Environmental and Experimental Botany 76 (2012) 60–67

Contents lists available at SciVerse ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Predicting germination in semi-arid wildland seedbeds. I. Thermal germination models

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ARTICLE INFO

Article history:
Received 23 March 2011
Received in revised form 31 August 2011
Accepted 7 October 2011

Keywords:
Bromus tectorum
Germination rate
Thermal time
Wildland restoration
Revegetation
Seeding
Fire rehabilitation

ABSTRACT

The key to stopping high-frequency or catastrophic wildfires in the western U.S.A. is the successful restoration of burned lands to functional plant communities. Developing models of seedling establishment for invasive and native species will help in the selection of species for restoration projects that are able to establish and compete with invasive species given the abiotic conditions of specific sites. Modeling germination is the first step in modeling seedling establishment. We developed thermal germination models and compared predicted and measured germination timing in incubators as a precursor to testing germination model prediction in field seedbeds. We incubated 11 revegetation species and three weed (*Bromus tectorum* L.) seedlots at constant temperatures to develop linear and curvilinear regression equations to estimate days to 10, 25, and 50% germination for each seedlot. We compared actual time to germination with predicted time for three field-simulated diurnal temperature regimes representing March, mid-March to mid-April, and May temperatures in a big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) plant community. *Bromus tectorum* seedlots germinated faster than perennial grasses and forbs, especially at cooler temperatures. However, most of the revegetation species had high and fast germination for a wide range of temperatures. Germination time generally fit constant temperatures well with R^2 values $\geq$ 0.85 for 33 of 40 linear equations and $\geq$0.80 for 40 of 48 curvilinear equations. Models overestimated germination time for field-simulated diurnal temperatures by 1–4 days for most seedlots. Model accuracy was sufficient for most seedlots to encourage subsequent testing of model accuracy under field conditions.

1. Introduction

The spread of the invasive annual grass, *Bromus tectorum* L. in the western United States has increased the frequency and extent of catastrophic fire in the region (D'Antonio and Vitousek, 1992; Knapp, 1998; Brooks et al., 2004). Plant materials are often chosen for rehabilitation seeding because of their known adaptation to the region or site. However, environmental conditions required for successful establishment are more restrictive than those required for mature plant persistence (Flerchinger and Hardegree, 2004; Hardegree et al., 2011). Improving seeding success involves selecting plant materials that function best in the establishment environment (Johnson, 1986; Call and Roundy, 1991). Recent emphasis on seeding native species for fire rehabilitation and sage-grouse (*Centrocercus urophasianus* Bonaparte) habitat improvement underscores the need to evaluate potential establishment of a wide range of plant materials in the functional environment (Crawford et al., 2004; Thompson et al., 2006).

Preadaptation of *B. tectorum* to the cold deserts of western North America has been attributed to its ability to germinate and grow roots during cool fall, winter or spring temperatures and then preempt soil moisture during the short time of spring soil water availability (Wilson et al., 1974; Hardegree et al., 2010). Similarly, successful fire rehabilitation to resist weed invasion depends upon sowing species that can germinate and grow roots sufficiently to avoid desiccation with summer drought (Johnson, 1986; Hardegree and Van Vactor, 2000; Roundy et al., 2007; Hardegree et al., 2010). Although *B. tectorum* germinates faster at cold temperatures than many potential fire rehabilitation species (Hardegree et al., 2010), many of these species may germinate fast enough at cool temperatures to establish. Development of a seedling establishment model based on the temperature conditions of the functional environment would allow screening and ranking of plant materials with highest probability of establishment.

Thermal accumulation models have been successfully used to predict the timing and rate of germination of weed seeds in

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doi:10.1016/j.envexpbot.2011.10.003

Table 1
Species, cultivar or collection seed source and collection date. UDWR, Utah Division of Wildlife Resources.

Species	Common name/collection	Source	Year collected
Achillea millefolium	'Eagle' yarrow	Eastern WA	2003
Achillea millefolium	Common yarrow	UDWR-Lot# 31053, WA	2003
Enceliopsis nudicaulis	Nakedstem sunray	Blind Valley, UT	2004
Linum lewisii	Lewis flax	Provo, UT	2001/2003
Linum perenne	'Appar' blue flax	UDWR-Lot# LHSIGNIA-245-1R	2003
Lupinus arbustus	Longspur lupine	Wells common garden/Deep Creek	2004
A. cristatum × *A. desertorum*	'Hycrest' crested wheatgrass	UDWR-Lot# 1377–9-127223	2003
Agropyron desertorum	'Nordan' desert wheatgrass	UDWR-Lot# 31347, MT	2003
Bromus tectorum	Cheatgrass	Lookout Pass, UT	2005
Bromus tectorum	Cheatgrass	Spanish Fork, UT	2002
Bromus tectorum	Cheatgrass	Skull Valley, UT	2005
Elymus elymoides	Bottlebrush squirreltail	UDWR-Sanpete Co., UT	2003
Elymus wawawaiensis	Snake River wheatgrass ('Secar' bluebunch wheatgrass)	UDWR-Lot# 31932, WA	2003
Psuedoroegneria spicata ssp. *spicata*	'Anatone' bluebunch wheatgrass	UDWR-Lot# LHSID3-445	2003

agricultural systems (Forcella et al., 2000; Vleeshouwers and Kropff, 2000), as well as that of seeds from temperature and water-limited ecosystems (Jordan and Haferkamp, 1989; Roundy and Biedenbender, 1996; Hardegree et al., 1999, 2003, 2008, 2010; Shrestha et al., 1999; Meyer et al., 2000; Hardegree, 2006; Wang et al., 2006; Meyer and Allen, 2009). These studies have shown species and seedlot-specific linear and non-linear germination rate responses to thermal time between T_b (the temperature below which germination will not occur), T_o (optimum or the temperature at which germination is most rapid), and T_m (maximum or the temperature above which germination will not occur). Use of these models to predict field germination based on temperature, rather than other environmental factors assumes that germination response is primarily a function of thermal accumulation and not other temperature factors such as magnitude of diurnal fluctuations or other aspects of thermal history (Hardegree, 2006). Because thermal progress toward germination occurs only for imbibed seeds, field models must also account for wet and dry seedbed conditions (Roundy et al., 2007).

Germination models should be verified under actual or simulated field seedbed conditions (Mueller and Bowman, 1989; Roundy and Biedenbender, 1996; Forcella et al., 2000; Hardegree, 2006; Meyer and Allen, 2009; Hardegree et al., 2010). Hardegree (2006) found that eight different thermal germination models had similar and high accuracy in predicting germination of Great Basin species from field-simulated temperatures. In an extensive analysis of multiple seed lots of perennial grasses and *B. tectorum*, Hardegree et al. (2010) developed a heat sum index to relate thermal-predicted germination time to simulated field seedbed temperatures. Fastest-germinating subpopulations of *B. tectorum* germinated faster than those of the perennial grasses, but germination time was similar for slower-germinating subpopulations.

As a first step to testing germination prediction in field seedbeds (Rawlins et al., 2011), we developed thermal time models for several potential western U.S.A. fire rehabilitation species and *B. tectorum* seedlots from constant temperature germination trials. We then used the models to predict time to germination at oscillating temperatures in an incubator programmed to simulate diurnal field seedbed temperatures. Our objectives were to: (1) determine the statistical fit of germination time to constant temperature for different seedlot subpopulations, and (2) determine the accuracy of thermal-time models to predict time to germination for diurnal-fluctuating temperatures.

2. Materials and methods

2.1. Model development

We developed thermal-time models for 11 seedlots of plants seeded or under consideration for fire rehabilitation seeding in the western U.S.A., as well as for three *B. tectorum* populations (Table 1). We conducted germination trials to determine time to 10, 25, and 50% subpopulations of germinable seeds for each seedlot at 7 constant temperatures (5, 10, 15, 20, 25, 30, 35 °C). The time to 10, 25,

Table 2
Total germination percentages for constant and diurnal simulated-field temperatures for AcmiE (*Achillea millefollium* 'Eagle'), Acmi (*Achillea millefolium* common), Ennu (*Enceliopsis nudicaulis*), Lile (*Linum lewisii*), Lipe (*Linum perenne* 'Appar'), Luar (*Lupinus arbustus*), AgcrAgdeH (*Agropyron cristatum* × *Agropyron desertorum* 'Hycrest'), AgdeN (*Agropyron desertorum* 'Nordan'), Elel (*Elymus elymoides*), Elwa (*Elymus wawawaiensis*), PsspA (*Psuedoroegneria spicata* 'Anatone'), BrteLP (*Bromus tectorum* Lookout Pass), BrteSF (*Bromus tectorum* Spanish Fork), BrteSV (*Bromus tectorum* Skull Valley). Different letters in a column indicate significantly different means of the arcsine of the square root of germination percentage by the Tukey test ($p < 0.05$).

Germination (%)										
Collection	Constant temperature (°C)							Diurnal temperature regime		
	5	10	15	20	25	30	35	March	March–April	May
AcmiE	8.3 b	24.2 d	37.5 de	50.0 bc	47.5 b	39.2 bc	13.3 c–e	22.5 e	23.3 d	90.8 ab
Acmi	0.8 b	3.3 e	18.3 f	70.0 ab	73.3 ab	65.0 a	55.8 ab	0.8 f	0.8 e	75.8 a–c
Ennu	6.7 b	24.2 d	29.2 ef	10.0 d	5.8 c	0.0 d	10.0 de	19.2 e	25.8 d	24.2 d
Lile	75.8 a	85.0 a	80.0 a	84.2 a	70.8 ab	57.5 ab	9.2 de	83.3 b–d	80.0 a–c	79.2 a–c
LipeA	53.3 a	70.0 a	58.3 b–d	64.2 ab	56.7 ab	31.7 c	3.3 e	72.5 cd	71.7 a–c	81.7 a–c
Luar	54.2 a	57.5 c	55.8 cd	33.3 cd	8.3 c	0.8 d	4.2 e	33.3 e	65.8 a–c	13.3 d
AgcrAgdeH	74.2 a	71.7 a–c	78.3 ab	67.5 ab	62.5 ab	51.7 a–c	25.0 cd	86.7 bc	79.2 a–c	84.2 a–c
AgdeN	63.3 a	72.5 a–c	81.7 a	70.8 ab	79.2 a	60.0 ab	74.2 a	75.8 b–d	79.2 a–c	75.0 a–c
Elel	48.3 a	59.2 bc	66.7 a–c	75.0 ab	53.3 ab	47.5 a–c	11. 7 de	78.3 b–d	60.8 c	88.3 ab
Elwa	68.3 a	78.3 a–c	78.3 ab	75.0 ab	65.8 ab	63.3 ab	61.7 ab	68.3 cd	69.2 a–c	62.5 c
PsspA	70.8 a	80.0 a–c	77.5 ab	76.7 ab	68.3 ab	66.7 a	27.5 cd	76.7 b–d	75.0 a–c	82.5 a–c
BrteLP	70.8 a	80.0 a–c	74.2 a–c	77.5 ab	70.8 ab	49.2 a–c	35.8 bc	91.7 b	81.7 a	71.7 bc
BrteSF	63.3 a	70.8 a–c	70.0 a–c	68.3 ab	67.5 ab	70.0 a	76.7 a	66.7 d	64.2 bc	71.7 bc
BrteSV	59.2 a	83.3 ab	82.5 a	77.5 ab	70.8 ab	56.7 a–c	61.7 ab	100.0 a	82.5 ab	95.0 a

and 50% germination was modeled separately to maximize model accuracy (Covell et al., 1986; Hardegree et al., 1999). Thirty seeds of each seedlot were placed on moist blotter paper in a petri-dish. One petri-dish of each seedlot was placed in each of four plastic bags (replicates), which were randomly assigned to a shelf within an incubation chamber. Incubation chambers were programmed to one of the seven constant temperatures. Bags were rotated on different shelves throughout the experiment. At each constant temperature, the time required for seed germination was recorded by counting germinated seeds every 1–3 days for 45 days or until germination ceased. Germination was recorded when the radicle was 2 mm in length. The only deviation from this protocol was that seeds of *Enceliopsis nudicaulis* (A. Gray) Nelson and *Lupinus arbustus* Douglas ex Lindl. were dusted with Captan fungicide wettable powder (N-trichloromethylthio-4-cyclohexene-1,2-dicarboximide) at the beginning of each trial to control fungal growth.

To obtain the percentage of germinable seeds for a constant temperature for a seedlot (Table 2), total germinated seeds for each constant temperature were divided by 30 seeds. However, to calculate days to a subpopulation germination percentage for each constant temperature and seedlot, the number of seeds germinated in daily counts was divided by the final maximum number of germinating seeds for that constant temperature and seedlot. Because germination was counted every 1–3 days, the number of days required to reach or exceed the subpopulation germination percentage was determined by interpolation from the cumulative germination curve (Covell et al., 1986; Roundy and Biedenbender, 1996; Hardegree et al., 1999; Hardegree, 2006).

Germination rate or the inverse of days (d^{-1}) to germination of the 10, 25, and 50% subpopulations was estimated for all seedlots as a function of incubation temperature using a combination of best-fit linear and nonlinear regression equations derived from the Table Curve® 2D curve-fitting program (Roundy et al., 2007). Linear and nonlinear regression models were chosen for best fit based on maximum R^2 and F-values with minimum residuals (Tables 3 and 4). Both linear regression equations and one or more curvilinear

Table 3
Statistics for linear regression equations fit to 1/days to 10, 25, and 50% subpopulation germination at constant suboptimal temperatures of 5, 10, and sometimes 15 °C and the diurnal temperatures ranges for which they were used to estimate germination time (0–5, 0–7, or 0–10 °C).

Species/collection	Sub-pop. (%)	Linear regressions					*P*-value
		Range (°C)	ddf[a]	R^2	SE[b]	*F*-stat	
Achillea millefolium 'Eagle'	10	0–10	2	0.99	0.008	462	0.0022
	25	0–5	4	0.90	0.022	31.6	0.0049
	50	0–10	4	0.89	0.044	21.6	0.0188
Achillea millefolium common	25	0–5	3	0.96	0.02	75.5	0.0032
	50	0–5	4	0.70	0.102	16.4	0.0048
Enceliopsis nudicaulis	10	0–5	3	0.78	0.012	10.9	0.0459
	50	0–5	6	0.64	0.017	10.9	0.0165
Linum lewisii	10	0–5	6	0.98	0.008	266	<0.0001
	25	0–5	6	0.98	0.009	190	<0.0001
	50	0–5	6	0.96	0.01	130	<0.0001
Linum perenne 'Appar'	10	0–5	6	0.99	0.002	8456	<0.0001
	25	0–5	6	0.99	0.004	2194	<0.0001
	50	0–5	6	0.99	0.004	977	<0.0001
Lupinus arbustus	10	0–5	6	0.71	0.011	14.5	0.0089
	25	0–5	6	0.86	0.005	37.7	0.0009
	50	0–5	5	0.87	0.004	33.6	0.0022
Agropyron cristatum × *A. desertorum* 'Hycrest'	10	0–7	6	0.97	0.012	189	<0.0001
	25	0–7	6	0.99	0.007	447	<0.0001
	50	0–7	6	0.85	0.015	35.1	0.001
Agropyron desertorum 'Nordan'	10	0–10	6	0.94	0.021	97.1	<0.0001
	25	0–5	6	0.96	0.014	134	<0.0001
	50	0–10	6	0.97	0.01	193	<0.0001
Bromus tectorum Spanish Fork	10	0–10	6	0.96	0.018	254	<0.0001
	25	0–5	6	0.97	0.019	206	<0.0001
	50	0–5	6	0.97	0.03	68.2	0.0002
Bromus tectorum Skull Valley	10	0–5	6	0.97	0.048	29	0.0017
	25	0–5	6	0.91	0.015	226	<0.0001
	50	0–5	6	0.80	0.029	72.4	0.0001
Bromus tectorum Lookout Pass	10	0–5	6	0.97	0.017	187	<0.0001
	25	0–5	6	0.91	0.026	58	0.0003
	50	0–5	6	0.80	0.034	24.2	0.0027
Elymus elymoides	10	0–5	6	0.97	0.012	164	<0.0001
	25	0–5	6	0.95	0.012	104	<0.0001
	50	0–5	5	0.75	0.016	15	0.0118
Psuedoroegneria spicata 'Anatone'	10	0–7	6	0.98	0.012	272	<0.0001
	25	0–5	6	0.99	0.010	278	<0.0001
	50	0–5	6	0.99	0.007	436	<0.0001
Elymus wawawaiensis	10	0–5	6	0.96	0.017	149	<0.0001
	25	0–5	6	0.96	0.016	127	<0.0001
	50	0–5	6	0.97	0.011	221	<0.0001

[a] Denominator degrees of freedom.
[b] Standard error of estimate.

Table 4
Statistics for curvilinear regression equations fit to 1/days to 10, 25, and 50% subpopulation germination at constant temperatures of 5, 10, 15, 20, 25, 30, 35 °C and the diurnal temperatures ranges for which they were used to estimate germination time up to 41 °C.

Species	Sub-pop. (%)	Curvilinear						*P*-value
		Range (°C)	ndf[a]	ddf[b]	R^2	SE[c]	*F*-stat	
Achillea millefolium 'Eagle'	10	>10–41	2	13	0.67	0.088	12.4	0.001
	25	>5–41	2	23	0.81	0.079	48.6	<0.0001
	50	>10–41	2	10	0.83	0.046	23.7	0.0002
Achillea millefolium common	10	0–30	2	19	0.94	0.061	150	<0.0001
		>30–41	3	18	0.95	0.06	103	<0.0001
	25	>5–35	2	14	0.88	0.036	48.8	<0.0001
		>35–41	2	14	0.84	0.04	39.0	<0.0001
	50	>5–41	2	13	0.83	0.032	32.1	<0.0001
Enceliopsis nudicaulis	10	>5–41	2	12	0.59	0.029	8.5	0.0050
	25	0–41	2	11	0.75	0.017	16.4	0.0005
	50	>5–41	3	15	0.85	0.014	27.7	<0.0001
Linum lewisii	10	>5–41	2	23	0.97	0.029	318	<0.0001
	25	>5–41	2	25	0.96	0.027	329	<0.0001
	50	>5–41	3	23	0.95	0.025	153	<0.0001
Linum perenne 'Appar'	10	>5–41	2	24	0.82	0.067	56.1	<0.0001
	25	>5–41	2	22	0.91	0.035	105	<0.0001
	50	>5–41	2	19	0.81	0.036	40.2	<0.0001
Lupinus arbustus	10	>5–41	4	13	0.88	0.014	23.9	<0.0001
	25	>5–41	4	13	0.95	0.007	58.9	<0.0001
	50	>5–41	3	10	0.86	0.008	20.3	0.0001
Agropyron cristatum × *A. desertorum* 'Hycrest'	10	>7–41	2	21	0.85	0.077	57.9	<0.0001
	25	>7–41	2	21	0.88	0.045	76.6	<0.0001
	50	>7–41	2	21	0.81	0.04	44.8	<0.0001
Agropyron desertorum 'Nordan'	10	>10–27	2	24	0.98	0.046	479	<0.0001
		>27–41	2	24	0.97	0.049	429	<0.0001
	25	>5–41	2	20	0.98	0.028	580	<0.0001
	50	>10–19.5	5	20	0.92	0.041	48	<0.0001
		>19.5–33.5	2	22	0.89	0.046	59.9	<0.0001
		>33.5–41	4	21	0.88	0.05	38.4	<0.0001
Bromus tectorum Spanish Fork	10	>10–41	2	25	0.60	0.552	18.5	<0.0001
	25	>5–41	2	20	0.93	0.087	129	<0.0001
	50	>5–41	2	25	0.95	0.047	232	<0.0001
Bromus tectorum Skull Valley	10	>5–22.5	2	23	0.65	0.112	21.1	<0.0001
		>22.5–41	2	23	0.59	0.121	16.3	<0.0001
	25	>5–41	3	22	0.72	0.076	19.1	<0.0001
	50	>5–27	2	22	0.77	0.053	36.5	<0.0001
Bromus tectorum Lookout Pass	10	>5–41	2	21	0.90	0.07	93	<0.0001
	25	>5–41	2	21	0.87	0.059	72.4	<0.0001
	50	>5–41	2	19	0.82	0.056	42.6	<0.0001
Elymus elymoides	10	>5–30	2	23	0.94	0.041	166	<0.0001
		>30–41	1	6	0.79	0.086	22.5	0.0032
	25	>5–41	2	25	0.83	0.046	62.1	<0.0001
	50	>5–41	2	18	0.80	0.038	35.5	<0.0001
Psuedoroegneria spicata 'Anatone'	10	>7–41	2	21	0.91	0.061	100	<0.0001
	25	>5–41	2	21	0.97	0.025	340	<0.0001
	50	>5–41	2	21	0.93	0.029	144	<0.0001
Elymus wawawaiensis	10	>5–41	2	25	0.96	0.056	294	<0.0001
	25	>5–41	4	23	0.92	0.06	66.3	<0.0001
	50	>5–41	4	23	0.88	0.052	41.6	<0.0001

[a] Numerator degrees of freedom.
[b] Denominator degrees of freedom.
[c] Standard error of estimate.

equations were used to obtain best fit over specific temperature ranges for specific seedlots. T_b and germination rates from 0–5, 0–7, and 0–10 °C hourly temperatures in diurnal-fluctuating temperature regimes were estimated using linear regression of the times to germination at 5, 10 and sometimes at 15 °C when linear with that at 5 and 10 °C according to the procedure of Roundy et al. (2007, Table 3). Germination rate at suboptimal temperatures is generally considered to be a linear function of incubation temperature (Hegarty, 1972), although Hardegree et al. (1999) determined that they could be curvilinear. Although estimates of germination rate near 0 °C were not necessary for the purposes of the present study, they may be necessary when estimating germination in field seedbeds. Curvilinear equations were used to estimate germination rates at temperatures above those used in linear equations (Roundy et al., 2007). In this laboratory study we did not have diurnal temperatures above 35 °C (Fig. 1). However, because we ultimately wanted to use these equations for field predictions, we needed to account for possible temperatures > 35 °C. For field application, we assumed that in field seedbeds germination would be erratic at temperatures > 35 °C. Therefore, we truncated germination rate to

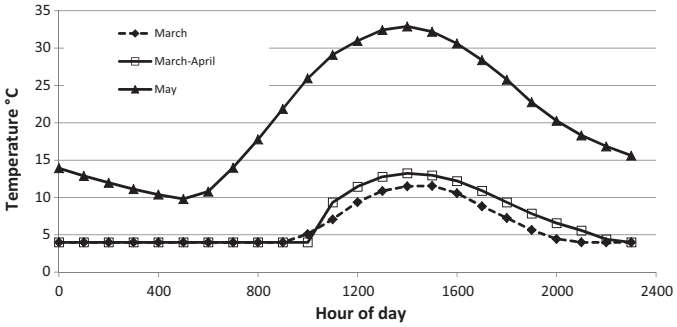

Fig. 1. Incubation chamber diurnal temperatures based on field soil temperatures for a cold, cool, or warm spring day (24-h) from soil temperatures recorded in an *Artemisia tridentata* community in Underdown Canyon, Shoshone Mountains, Nevada during March, mid-March to mid-April, and May when the seedbed was wet (Roundy et al., 2007).

0 at >41 °C when curvilinear estimates of rate did not reach 0 by that temperature (Roundy et al., 2007; Fig. 2). In cases where one curvilinear equation did not provide good fit over the range of constant temperatures, we applied a series of curvilinear equations to obtain best fit (Table 4).

2.2. Spring diurnal temperatures

Diurnal field temperatures were simulated in incubation chambers to compare germination rates and to test model accuracy. Incubation chambers were programmed with one of three diurnal temperature regimes (Fig. 1). The same diurnal temperature regime was repeated each day for the length of each separate diurnal trial. Diurnal temperature regimes were hourly soil temperature averages measured with thermocouples buried 1–3 cm deep in a Wyoming big sagebrush (*Artemisia tridentata* Nutt ssp. *wyomingensis* Beetle & Young) – dominated community in Underdown Canyon, Shoshone Mountains, Nevada, during March 2003, mid-March to mid-April 2005, and May 2002 when the seedbed was wet (≥−1.5 MPa, Roundy et al., 2007). These cold, cool, and warm spring temperature oscillations were used to simulate the seedbed temperature environment of species sown in fire rehabilitation projects. Most species are seeded in late fall and germination is generally expected to occur in the spring before the seedbed dries. Minimum late-fall diurnal temperatures could not be simulated below 4 °C due to incubator limitations. The incubator internal temperature probe was observed to read within ±0.5 °C of set or expected ramping temperature. The same methodology used in constant temperature trials for determining actual time to germination was used in the fluctuating temperature trials.

Progress toward germination was estimated for diurnal-fluctuating temperature regimes from each programmed hourly temperature of incubation using the appropriate linear or curvilinear equation for that temperature range (Roundy and Biedenbender, 1996; Roundy et al., 2007). Progress toward germination for each hour is the regression-estimated germination rate or inverse of days required for a subpopulation to germinate at that hourly temperature and divided by 24 h per day. The estimated time required for germination of a subpopulation is the total time elapsed between the start of the germination trial and the time when regression-estimated hourly progress toward germination sums to 1 (Roundy and Biedenbender, 1996). When regression equations predicted a negative progress toward germination for a given hourly temperature, progress toward germination for that hour was set to zero.

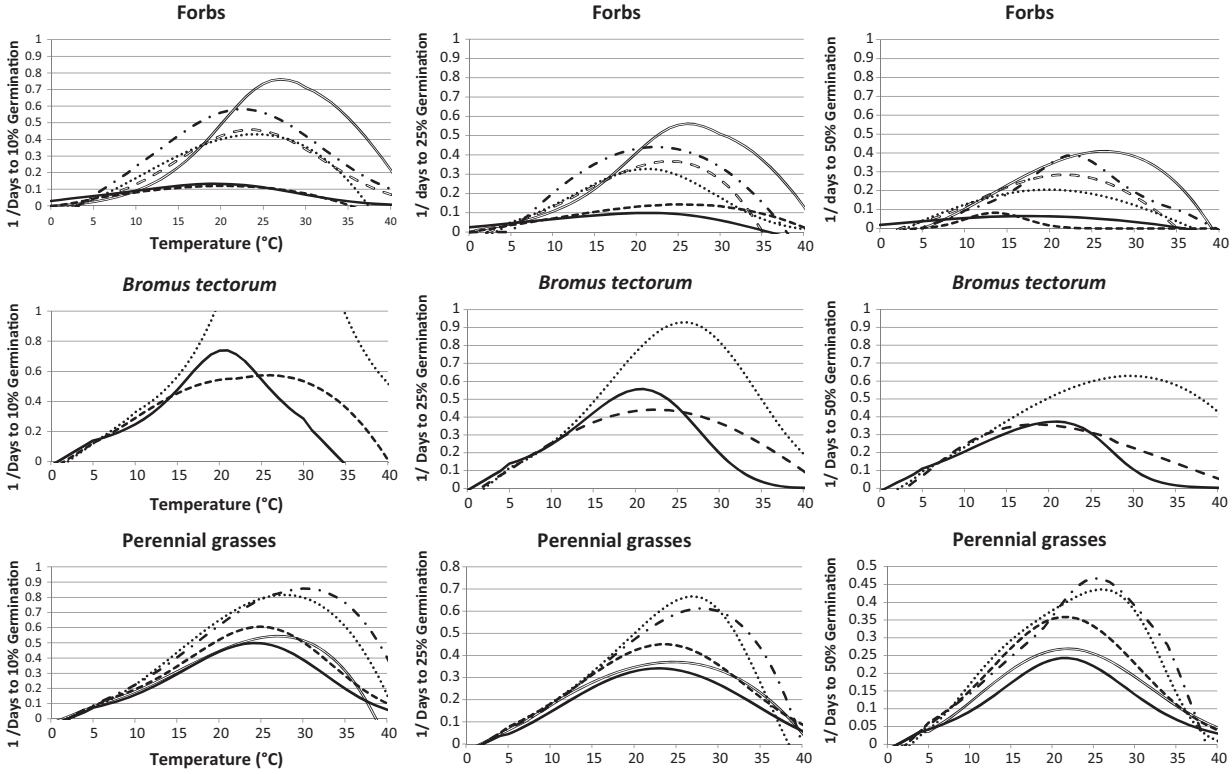

Fig. 2. Combined linear and curvilinear regression estimates of 1/days to 10, 25, or 50% germination as a function of incubation temperature for forbs: *Achillea millefolium* 'Eagle' – dash-dot, *A. millefolium* common – open line, *Enceliopsis nudicaulis* – dashed line, *Linum lewisii* – open dashed, *L. perenne* 'Appar' – dots, *Lupinus arbustus* – solid line; *Bromus tectorum* seedlots: Lookout Pass – solid line, Spanish Fork-dots, Skull Valley – dashed; perennial grasses: *Agropyron cristatum* × *A. desertorum* 'Hycrest' – open line, *A. desertorum* 'Nordan' – dash-dot, *Elymus elymoides* – solid line, *E. wawawaiensis* – dot, *Psuedoroegneria spicata* 'Anatone' – dashed.

2.3. Statistical analysis

Mixed model analysis of variance (SAS Institute Inc., 2001) was used to determine effects of seedlot and incubation temperature on the arcsine of the square root of total germination percentage and effects of seedlot and diurnal temperature on days to 10, 25, and 50% germination. Germination model accuracy for each seedlot and subpopulation was evaluated for diurnal temperatures by subtracting actual measured time to germination for a subpopulation from model-predicted germination time. Mixed model analysis of variance was conducted on the difference values. Tukey's mean separation test ($P < 0.05$) was used to determine significant differences among total germination and germination time responses for different seedlots or diurnal temperature regimes for germination subpopulations.

3. Results

3.1. Total germination responses to temperature

The interaction of seedlot and temperature was significant ($P < 0.0001$) for total germination. Most grass species exhibited high germination (>50%) at all constant and diurnal temperatures, even at 5 °C (Table 2). Three perennial grasses, *Agropyron cristatum* x *A. desertorum* Hycrest, *Elymus elymoides* 'Sanpete', and *Psueudoroegneria spicata* 'Anatone', one annual grass, *B. tectorum* Lookout Pass, and three forbs, *Linum lewisii*, *L. perenne* 'Appar', and *Lupinus arbustus*, had higher germination at 5 than 35 °C ($P < 0.05$). Most forbs had highest germination at moderate temperatures, while *L. arbustus* germinated best at cool to moderate temperatures. *Achillea millefolium* common had low germination at the cooler constant temperatures and the March and March–April diurnal temperatures while *L. arbustus* germinated best under the March diurnal temperature. All seedlots had at least 50% germination at some temperatures, except *E. nudicaulis*, which had highest germination of 29.2% at 15 °C. The perennial grasses, *L. arbustus*, and *Linum* seedlots had similar total germination as the *B. tectorum* seedlots at cooler temperatures (≤15 °C, $P < 0.05$). The *Achillea* seedlots had lower germination than the *B. tectorum* seedlots at those cooler temperatures, but similar germination at moderate temperatures (20–30 °C).

3.2. Model fit and germination rate responses to constant temperatures

Overall model fit of germination rate as a function of constant temperature was high with linear equation R^2 values ranging from 0.64 to 0.99 with 33 of 40 equations having an $R^2 \geq 0.85$ (Table 3). Model R^2 values for curvilinear equations ranged from 0.59 to 0.98, and 40 of the 48 equations had an $R^2 \geq 0.80$ (Table 4). Linear regression intercepts or estimated base temperatures were close to 0 °C for the 10, 25, and 50% subpopulations, across most seedlots. *E. nudicaulis* consistently had both lower germination percentages and lower R^2 values. The *B. tectorum*, perennial grasses, *Linum*, and *Achillea* seedlots all had slightly decreasing R^2 values with increasing subpopulation percentage from 10 to 50% for linear regressions using cooler temperatures. The perennial grass and *Linum* seedlots had R^2 values as high as those of the *B. tectorum* seedlots for these linear equations. For the curvilinear equations, the perennial grasses and *Linum* seedlots had higher R^2 values than the *B. tectorum* seedlots.

Most seedlots had similar responses of increasing germination rate above 5 °C to a T_o of 20–25 °C, and decreasing rate at temperatures > 30 °C (Fig. 2). The 10 and 25% subpopulations generally had higher T_o than the 50% subpopulations. The *Achillea* and *Linum* seedlots had most rapid germination at warmer temperatures with the 'Eagle' seedlot having a T_o of 5 °C greater than the other forbs. The *Linum* seedlots had intermediate germination rates, while rates of *E. nudicaulis* and *L. arbustus* were lowest. *Elymus wawaiensis* and *Agropyron desertorum* 'Nordan' had a similar temperature range for T_o (25–30 °C) as the Spanish Fork *B. tectorum* seedlot, but not nearly as high of a germination rate at T_o. The Lookout Pass seedlot of *B. tectorum* had the lowest T_o, 20 °C.

The ability of *B. tectorum* to germinate quickly at cool temperatures was evident from linear regression estimates, as well as responses to the March diurnal temperature. Estimated time to 10, 25, and 50% germination for the *B. tectorum* seedlots at 5 °C was 7.9, 8.5, and 11.4 days. This was 4.6, 7.1, and 10.7 days faster than the perennial grass seedlots, and 12.7, 13.6, and 14 days faster than the fastest-germinating forb seedlots. *A. desertorum* 'Nordan' required the least time of any of the perennial grasses to germinate in the March and April diurnal temperatures (Table 5). *Elymus elymoides* consistently required the most time of any grass to reach the subpopulation germination percentages in all diurnal spring temperatures except for the fastest 10% subpopulation incubated in May temperatures. Most seedlots required the least time to germinate in the May diurnal temperatures (Table 5).

3.3. Accuracy of model predictions for diurnal temperatures

Main effects of subpopulation, diurnal temperature, and seedlot were all significant ($P < 0.01$) for the difference between predicted and measured days to a germination percentage, as was the three-way interaction of these factors. In general, differences were least for the annual and perennial grasses and *L. arbustus*, intermediate for the *Linum* species, high for the *Achillea* seedlots, and highest for *E. nudicaulis* (Table 5). Over all species and subpopulations, models overestimated days to a germination percentage by 3.4 days for the March diurnal temperature and overestimated by significantly ($P < 0.05$) fewer days (1.6 and 1.8) for the mid-March to mid-April and May diurnal temperatures. Exceptions to greater overestimation at the March diurnal temperatures were *E. nudicaulis* and *L. arbustus* which both had much faster measured germination and much greater overestimation for the May than the cooler temperature regimes (Table 5). However, the total germination of *L. arbustus* was low (13.3%) under May diurnal temperatures (Table 2). Germination of the 50% subpopulation of *A. millefolium* 'Eagle' was especially slow for the cooler March and mid-March to mid-April diurnal temperatures (21.2 and 19.7 days, Table 5) and the model especially overestimated time to 50% germination for these diurnal temperatures (13.9 and 11.8 days).

3.4. Discussion

To be useful, germination models must accurately predict germination under simulated and actual field conditions. The thermal-time model predicted germination time for simulated field temperatures very well for most seedlots for most diurnal temperatures. In almost every case, the model overestimated days to a subpopulation germination percentage. It especially overestimated germination time for *A. millefolium* common under March temperatures and the 50% subpopulation of *E. nudicaulis* under warmer temperatures (Table 5). Overestimation of time to germination at low temperatures has been attributed to errors in temperature control or sensitivity of germination rate to near-base temperatures (Hardegree et al., 1999). A possible reason that the model overestimated germination time, especially for the March diurnal temperatures is underestimation of progress toward germination at cooler temperatures (0–5 °C). Our minimum simulated diurnal temperature (4 °C) was higher than actual minimum temperatures measured in the field, but the March and March–April

Table 5
Measured days to a subpopulation germination percentage and difference between estimated and measured days for three diurnal temperature regimes for AcmiE (Achillea *millefollium* 'Eagle'), Acmi (*Achillea millefolium* common), Ennu (*Enceliopsis nudicaulis*), Lile (*Linum lewisii*), Lipe (*Linum perenne* 'Appar'), Luar (*Lupinus arbustus*), AgcrAgdeH (*Agropyron cristatum* x *Agropyron desertorum* 'Hycrest'), AgdeN (*Agropyron desertorum* 'Nordan'), Elel (*Elymus elymoides*), Elwa (*Elymus wawawaiensis*), PsspA (*Psuedoroegneria spicata* 'Anatone'), BrteLP (*Bromus tectorum* Lookout Pass), BrteSF (*Bromus tectorum* Spanish Fork), BrteSV (*Bromus tectorum* Skull Valley). A positive difference value indicates the model overestimated time to germination while a negative value indicates underestimation by the number of days difference.

Sub-population	Collection	March		March–April		May	
		Measured (days)	Difference (days)	Measured (days)	Difference (days)	Measured (days)	Difference (days)
10%	AcmiE	7.38	2.29	5.36	2.30	1.44	0.49
	Acmi	16.03	7.88	17.64	0.17	2.30	0.18
	Ennu	13.58	7.09	17.76	0.78	0.92	6.01
	Lile	11.36	4.68	9.58	2.97	1.39	0.48
	LipeA	10.53	4.01	8.87	1.97	0.90	1.19
	Luar	14.88	0.27	13.59	0.53	1.62	2.04
	AgcrAgdeH	8.03	2.05	6.60	1.98	1.08	1.19
	AgdeN	4.78	3.85	6.28	0.84	1.45	0.27
	Elel	10.40	1.48	8.38	1.37	1.33	1.27
	Elwa	8.14	1.23	7.66	−0.16	4.48	0.15
	PsspA	7.91	1.71	7.40	0.60	1.02	1.12
	BrteLP	3.65	2.89	5.17	0.45	3.11	0.14
	BrteSF	3.69	2.01	3.50	1.38	6.83	0.16
	BrteSV	3.66	2.92	4.76	0.86	1.64	0.82
25%	AcmiE	10.54	−1.33	6.81	0.73	1.96	0.52
	Acmi	16.78	8.71	18.09	0.76	2.69	0.13
	Ennu	22.84	0.93	22.23	−1.69	1.43	3.50
	Lile	12.42	3.29	10.44	2.23	1.82	0.77
	LipeA	11.85	4.65	9.57	3.14	1.25	2.00
	Luar	19.51	0.06	18.67	−0.26	2.23	2.88
	AgcrAgdeH	9.33	2.25	8.07	1.55	1.77	1.44
	AgdeN	7.38	3.58	6.93	2.03	2.00	0.44
	Elel	12.00	1.96	9.27	2.23	2.10	1.21
	Elwa	9.17	1.58	8.20	0.59	5.91	0.21
	PsspA	8.94	1.73	8.06	0.73	1.53	1.23
	BrteLP	4.62	2.01	6.93	−1.22	3.66	0.13
	BrteSF	4.73	2.52	4.25	1.59	11.30	0.49
	BrteSV	4.66	2.84	5.46	1.04	2.14	0.93
50%	AcmiE	21.19	13.87	19.69	11.78	2.63	1.66
	Acmi	18.03	12.42	18.84	1.09	3.36	0.10
	Ennu	36.05	3.42	26.28	12.72	2.66	16.73
	Lile	13.73	3.98	12.44	1.48	2.96	1.36
	LipeA	14.01	4.45	11.48	3.23	1.67	2.06
	Luar	25.87	−1.34	22.31	0.77	3.53	7.73
	AgcrAgdeH	11.67	4.74	10.40	3.02	2.95	1.87
	AgdeN	9.38	4.46	8.55	3.00	2.81	0.37
	Elel	14.98	3.60	11.11	4.51	3.92	1.16
	Elwa	12.03	1.72	9.43	1.28	11.86	0.38
	PsspA	10.45	3.01	8.70	2.01	2.15	1.49
	BrteLP	6.24	1.93	9.83	−2.83	4.68	−1.06
	BrteSF	6.47	2.24	5.50	2.00	18.00	0.59
	BrteSV	6.32	3.30	6.68	1.07	2.94	0.84
Standard error range		1.88–3.73	1.26–1.45	1.93–3.83	1.26–2.51	1.39	1.26

diurnal regimes were at this temperature for 10 and 9 h each day (Fig. 1). Because incubators tend to freeze when programmed at temperatures < 5 °C, it has been difficult to determine germination responses at cool temperatures. The minimum temperature used to develop our thermal models was 5 °C. Hardegree et al. (2008, 2010) developed germination models using a minimum temperature of 3 °C. Hardegree et al. (2010) ranked ability to germinate at cooler simulated-field temperatures as *B. tectorum* > *P. spicata* > *E. elymoides* as we also found.

It is unlikely that use of linear equations for temperatures of 5–10 °C, and sometimes 15 °C greatly overestimated progress toward germination at the 4 °C minimum temperature of our coolest diurnal curves. Our approach essentially fits that of Hardegree et al. (1999) who reduced their low-temperature estimation errors by creating a separate linear equation for each 5 °C increment in temperature in the 5–20 °C range. Linear regression intercept differences among most of our seedlots were <0.02 for the different subpopulations. Errors from over-estimation could be exacerbated in the field with minimum temperatures lower than 4 °C. Hardegree et al. (2010) noted that, although germination rates are relatively similar at these cooler temperatures, small inverse rate differences equate to large actual germination time differences. The accuracy of thermal-time models such as ours depends on how fast progress toward germination is in relation to how long seedbeds are actually at these low temperatures and enough water remains unfrozen in seeds to allow germination processes to proceed. Prediction of field germination behavior must involve accounting for thermal progress toward germination only when seedbeds are wet and seeds are expected to be imbibed (Roundy et al., 2007).

A high R^2 value, but consistent or large difference between estimated and measured time to germination could also indicate that seeds are stimulated to germinate faster by factors other than thermal accumulation. Thermal-time models for most of our seedlots had high R^2 values, but overestimated germination time. Thermal models are built on response to constant temperature, but the

germination rate and dormancy loss of many species is stimulated by alternating temperatures and other aspects of temperature pattern (Probert, 1992; Hardegree et al., 1999). It should be expected that species that have very low total germination percentages at constant temperatures, but high germination percentages at alternating temperatures will have inaccurate prediction of germination timing using thermal time models. Thermal time modeling of such species is not representative of most of the seed population, but a small subpopulation of seeds that can germinate at constant temperatures. This appears to be the case with some of the forbs in our study, such as the large overestimation of time to germination of the *Achillea* seedlots, and especially *A. millefolium* common in the March diurnal temperature. Higher total germination at a range of constant temperatures allows more confidence in using thermal time prediction of germination rates because relatively more seeds are represented in each subpopulation. Where total germination is low for most constant temperatures, a high percentage of dormant seeds is indicated, and prediction of germination timing using thermal accumulation may be inaccurate, as seen for *E. nudicaulis* (Tables 2 and 5).

4. Conclusion

Thermal-time models allow estimation of potential germination under the dynamic temperatures of field seedbeds and could be very useful in selecting plant materials for fire rehabilitation and restoration seedings for specific sites and years. Thermal-time models overestimated germination time for field-simulated temperatures by <1–4 days for most seedlots. This generally high degree of accuracy supports use of thermal models to predict field germination for non-dormant seeds. Thermal model predictions should be compared with actual field germination to best determine suitability for species selection. Thermal modeling was sufficiently accurate enough for many seedlots to incorporate its use into a wet thermal model. This model predicts germination by accumulating thermal progress toward germination only when seedbeds are wet and seeds presumed to be imbibed (Roundy et al., 2007; Rawlins et al., 2011). Seedling establishment models require accurate prediction of both germination and seedling root growth in order to best predict seedling survival and establishment potential (Forcella et al., 2000; Vleeshouwers and Kropff, 2000).

Acknowledgements

We thank Mitchell Rawlins for assistance in data management. We thank the USDA Forest Service Rocky Mountain Station and Brigham Young University for financial support.

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