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

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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 ≥ 0.85 for 33 of 40 linear equations and ≥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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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