weight exclusion limit of 3500 which excludes the higher molecular weight PEG but allows water to pass through to the seeds. The water in the membrane, however, equilibrates with the solution reservoir and is held at a matric potential equal to the osmotic potential of the PEG solution.

PEG was mixed with water to yield solutions with a water potential of 0, −0.33, −0.1, −0.4, −0.7, −1.0, −1.3, −1.6, −1.9, −2.2 and −2.5 MPa. These solutions were mixed separately for each temperature regime to account for the thermal dependence of PEG-solution water potential (Michel and Radcliffe, 1995). Each water potential treatment was replicated in three germination vials within each environmental chamber for a total of nine vials for each combination of seedlot and temperature regime.

Six seedlots, 12 temperatures, 11 water potentials, 3 chamber-replications and 3 within-chamber/vial replications made for a total of 7128 germination vials. This number of vials could not be monitored simultaneously as there were only 36 environmental chambers available with a maximum capacity of 80 vials each. Seed germination was also expected to take much longer in the cooler temperature regimes. All 3 and 6 °C treatment vials were, therefore, loaded on the first day of the experiment in 18 of the 36 environmental chambers. One-third of the 9, 15, 21, 27, 33 and 36 °C-treatment vials were also loaded on the first day of the experiment. Loading order for the different water potential treatments within each temperature regime was randomized, but all nine vials for each specific combination of seedlot, temperature and water potential were always loaded on the same day.

Each vial was loaded with 30 seeds of a given seedlot and monitored every day for seed germination. Seeds were dusted with Captan fungicide powder (5% *N*-trichloromethylthio-4-cyclohexene-1,2-dicarboximide, wettable powder) at the beginning of each experimental run and as needed, thereafter, to minimize fungal growth. Seeds were counted and removed when they exhibited radicle extension ≥ 2 mm. All data were entered into a spreadsheet every 5–7 days, and complete sets of nine replicate vials evaluated for cumulative germination response. Cumulative germination curves, of total germination percentage as a function of time, were inspected for each treatment until a clear plateau of germination response

was achieved. At this time, all nine vials of a given treatment were removed and replaced with nine vials of the next seedlot and water potential treatment on the randomized list. When all treatments for a given temperature regime were completed, the three environmental chambers were reprogrammed for a new temperature. This process was repeated until all temperature and water potential treatment combinations were tested. Vial order within each chamber was randomized within three replicated blocks. All vials were included in the initial randomization so that some reordering took place when treatments were terminated and replaced. The last treatments were evaluated and the experiment terminated 120 days after the first vials were loaded.

2.3. Germination model development

Germination counts for the three treatment vials within a given environmental chamber were pooled and the three chamber-values used as replicate samples for model development. Cumulative germination percentage was calculated for each combination of seedlot, temperature, and water potential treatment for each day of the experiment. Seed populations were considered to be composed of subpopulations based on relative germination rate (Garcia-Huidobro et al., 1982; Benech Arnold et al., 1990). Days required to achieve 10, 25 and 50% germination 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 (Hardegree and Van Vactor, 2000).

Alternative regression equations were surveyed to identify specific types of models that would adequately characterize germination rate as a function of temperature and water potential for the three target subpopulations. A computer program (TableCurve3D^{TM}, Jandel Scientific) was used to screen regression equations to determine models with the best data fit. Optimized models for each seedlot and subpopulation were ranked for model fit using the coefficient of determination (r^2). Highly ranked models were compared to identify a single model that provided relatively good fit across all seedlots and subpopulations. The best overall model fit was a non-linear Lorentzian function

of the form:

$$R = a + \frac{b}{1+[(T-c)/d]^2} + \frac{e}{1+[(-10\psi-f)/g]^2}$$
$$+ \frac{h}{\{1 + [(T-c)/d^2][1 + (-10\psi-f)/g]^2\}} \quad (1)$$

where R is germination rate (day^{-1}), T is temperature (°C), ψ is water potential (MPa) and a–f are seedlot-specific model coefficients.

2.4. Historical germination simulation

SHAW-model estimates of temperature and water potential at 2-cm depth and germination model coefficients were input into Eq. (1) to estimate per-day germination rate for each seedlot and subpopulation for every hour between October 1, 1962 and September 30, 1999. Per-day rates were divided by 24 to obtain per-hour rate estimates. Germination rate was set to zero for temperature and water potential combinations that were outside the range of treatment conditions that resulted in germination during the laboratory experiment. Germination-time was estimated for every seedlot for a simulated planting time of 08:00 h for every day during the 38-year test period. Per-hour germination rate estimates represent the fractional progress toward germination for a given subpopulation during that hour (Hardegree et al., 1999). Germination time for a given subpopulation was estimated to occur when the sum of hourly, post-planting, germination rate estimates became equal to 1 (Phelps and Finch-Savage, 1997; Hardegree et al., 1999).

3. Results

Total precipitation during 1962–1999 hydrologic years (October 1–September 30) ranged from 126 to 428 mm (Fig. 1). On average, most precipitation during this period fell in late-fall, winter and spring but there was relatively high variability among different years (Fig. 2). The period between March 1 and May 31 is critical for plant establishment in this region because precipitation is relatively high, and temperatures (Fig. 3) are usually between base and optimal temperature for germination of the species tested in this experiment (Hardegree et al., 1999). Precipitation
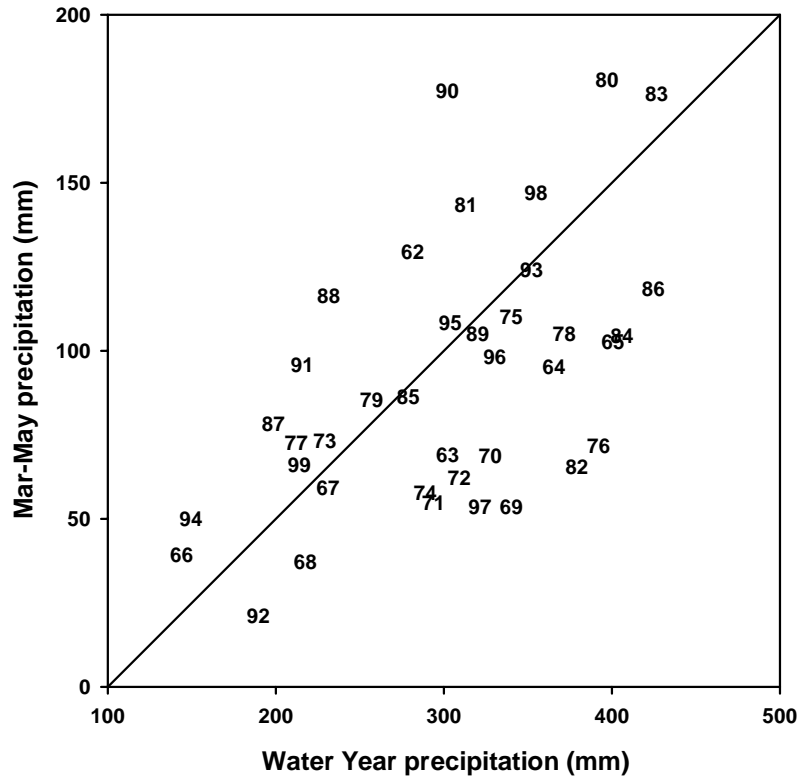
Fig. 1. Relationship between total precipitation during the water year (October–September) and total precipitation during the period March–May as a function of water year for the Boise/Orchard meteorological record (1962–1999).
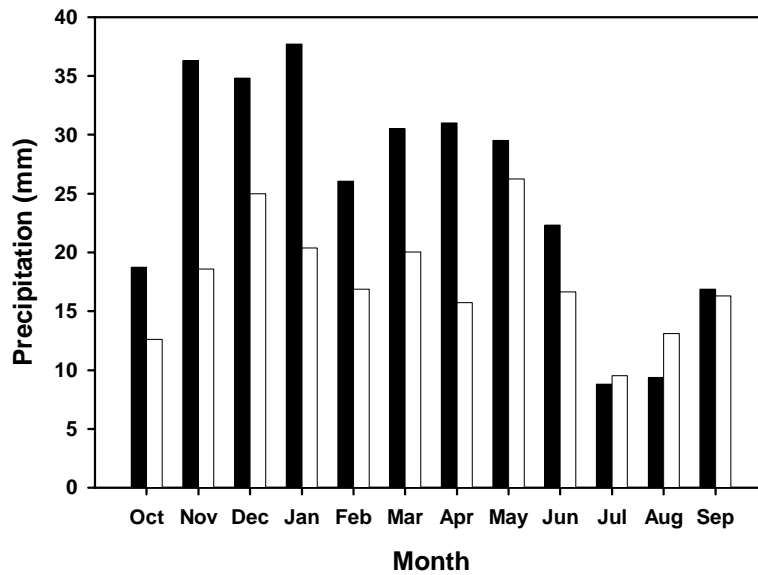

Fig. 2. Mean (solid bars) and standard deviation (hollow bars) of precipitation as a function of month during the 38-year test period.
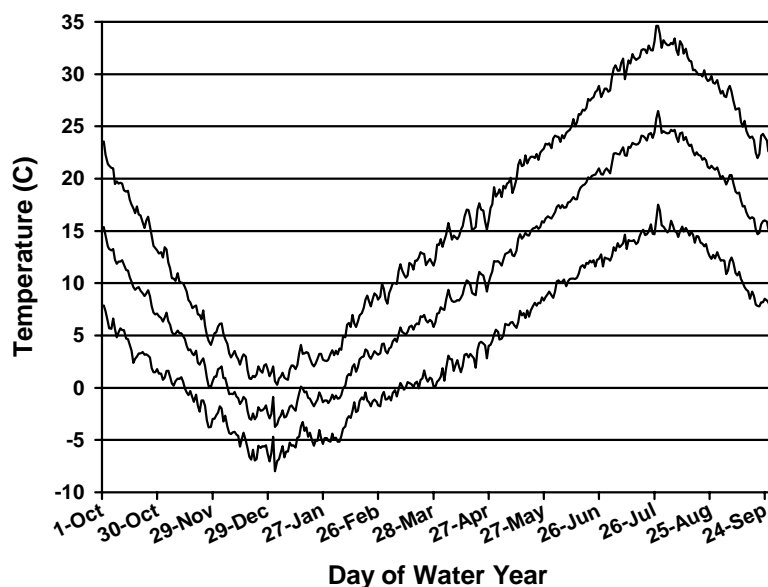
Fig. 3. Daily mean, mean-maximum and mean-minimum air temperature for the 38-year test period.

between March and May over the 38-year test period ranged from 21 to 181 mm (Fig. 1). Ranking of a given year as a function of precipitation is dependent upon on the time period under consideration (Fig. 1). 1980 and 1982, for example, were very similar in total precipitation during the 12-month hydrologic year (399 and 381 mm, respectively) but 1982 had only one-third as much precipitation, as 1980 (65 mm versus 181 mm), during the period between March and May (Fig. 1).

Total germination percentage and mean days to germinate for the 10, 25 and 50% subpopulations are presented in Table 1 for all temperature treatments at 0 MPa. *Bromus tectorum* exhibited relatively higher germination rate (lower days to germinate) than the native grass species, across all temperature treatments, for the 10 and 25% subpopulations. Absolute differences in days required for germination were smaller among all seedlots in the intermediate temperature range.

A Lorentzian model was selected for estimating germination rate as a function of temperature and water potential because this type of equation consistently exhibited a relatively high degree of fit across all seedlots and subpopulations for which regression models were optimized. The sole exception to high model fit

was the 10%-subpopulation for the Orchard seedlot of *B. tectorum*. These data were divided into two modeling ranges, ≤ 24 and $>24\,^\circ$C, which greatly improved model fit. Table 2 summarizes regression statistics for each seedlot and subpopulation.

There was relatively high variability in the annual and seasonal distribution of seedbed microclimate among and between years. This resulted in relatively high variability in mean estimates of germination time as a function of planting day (Fig. 4). Long-term patterns of simulated germination time, however, were consistent with average precipitation and temperature estimates. The most rapid germination times were registered in spring when both moisture and temperature conditions are most likely to be favorable for growth (Figs. 2 and 4). Daily germination rate summations are an index of the relative favorability of seedbed microclimate on a given day. As germination rate is the inverse of germination time, rate estimates represent the percent progress toward germination for a given subpopulation and time period. Fig. 5 shows the average, seasonal distribution of daily germination rate summations as a function of seedlot for three seed subpopulations. A high average-daily-rate summation indicates relatively favorable microclimatic conditions for germination. As the microclimatic

Table 1
Germination rate indices (days to 10, 25 and 50% germination) and total germination percentage (G) as a function of seedlot and temperature for the 0 MPa water potential treatments

Index	Species	Seedlot	Temperature (°C)										
			3	6	9	12	15	18	21	24	27	30	33
D10	*B. tectorum*	Kuna	10.0 (0.5)	5.7 (0.2)	3.6 (0.3)	1.9 (0.3)	1.3 (0.0)	1.2 (0.0)	3.1 (0.0)	0.3 (0.1)	0.2 (0.0)	0.6 (0.3)	1.1 (0.5)
		Orch	9.7 (2.3)	5.3 (0.4)	3.1 (0.2)	2.1 (0.0)	1.2 (0.0)	1.1 (0.0)	0.6 (0.1)	0.3 (0.0)	2.3 (0.0)	0.5 (0.3)	1.3 (0.8)
	E. multisetus	GV	13.4 (0.3)	7.0 (0.8)	4.6 (0.2)	2.9 (0.3)	2.2 (0.0)	2.0 (0.2)	1.8 (0.2)	1.3 (0.1)	1.7 (0.3)	1.4 (0.1)	2.4 (0.2)
		SH	17.8 (0.6)	9.4 (1.3)	5.4 (0.1)	3.5 (0.1)	2.9 (0.1)	2.1 (0.1)	1.5 (0.1)	1.2 (0.1)	1.6 (0.0)	2.0 (0.2)	5.4 (2.6)
	P. spicata	MOPX	17.1 (0.2)	9.3 (0.5)	5.5 (0.3)	4.2 (0.1)	2.9 (0.3)	2.4 (0.1)	1.9 (0.2)	2.2 (0.4)	2.0 (0.2)	3.6 (0.7)	10.1 (1.1)
		P4	26.3 (6.3)	13.1 (0.4)	8.3 (0.9)	5.2 (0.1)	4.0 (0.1)	2.9 (0.3)	2.5 (0.1)	2.6 (0.2)	2.2 (0.0)	2.8 (0.0)	5.7 (1.6)
D25	*B. tectorum*	Kuna	11.4 (0.9)	7.0 (0.3)	4.2 (0.2)	2.2 (0.3)	1.7 (0.1)	1.5 (0.1)	3.4 (0.0)	0.7 (0.2)	0.6 (0.1)	1.3 (0.6)	2.2 (0.9)
		Orch	12.0 (3.9)	6.5 (0.5)	3.5 (0.2)	2.4 (0.0)	1.5 (0.1)	1.4 (0.0)	1.2 (0.0)	0.7 (0.0)	2.8 (0.1)	0.8 (0.3)	4.7 (3.4)
	E. multisetus	GV	14.3 (0.4)	7.8 (0.5)	5.0 (0.2)	3.6 (0.3)	2.4 (0.0)	2.4 (0.2)	2.2 (0.1)	1.7 (0.2)	2.0 (0.2)	2.0 (0.2)	3.1 (0.4)
		SH	21.0 (0.7)	10.8 (1.0)	6.7 (0.5)	4.1 (0.2)	4.5 (0.8)	2.6 (0.1)	2.4 (0.2)	1.9 (0.1)	2.3 (0.1)	2.8 (0.2)	–
	P. spicata	MOPX	21.0 (0.7)	10.1 (0.4)	6.9 (0.2)	4.6 (0.2)	3.4 (0.3)	3.0 (0.3)	2.5 (0.2)	2.9 (0.4)	3.0 (0.1)	–	–
		P4	41.7 (16.8)	14.6 (0.9)	8.9 (0.7)	6.2 (0.5)	4.4 (0.1)	3.5 (0.3)	3.0 (0.1)	3.0 (0.2)	2.5 (0.0)	3.9 (0.1)	11.7 (3.4)
D50	*B. tectorum*	Kuna	–	13.8 (0.3)	9.6 (2.2)	3.4 (0.4)	5.6 (0.4)	2.8 (0.5)	3.8 (0.0)	1.3 (0.2)	1.2 (0.3)	3.0 (1.2)	5.4 (1.0)
		Orch	–	9.3 (0.4)	4.3 (0.3)	2.8 (0.0)	3.3 (1.5)	1.7 (0.0)	1.8 (0.0)	1.5 (0.2)	4.0 (0.3)	1.4 (0.2)	–
	E. multisetus	GV	15.9 (0.3)	9.0 (0.4)	5.4 (0.1)	4.2 (0.3)	2.9 (0.0)	3.5 (0.9)	2.6 (0.0)	2.2 (0.1)	2.4 (0.2)	2.5 (0.1)	6.1 (0.8)
		SH	32.9 (2.1)	17.8 (3.5)	13.9 (1.2)	6.5 (0.4)	–	5.2 (0.3)	3.3 (0.4)	–	6.1 (1.9)	–	–
	P. spicata	MOPX	29.7 (3.3)	12.0 (0.6)	8.1 (0.6)	5.2 (0.2)	4.0 (0.3)	3.7 (0.4)	3.4 (0.3)	4.5 (1.1)	7.5 (1.8)	–	–
		P4	–	–	10.4 (0.2)	7.0 (0.6)	5.0 (0.1)	4.0 (0.4)	3.8 (0.1)	3.7 (0.1)	3.3 (0.1)	13.2 (3.2)	–
G	*B. tectorum*	Kuna	43.7 (4.9)	51.9 (2.6)	64.4 (5.5)	76.3 (1.6)	66.3 (3.3)	64.1 (4.5)	74.4 (4.0)	79.3 (1.6)	74.5 (3.9)	63.3 (3.3)	57.4 (4.3)
		Orch	52.2 (12.2)	53.2 (3.3)	62.2 (3.6)	71.1 (5.8)	69.9 (7.8)	77.0 (3.2)	71.9 (0.7)	73.3 (5.3)	57.0 (5.2)	67.4 (3.5)	41.5 (8.7)
	E. multisetus	GV	86.3 (2.1)	94.1 (1.0)	94.1 (2.0)	91.9 (1.6)	94.1 (3.0)	93.0 (2.1)	91.6 (2.4)	95.6 (0.0)	91.5 (2.3)	87.8 (0.0)	85.9 (2.1)
		SH	51.1 (2.9)	66.3 (7.2)	55.2 (2.0)	69.0 (5.3)	46.8 (9.4)	60.4 (3.0)	58.9 (8.7)	47.4 (3.5)	53.3 (1.3)	46.7 (5.1)	11.5 (5.8)
	P. spicata	MOPX	73.3 (5.5)	82.6 (4.9)	85.2 (2.7)	85.2 (2.6)	83.8 (0.5)	81.9 (0.4)	79.9 (2.7)	65.6 (5.0)	76.3 (5.5)	20.0 (2.3)	23.0 (3.9)
		P4	42.2 (13.3)	50.0 (2.8)	77.0 (2.7)	74.4 (5.3)	83.3 (2.2)	84.4 (3.4)	80.7 (0.7)	80.6 (3.1)	74.3 (3.6)	55.2 (2.9)	42.6 (5.3)

Numbers in parentheses represent 1 S.E.M.

Table 2
Lorentzian germination-model fit as a function of species, seedlot and subpopulation

Species	Origin	Subpopulation (%)	Adjusted r^2	S.E.M.
B. tectorum	Kuna Butte, ID	10	0.68	0.45
B. tectorum	Kuna Butte, ID	25	0.70	0.20
B. tectorum	Kuna Butte, ID	50	0.68	0.12
B. tectorum[a]	Orchard, ID	10	0.86	0.21
B. tectorum[b]	Orchard, ID	10	0.71	0.64
B. tectorum	Orchard, ID	25	0.75	0.19
B. tectorum	Orchard, ID	50	0.77	0.11
P. spicata	Multiple origin polycross	10	0.86	0.06
P. spicata	Multiple origin polycross	25	0.85	0.05
P. spicata	Multiple origin polycross	50	0.88	0.03
P. spicata	Ainsworth, BC	10	0.91	0.04
P. spicata	Ainsworth, BC	25	0.91	0.03
P. spicata	Ainsworth, BC	50	0.89	0.03
E. multisetus	Paradise Valley, NV	10	0.86	0.07
E. multisetus	Paradise Valley, NV	25	0.85	0.06
E. multisetus	Paradise Valley, NV	50	0.85	0.05
E. multisetus	Gem Co., ID	10	0.88	0.06
E. multisetus	Gem Co., ID	25	0.84	0.06
E. multisetus	Gem Co., ID	50	0.75	0.05

[a] Below 24 °C.
[b] Above 24 °C.

conditions underlying Fig. 5 are the same for all plant materials, the average-daily-rate summation is also an index of relative germinability among seedlots. The two cheatgrass seedlots consistently showed the highest germination rate summations for the 10 and 25% subpopulations.

Integration of rate summations over time provides a time-specific index of relative germination performance. Table 3 provides mean germination rate summations across all test years for two periods: the hydrologic year and the March–May establishment period. In general, cheatgrass exhibited substantially higher seasonal and annual germination rate summations relative to the other seedlots for the 10 and 25% subpopulations. Relative ranking of seedlots was also similar between 10 and 25% subpopulations. Germination rate summations for a given seedlot were dependent upon precipitation for the time-period in question. Fig. 6 shows the variability in germination rate summations for the 25% subpopulations as a function of precipitation for both the hydrologic year and March–May establishment period.

Interpretation of measured-germination and estimated-model results were affected by relatively low total germinability of the cheatgrass seedlots and the SH seedlot of squirreltail (Table 1). Germination of the latter seedlots often did not exceed 50% at even moderate levels of water stress, which limited the utility of rate comparisons for the median subpopulations (Tables 1 and 3; Fig. 5).

Each seedlot and subpopulation had a different range of microclimatic conditions under which germination was detected in the laboratory. The average percentage of time spent in the germinable range of seedbed microclimate during the simulated test period, across all seedlots, was estimated to be less than 30%. The simulated-microclimatic data were sorted separately for each seedlot and subpopulation to screen out hours that were spent outside the germinable range. The remaining hours were sorted to determine the amount of time spent in each category of temperature and water potential. Fig. 7 shows these data expressed as a percentage of time spent below a given temperature or water potential for the 10th percentile seed subpopulation.

The data in Fig. 7 do not take into account the relative effect of temperature and water potential on germination rate. An hourly germination rate was calculated for every temperature and water potential
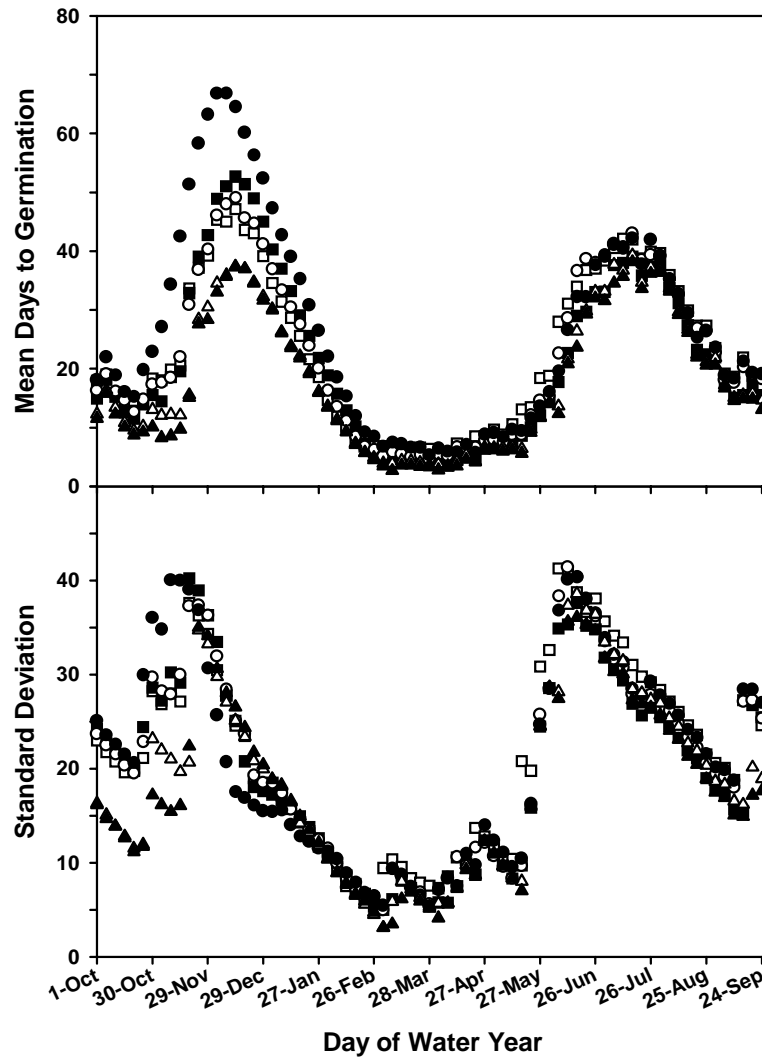
Fig. 4. Mean and standard deviation of simulated-days required to reach 10% germination as a function of planting date for the 38-year test period (open triangle, Kuna, *B. tectorum*; closed triangle, Orch, *B. tectorum*; open circle, MOPX, *P. spicata*; closed circle, P4, *P. spicata*; open square, GV, *E. multisetus*; closed square, SH, *E. multisetus*). Only every 5th day is presented for clarity.

combination used in Fig. 7 and summed for each seed-lot. Fig. 8 shows the percentage of this rate sum that can be attributed to germination in different ranges of temperature and water potential. Fig. 8, therefore, represents the relative progress made toward germination, as a function of temperature and water potential, for all time spent within the germinable range of seedbed microclimate during the 38-year simulation.

4. Discussion

Total germination percentage and germination rate, or derivative indices, are often used to make treatment comparisons and to rank relative germinability of seed populations (Scott et al., 1984; Brown and Mayer, 1988). In the past, the most common method for evaluating germinability among rangeland seedlots was to compare total germination percentage and an
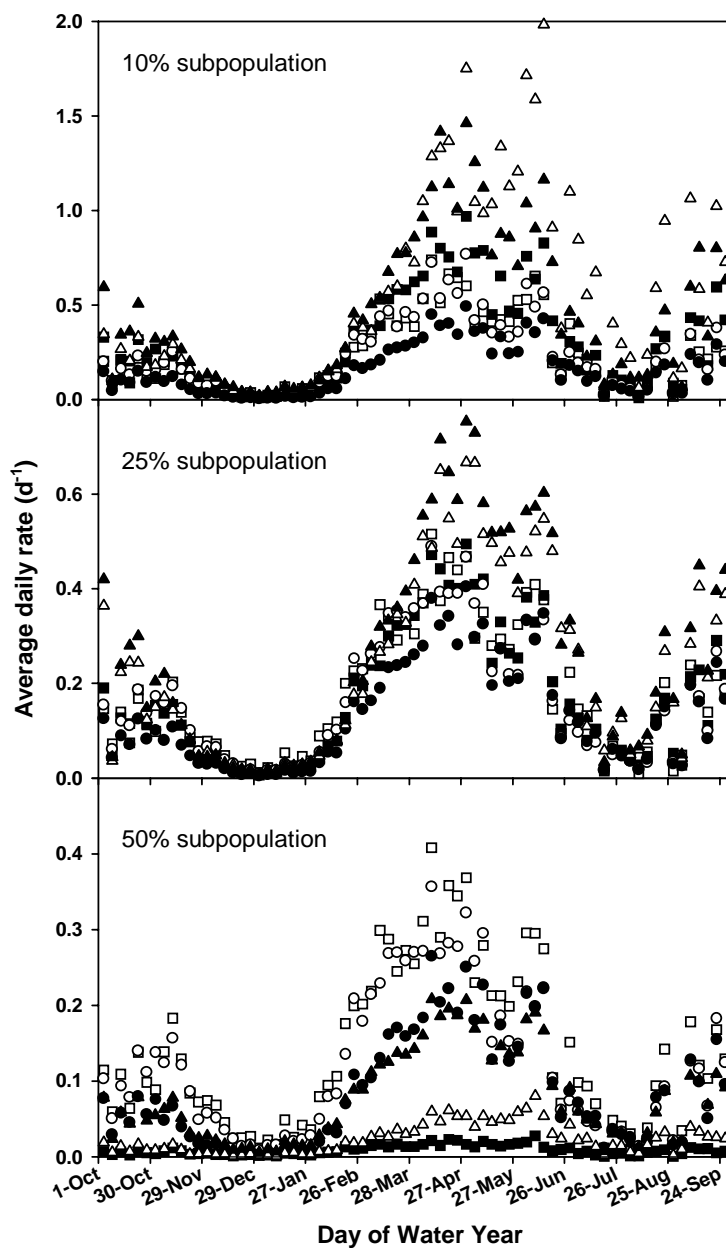
Fig. 5. Mean of daily germination rate summation as a function of seedlot and subpopulation for the 38-year test period (open triangle, Kuna, *B. tectorum*; closed triangle, Orch, *B. tectorum*; open circle, MOPX, *P. spicata*; closed circle, P4, *P. spicata*; open square, GV, *E. multisetus*; closed square, SH, *E. multisetus*). Only every 5th day is presented for clarity.

Table 3
Subpopulation rate sums as a function of species, subpopulation and time period

Time period	Species	Seedlot	Subpopulation (%)		
			10	25	50
Hydrologic year	*B. tectorum*	Kuna	189.5 (11.1)	85.6 (3.8)	8.3 (0.5)
		Orch	166.7 (7.4)	95.3 (4.2)	28.6 (1.4)
	P. spicata	MOPX	84.0 (4.3)	60.2 (2.6)	44.1 (1.9)
		P4	56.4 (2.8)	47.8 (2.4)	30.8 (1.6)
	E. multisetus	GV	88.0 (5.0)	63.6 (3.4)	50.5 (2.6)
		SH	111.3 (5.3)	61.1 (2.7)	3.3 (0.2)
March–May	*B. tectorum*	Kuna	86.8 (6.6)	40.7 (1.9)	3.9 (0.3)
		Orch	84.2 (4.5)	46.2 (2.1)	14.1 (0.9)
	P. spicata	MOPX	43.1 (2.9)	31.2 (1.7)	22.8 (1.3)
		P4	28.7 (1.8)	24.4 (1.5)	16.0 (1.0)
	E. multisetus	GV	43.2 (3.4)	31.5 (2.3)	25.1 (1.7)
		SH	57.3 (3.3)	31.5 (1.7)	1.5 (0.1)

Numbers in parentheses represent ±1 S.E.M.

index of germination rate at one or two test temperatures (Wester, 1991). These indices have several characteristics that limit their utility for making inferences about seed population response. Indices that rely on a measure of germination percentage can underestimate potential response if the treatment is terminated prematurely (Romo and Eddleman, 1995). Indices of mean germination time are affected by the total number of seeds that germinate. This can confound a comparison of treatment means because the genetic subpopulations being compared are not identical. Median germination time of the total number of seeds planted is a better indicator of population-specific germination rate, but can only be used when total germination percentage exceeds 50%.

Table 1 displays germination percentage and germination times at 0 MPa as a function of temperature for the seedlots tested in this study. The germination rate data for median germination are similar in scope and are consistent with previous studies of thermal germination response (Hardegree, 1994a,b; Hardegree et al., 1999, 2002; Hardegree and Van Vactor, 1999, 2000). It is difficult to assess the ecological importance of these treatment differences, however, because they do not account for water stress effects, and assign equal statistical importance to all test treatments, regardless of their probability of occurrence in a realistic field scenario.

Germination response models can be used to generate coefficients that integrate potential response over a wide range of temperature and moisture conditions, and for all seeds in a given seed population (Arnold, 1959; Garcia-Huidobro et al., 1982; Covell et al., 1986; Hardegree et al., 1999). Arnold (1959) used an iterative procedure to optimize base-temperature estimates and to calculate thermal-time coefficients from variable-temperature response data. Garcia-Huidobro et al. (1982) measured constant-temperature germination response and expanded response modeling to consider within-population variability in germination rate. Covell et al. (1986) used probit analysis and logistic regression to quantify this variability in germination rate among different seed populations. Gummerson (1986) used a similar approach to quantify water stress effects on germination rate, and subsequent authors have constructed hydrothermal-probit models to describe the interactive effects of both water and temperature (Dahal and Bradford, 1990, 1994; Christensen et al., 1996; Finch-Savage et al., 1998; Cheng and Bradford, 1999; Roman et al., 1999; Shrestha et al., 1999; Meyer et al., 2000). Phelps and Finch-Savage (1997) and Kebreab and Murdoch (1999) have questioned the predictive accuracy of these models which make significant assumptions about model shape. Hardegree et al. (1999) developed an alternative regression approach which eliminates certain assumptions regarding base temperatures and the linearity of rate response among seed subpopulations. McDonald (2002a) tested the Hardegree et al. (1999) model and determined that it was more
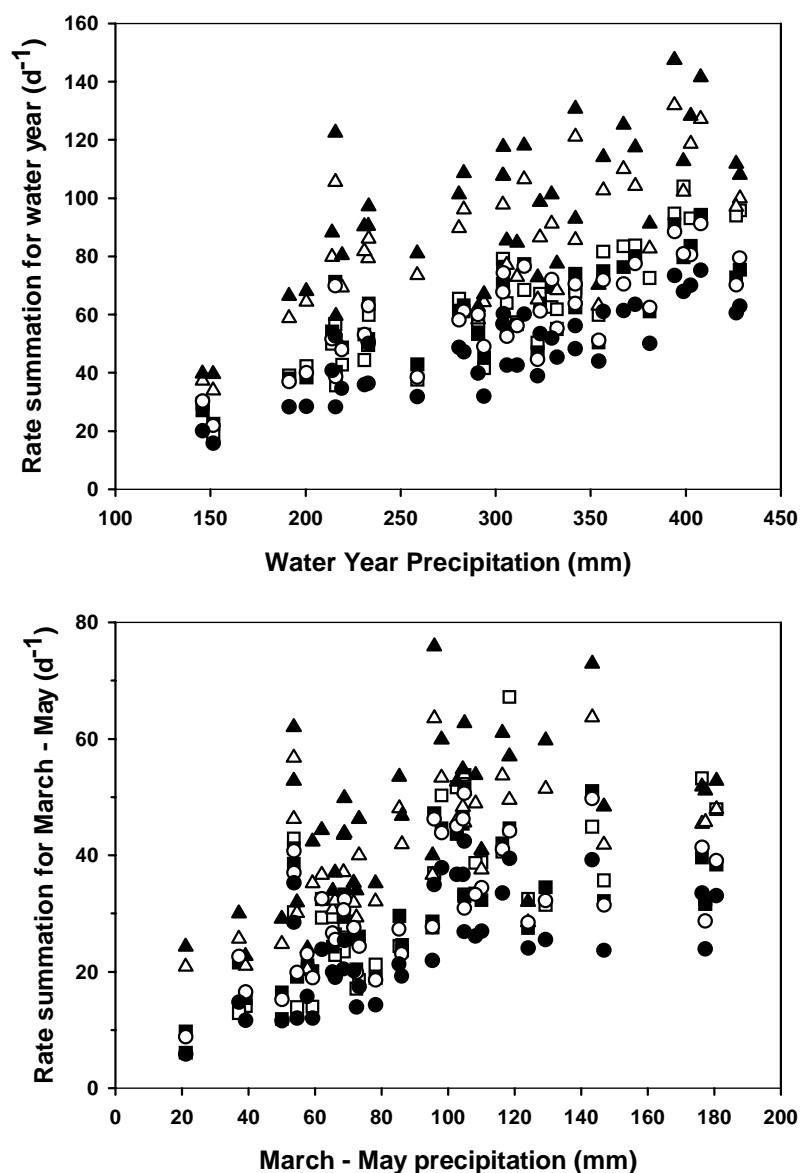
Fig. 6. Water-year and March–May rate summations for the 25th germination percentile as a function of seedlot and precipitation amount (open triangle, Kuna, *B. tectorum*; closed triangle, Orch, *B. tectorum*; open circle, MOPX, *P. spicata*; closed circle, P4, *P. spicata*; open square, GV, *E. multisetus*; closed square, SH, *E. multisetus*).

accurate than those described by Garcia-Huidobro et al. (1982) and Covell et al. (1986) in predicting constant-temperature germination response of several tropical and subtropical legumes. The Hardegree et al. (1999) model was less accurate at predicting germination response to variable-temperature for these legume species (McDonald, 2002b). Hardegree and Van Vactor (1999), however, were more successful at predicting variable-temperature germination response of four perennial bunchgrass species.

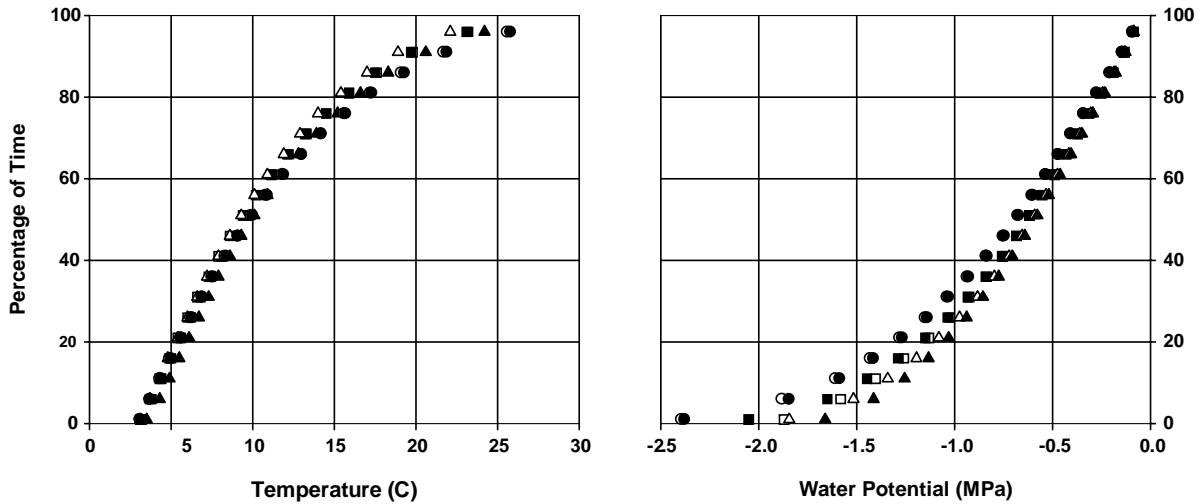Thermal and hydrothermal model coefficients can be compared directly to rank relative-potential

Fig. 7. Percentage of time, during the 38-year test period, spent below the maximum temperature and water potential while in the germinable range of seedbed microclimate, as a function of seedlot, for the 10th-percentile seed subpopulations (open triangle, Kuna, *B. tectorum*; closed triangle, Orch, *B. tectorum*; open circle, MOPX, *P. spicata*; closed circle, P4, *P. spicata*; open square, GV, *E. multisetus*; closed square, SH, *E. multisetus*).

performance of seedlots (Covell et al., 1986; Ellis et al., 1986, 1987; Jordan and Haferkamp, 1989; Fidanza et al., 1996; Holshouser et al., 1996). Hardegree and Van Vactor (2000) suggested that such models could be used more effectively by estimating

relative germination response under a broad range of alternative, simulated environmental conditions. Previous historical simulations of this type (Hardegree and Van Vactor, 2000; Hardegree et al., 2002) were limited to thermal response and assumed adequate
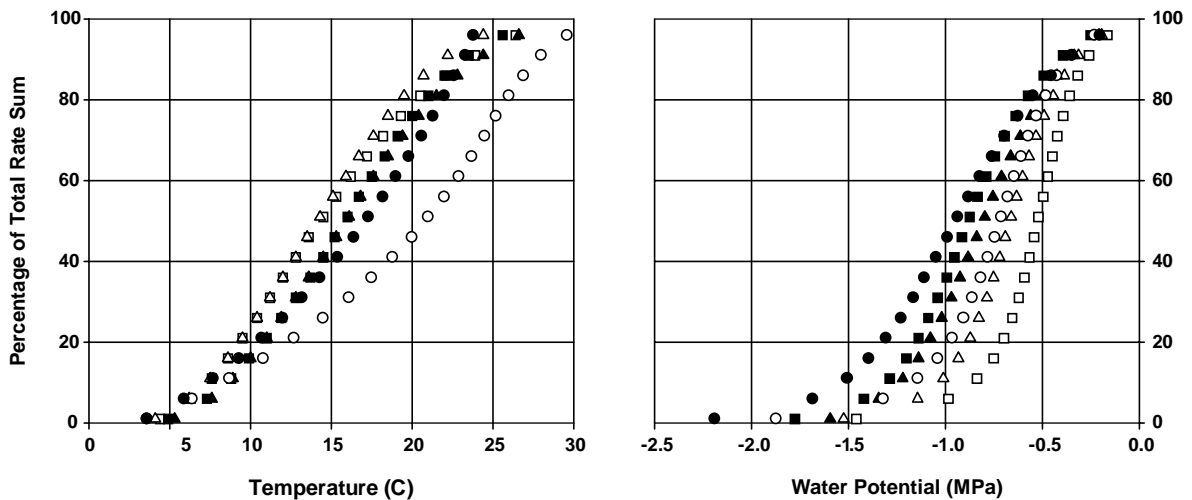

Fig. 8. Percentage of the total rate sum, during the 38-year test period, accrued below the maximum temperature and water potential while in the germinable range of seedbed microclimate, as a function of seedlot, for the 10th-percentile seed subpopulations (open triangle, Kuna, *B. tectorum*; closed triangle, Orch, *B. tectorum*; open circle, MOPX, *P. spicata*; closed circle, P4, *P. spicata*; open square, GV, *E. multisetus*; closed square, SH, *E. multisetus*).

water availability subsequent to planting. More realistic simulations require analysis of hydrothermal germination response relative to field variability of both temperature and water (Weaich et al., 1996). In the current study, alternative regression models were evaluated to provide the best fit of germination rate as a function of both temperature and water potential. The objective here was to minimize assumptions regarding model shape and to maximize predictive accuracy.

Fig. 4 is the first step in assessing potential seedlot performance as a function of both hydrothermal germination response and expected patterns of seedbed microclimate. The data in Fig. 4 represent the average number of days required to reach 10% germination, as a function of seedlot, subpopulation and planting date, averaged across all 38 test years. The annual and seasonal variability in precipitation and temperature (Figs. 1–3) result in a relatively large range of predicted germination times across years. The sample standard deviation of germination time is roughly the same order of magnitude as the mean germination time in Fig. 4. The data in Fig. 4 sum inverse-germination rate estimates between planting and germination. An alternative method of comparison is to evaluate mean-daily germination rates as a function of planting date (Fig. 5). Fig. 5 integrates microclimatic conditions and potential germination response into an index of the seasonal pattern of relative germinability. An inverse rate of 0.1, 0.5, 1.0 and 2.0 would result in germination times of 10, 2, 1 and 0.5 days, respectively, under the conditions present on a given day.

Summation of hourly or daily germination rates can be used to integrate potential germination response for comparison of different seedlots, seasons or years. Annual and March–May rate sums are shown in Fig. 6 for the 25% subpopulations as a function of seedlot and precipitation. Effective germination is shown to be related to precipitation amount but there is still a significant amount of variability in response. Table 3 lists annual and March–May rate sum averages for each subpopulation calculated across all 38 test years. These rate sums integrate expected seedbed microclimate and potential seedlot response into a single comparative index. The two cheatgrass seedlots show higher rate sums than the other two species for the 10 and 25% seed subpopulations. The relative ranking of seedlots is reflected in the relative positioning of rate

summations in Figs. 5 and 6 and germination times in Fig. 4.

Previous studies have hypothesized that the ability to germinate rapidly at low temperature contributes to the success of cheatgrass (Harris and Wilson, 1970; Wilson et al., 1974). This hypothesis is supported by laboratory evidence demonstrating statistically significant differences in relative germination rate in a fixed, low-temperature test environment (Hardegree, 1994a,b). The ecological significance of rate differences measured in previous studies is more difficult to assess. The current study showed that the relative germination advantage of cheatgrass persists across a wide number of historically-simulated, field-variable conditions of seedbed microclimate. The ecological advantage of rapid germination rate per se, however, may not be as significant as the relative effect of seed numbers in the field. The density of viable cheatgrass seed after wildfire may be on the order of 10,000 seeds m^{-2} (Humphrey and Schupp, 2001). At typical seeding rates for the perennial species tested in this experiment, one would not expect to have more than about 200–500 seeds m^{-2} either planted or broadcast (Jensen et al., 2001). This would increase the comparative advantage of cheatgrass by an order of magnitude relative to the rate sum differences shown in Figs. 5 and 6 and Table 3.

Finch-Savage and Phelps (1993) and Finch-Savage et al. (1998) have suggested that thermal response may be the primary predictor of field performance above a threshold level of water availability. In this study, over a 38-year simulation, the time spent in the germinable range was a continuous function of both temperature and water potential. Approximately 30% of the hours in the test period were within the germinable domain of all 10 and 25% seed subpopulations. Within the subset of hours in the germinable range, Fig. 7 shows the relative time spent as a function of temperature and water potential for the 10% seed subpopulation. Sixty percent of the time spent in the germinable range occurred in the temperature interval of about 5–17 °C and the water potential range of about −0.3 to −1.2 MPa. Hours spent in each microclimatic sub-domain are not indicative of the relative progress made toward germination, however. Fig. 8 shows the relative contribution of different conditions of temperature and water potential toward germination, relative to the integrated rate sum across the 38-year test period. The threshold

described by Finch-Savage and Phelps (1993) and Finch-Savage et al. (1998) is perhaps best defined in terms of probability. Eighty percent of the positive germination response across the whole time-frame occurs above about −0.7 MPa for the GV squirreltail seedlot but above about −1.3 MPa for the P4 seedlot of bluebunch wheatgrass (Fig. 8). Time spent in the germinable range of temperature conditions is more evenly distributed between about 5 and 25 °C (Fig. 7).

There are a number of assumptions inherent in this modeling approach that need additional discussion and further study. Accuracy in prediction of soil temperature and water status with the SHAW model have been the subject of previous studies (Flerchinger and Pierson, 1991, 1997). We did not evaluate the impact of SHAW-model uncertainty on our germination model predictions but assumed that random errors in model predictions would average out in our long-term simulations. We also did not account for the discontinuous nature of germination progress under field conditions of seedbed microclimate. In our analysis we accumulated progress toward germination during favorable periods of seedbed microclimate but set germination response under all other seedbed conditions to zero. Under some conditions, seeds equilibrated at subgermination water content can experience a natural form of seed priming that may enhance subsequent germinability (Wallace, 1960; Lush and Groves, 1981). Seed priming effects may persist even if the seeds dry back during the interim period (Hardegree, 1994a). A more common scenario involves a reduction in seed viability and vigor from respiratory losses at subgermination water content (Hardegree and Emmerich, 1992b). Potentially negative impacts of any seed storage environment are generally exacerbated at higher temperatures (McDonald, 1999). Our study considered only the non-dormant seeds of the specific populations tested. Our inferences, therefore, do not necessarily apply to seeds of these species that were collected, processed or stored in other ways.

5. Conclusions

One objective of this study was to determine whether microclimatic knowledge and information could be used to improve revegetation and restoration success rates on cheatgrass-affected rangelands.

Allen and Meyer (1998) suggested that medium and long-term weather forecasting could be used to predict the probability of favorable seedbed conditions that would warrant expenditure of restoration funds. In our study, we demonstrated a methodology that links weather and climate information to relative germination performance. Management implementation of this concept, however, may require that we separate short-term objectives of soil stabilization and longer-term biodiversity objectives.

Emergency fire rehabilitation policy generally prioritizes establishment of plants that will both stabilize the soil and compete successfully with invasive weeds (Bureau of Land Management, 1999). Funds for burn rehabilitation are generally earmarked for expenditure in the year following the fire. Under this relatively short planning horizon, there is minimum flexibility regarding number of acres to be treated and availability of seed. Under this planning scenario, weather forecast information may only be useful in two areas: selection of species to seed; and decisions regarding weed control methods. Emergency fire rehabilitation policy encourages use of native species but only if they are capable of surviving under conditions of weed competition and drought (Bureau of Land Management, 1999). If one recognizes that initial establishment is critically dependent upon water availability, it may be prudent to select more easily established non-native species for burn rehabilitation under certain conditions, regardless of native seed availability. These conditions might be met if the burned area was previously dominated by cheatgrass; and either weather forecasts predict drought, or post-fire cheatgrass control is not feasible. Indeed, cheatgrass control methods may actually reduce soil stability if planted species do not successfully establish.

Weather forecast information and seedbed modeling may be more applicable to longer-term restoration objectives. Historical weather probabilities can be used to predict the frequency of occurrence of years in which native-plant establishment is optimal. Treatment sites can be identified well ahead of time and seed can be obtained and stored in anticipation of favorable planting conditions. Cheatgrass control measures could be utilized only in years where there is a high probability of favorable native-plant establishment. A restoration scenario of this type would also be applicable in areas that are currently occupied by non-native species that

were planted for emergency rehabilitation. This scenario, however, would require significant modification to the current system of restoration planning, both in the area of seeding logistics and funding.

Future research is needed to adapt current weather forecast models for use in microclimatic modeling applications; to test the utility of these models under field conditions; and to assess the economic feasibility of forecast-modeling applications. There are relatively few studies of hydrothermal germination response of rangeland species (Allen and Meyer, 1998; Allen et al., 2000; Meyer et al., 2000). Additional research is needed to evaluate within and between-species variability in hydrothermal germination response. Christensen et al. (1996), Allen and Meyer (1998), Cheng and Bradford (1999), Meyer et al. (2000) and Bradford (2002) have begun to model and evaluate the relationships between hydrothermal germination time, priming and seed dormancy relations. Future simulations of potential germination response will need to integrate both positive and negative impacts of seedbed microclimate on potential establishment success.

Acknowledgements

References

Allen, P.S., Meyer, S.E., 1998. Ecological aspects of seed dormancy loss. Seed Sci. Res. 8, 183–191.

Allen, P.S., Meyer, S.E., Khan, M.A., 2000. Hydrothermal time as a tool in comparative germination studies. In: Black, M., Bradford, K.J., Vazquez-Ramos, J. (Eds.), Seed Biology: Advances and Applications. CAB International, Wallingford, Oxon, pp. 401–410.

Arnold, C.Y., 1959. The determination and significance of the base temperature in a linear heat unit system. J. Am. Soc. Hortic. Sci. 74, 430–445.

Benech Arnold, R.L., Ghersa, C.M., Sanchez, R.A., Insausti, P., 1990. Temperature effects on dormancy release and germination rate in Sorghum halepense (L.) Pers. seeds: a quantitative analysis. Weed Res. 30, 81–89.

Bradford, K.J., 2002. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. Weed Sci. 50, 248–260.

Brown, R.F., Mayer, D.G., 1988. Representing cumulative germination. 1. Germination indices. Ann. Bot. 61, 117–125.

Bureau of Land Management, 1999. Emergency Fire Rehabilitation Handbook. U.S. Department of Interior, Bureau of Land Management Handbook H-1742, Washington DC, 35 pp.

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

Cheng, Z.Y., Bradford, K.J., 1999. Hydrothermal time analysis of tomato seed germination responses to priming treatments. J. Exp. Bot. 50, 89–99.

Christensen, M., Meyer, S.E., Allen, P.S., 1996. A hydrothermal time model of seed after-ripening in Bromus tectorum L. Seed Sci. Res. 6, 155–163.

Covell, S., Ellis, R.H., Roberts, E.H., Summerfield, R.J., 1986. The influence of temperature on seed germination rate in grain legumes. I. A comparison of chickpea, lentil, soyabean and cowpea at constant temperatures. J. Exp. Bot. 37, 705–715.

Dahal, P., Bradford, K.J., 1990. Effects of priming and endosperm integrity on seed germination rates of tomato genotypes. II. Germination at reduced water potential. J. Exp. Bot. 41, 1441–1453.

Dahal, P., Bradford, K.J., 1994. Hydrothermal time analysis of tomato seed germination at suboptimal temperature and reduced water potential. Seed Sci. Res. 4, 71–80.

Ellis, R.H., Covell, S., Roberts, E.H., Summerfield, R.J., 1986. The influence of temperature on seed germination rate in grain legumes. II. Interspecific variation in chickpea (Cicer arietinum L.) at constant temperature. J. Exp. Bot. 37, 1503–1515.

Ellis, R.H., Simon, G., Covell, S., 1987. The influence of temperature on seed germination rate in grain legumes. III. A comparison of five faba bean genotypes at constant temperatures using a new screening method. J. Exp. Bot. 38, 1033–1043.

Fidanza, M.A., Dernoeden, P.H., Zhang, M., 1996. Degree-days for predicting smooth crabgrass emergence in cool-season turfgrasses. Crop Sci. 36, 990–996.

Finch-Savage, W.E., Phelps, K., 1993. Onion (Allium cepa) seedling emergence patterns can be explained by the influence of soil temperature and water potential on seed germination. J. Exp. Bot. 44, 407–414.

Finch-Savage, W.E., Steckel, J.R.A., Phelps, K., 1998. Germination and post-germination growth to carrot seedling emergence: predictive threshold models and sources of variation between sowing occasions. New Phytol. 139, 505–516.

Flerchinger, G.N., Hanson, C.L., 1989. Modeling soil freezing and thawing on a rangeland watershed. Trans. ASAE 32, 1551–1554.

Flerchinger, G.N., Pierson, F.B., 1991. Modeling plant canopy effects on variability of soil temperature and water. Agric. For. Meteorol. 56, 227–246.

Flerchinger, G.N., Pierson, F.B., 1997. Modeling plant canopy effects on variability of soil temperature and water: model calibration and validation. J. Arid Environ. 35, 641–653.

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., Baker, J.M., Spaans, E.J.A., 1996a. A test of the radiative energy balance of the SHAW model for snowcover. Hydrol. Proc. 10, 1359–1367.

Flerchinger, G.N., Hanson, C.L., Wight, J.R., 1996b. Modeling evapotranspiration and surface energy budgets across a watershed. Water Resour. Res. 32, 2539–2548.

Garcia-Huidobro, J., Monteith, J.L., Squire, G.R., 1982. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S & H). I. Constant temperature. J. Exp. Bot. 33, 288–296.

Gummerson, R.J., 1986. The effect of constant temperatures and osmotic potentials on the germination of sugar beet. J. Exp. Bot. 37, 729–741.

Hardegree, S.P., 1994a. Matric priming increases germination rate of Great Basin native perennial grasses. Agron. J. 86, 289–293.

Hardegree, S.P., 1994b. Drying and storage effects on germination of primed grass seeds. J. Range Manage. 47, 196–199.

Hardegree, S.P., Burgess, M.D., 1995. Datalogger control of environmental chambers for variable-temperature germination experiments. J. Range Manage. 48, 554–556.

Hardegree, S.P., Emmerich, W.E., 1992a. Effect of matric-priming duration and priming water potential on germination of four grasses. J. Exp. Bot. 43, 233–238.

Hardegree, S.P., Emmerich, W.E., 1992b. Seed germination response of four southwestern range grasses to equilibration at subgermination matric-potentials. Agron. J. 84, 994–998.

Hardegree, S.P., Van Vactor, S.S., 1999. Predicting germination response of four cool-season range grasses to field-variable temperature regimes. Environ. Exp. Bot. 41, 209–217.

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., Van Vactor, S.S., Pierson, F.B., Palmquist, D.E., 1999. Predicting variable-temperature response of non-dormant seeds from constant-temperature germination data. J. Range Manage. 52, 83–91.

Hardegree, S.P., Jones, T.A., Van Vactor, S.S., 2002. Variability in thermal response of primed and non-primed seeds of squirreltail [*Elymus elymoides* (Raf.) Swezey and *Elymus multisetus* (J.G. Smith) M.E. Jones]. Ann. Bot. 89, 311–319.

Harris, G.A., Wilson, A.M., 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. Ecology 51, 530–534.

Hayhoe, H.N., 1994. Field testing of simulated soil freezing and thawing by the SHAW model. Can. Agric. Eng. 36, 279–285.

Holshouser, D.L., Chandler, J.M., Wu, H.I., 1996. Temperature-dependent model for non-dormant seed germination and rhizome bud break of johnsongrass (*Sorghum halepense*). Weed Sci. 44, 257–265.

Humphrey, L.D., Schupp, E.W., 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. West. N. Am. Nat. 61, 85–92.

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

Jordan, G.L., Haferkamp, M.R., 1989. Temperature response and calculated heat units for germination of several range grasses and shrubs. J. Range Manage. 42, 41–45.

Kebreab, E., Murdoch, A.J., 1999. Modelling the effects of water stress and temperature on germination rate of *Orobanche aegyptiaca* seeds. J. Exp. Bot. 50, 655–664.

Klute, A., 1986. Water retention: laboratory methods. In: Klute, A. (Ed.), Methods of Soil Analysis, Part 1, Physical and Mineralogical Methods. American Society of Agronomy, Madison, pp. 635–662.

Lush, W.M., Groves, R.H., 1981. Germination, emergence and surface-establishment of wheat and ryegrass in response to natural and artificial hydration/dehydration cycles. Aust. J. Agric. Res. 32, 731–739.

McDonald, M.B., 1999. Seed deterioration: physiology, repair and assessment. Seed Sci. Tech. 27, 177–237.

McDonald, C.K., 2002a. Germination response to temperature in tropical and subtropical pasture legumes. 1. Constant temperature. Aust. J. Exp. Agric. 42, 407–419.

McDonald, C.K., 2002b. Germination response to temperature in tropical and subtropical pasture legumes. 2. Alternating temperatures. Aust. J. Exp. Agric. 42, 421–429.

Meyer, S.E., Debaene-Gill, S.B., Allen, P.S., 2000. Using hydrothermal time concepts to model seed germination response to temperature, dormancy loss and priming effects in *Elymus elymoides*. Seed Sci. Res. 10, 213–223.

Michel, B.E., Radcliffe, D., 1995. A computer program relating solute potential to solution composition for five solutes. Agron. J. 87, 126–130.

Phelps, K., Finch-Savage, W.E., 1997. A statistical perspective on threshold type germination models. In: Ellis, R.H., Black, M., Murdoch, A.J., Hong, T.D. (Eds.), Basic and Applied Aspects of Seed Biology. Kluwer Academic Publishers, Dordrecht, pp. 361–368.

Pierson, F.B., Wight, J.R., 1991. Variability of near-surface soil temperature on sagebrush rangeland. J. Range Manage. 44, 491–497.

Roman, E.S., Thomas, A.G., Murphy, S.D., Swanton, C.J., 1999. Modeling germination and seedling elongation of common lambsquarters (*Chenopodium album*). Weed Sci. 47, 149–155.

Romo, J.T., Eddleman, L.E., 1995. Use of degree-days in multiple-temperature experiments. J. Range Manage. 48, 410–416.

Roundy, B.A., Call, C.A., 1988. Revegetation of arid and semiarid rangelands. In: Tueller, P.T. (Ed.), Vegetation Science Applications for Rangeland Analysis and Management. Kluwer Academic Publishing, Dordrecht, pp. 607–635.

Scott, S.J., Jones, R.A., Williams, W.A., 1984. Review of data analysis methods for seed germination. Crop Sci. 24, 1192–1199.

Shrestha, A., Roman, E.S., Thomas, A.G., Swanton, C.J., 1999. Modeling germination and shoot-radicle elongation of *Ambrosia artemisiifolia*. Weed Sci. 47, 557–562.

Wallace, H.A.H., 1960. Factors affecting subsequent germination of cereal seeds sown in soils of subgermination moisture content. Can. J. Bot. 38, 287–306.

Weaich, K., Bristow, K.L., Cass, A., 1996. Simulating maize emergence using soil and climate data. Agron. J. 88, 667–674.

Wester, D.B., 1991. A Summary of Range Plant Seed Germination Research. International Center for Arid and Semiarid Land Studies (ICASALS) No. 91-2.

Wilson, A.M., Wonderchek, D.E., Goebel, C.J., 1974. Responses of range grass seeds to winter environments. J. Range Manage. 27, 120–122.

Young, J.A., Longland, W.S., 1996. Impact of alien plants on Great Basin rangelands. Weed Tech. 10, 384–391.

Young, J.A., Evans, R.A., Eckert, R.E., Kay, B.L., 1987. Cheatgrass. Rangelands 9, 266–270.