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Predicting germination in semi-arid wildland seedbeds II. Field validation of wet thermal-time models

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ABSTRACT

Accurate prediction of germination for species used for semi-arid land revegetation would support selection of plant materials for specific climatic conditions and sites. Wet thermal-time models predict germination time by summing progress toward germination subpopulation percentages as a function of temperature across intermittent wet periods or within singular wet periods. Wet periods may be defined by any reasonable seedbed water potential above which seeds are expected to imbibe sufficiently to germinate. These models may be especially applicable to the *Artemisia* steppe of the western U.S.A. where water availability limits germination in summer and early fall while cool temperatures limit germination in late fall, winter, and spring when soil water is available. To test accuracy of wet thermal-time models we placed seedbags with seeds of five species commonly used in wildland revegetation, as well as two collections of the invasive annual grass, *Bromus tectorum* L. into *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young zone seedbeds for 19 field incubation periods over four seasons. Hourly surface (1–3 cm) soil temperatures and soil water potentials were measured near the seedbags. These data were input into thermal-time models which predicted time to germination for each seedbag retrieval date. Binomial data representing agreement (1) or lack of agreement (0) of predicted and actual germination for each retrieval date were analyzed using logistic regression. Thermal summation method, season, water potential threshold, and species most affected accuracy of predictions ($P < 0.0002$). A model which defined a wet period as ≥ -1.5 MPa soil water potential and summed progress toward germination across intermittent wet periods was most accurate in predicting actual germination by a retrieval date. Across all species, this model correctly predicted that germination would occur in seedbags 75–95% of the time over the latewinter to mid-spring seasons, but only 50–71% of the time for the fall-early winter season when time of soil water availability was least. Although the wet thermal-time model overestimated time to germination for some species and seasons, its accuracy should be high enough to evaluate germination potential by mid-spring for different species, sites, and climatic conditions.

1. Introduction

Seedings of perennial species for fire rehabilitation in *Artemisia tridentata* Nutt. (big sagebrush) ecosystems in the western United States often fail due to lack of adequate precipitation (Hardegree et al., 2011). Predicting germination of revegetation species in relation to soil temperature and water conditions is the first step in developing seedling-establishment models to better evaluate seeding potential of desirable plant materials (Vleeshouwers and Kropff, 2000; Grundy, 2003; Rawlins et al., 2011). In cold desert *A. tridentata* communities, cool soil temperatures limit germination in late fall, winter, and spring, when seedbed water is available, while soil water availability limits germination in early fall, spring, and summer when temperatures are warm (Roundy et al., 2007). To establish in this environment, seeds must germinate and grow roots sufficiently to persist as soil water is quickly lost in late spring and summer (Evans et al., 1970). Therefore, models must quantify effects of dynamic soil temperatures and water potentials on seed population germination rate.

Germination time has been predicted in relation to limiting temperature and water potential thresholds using hydrothermal models (Gummerson, 1986; Finch-Savage and Phelps, 1993; Allen et al., 1999; Roman et al., 1999; Meyer et al., 2000; Hardegree et al., 2003; Rawlins et al., 2011). Such models are difficult to validate in the field because sensors are lacking which can continuously and accurately measure a wide range of seedbed water potentials at the scale and near-surface location of seeds (Taylor et al., 2007). Roundy et al. (2007) simplified the model by summing thermal progress toward germination only when the seedbed water potential is above a given threshold. Progress toward germination

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Table 1
Seasonal planting and retrieval dates and number of days in the ground for 19 seedbag field incubation periods.

2005–2006			2006–2007		
Planting	Retrieval	# of days	Planting	Retrieval	# of days
Fall-early winter					
15 October	6 December	52	24 October	9 November	16
			24 October	16 November	23
			24 October	30 November	37
Fall-late winter					
15-October	19 January	96	24 October	21 February	120
Late winter–early spring					
27 February	16 March	17	21 February	8 March	15
27 February	28 March	29	21 February	20 March	27
27 February	11 April	43			
27 February	25 April	57			
Late winter–mid-spring					
28 March	11 April	14	20 March	5 April	16
11 April	25 April	14	21 February	5 April	43
27 February	10 May	72	21 February	18 April	56
			5 April	18 April	13

may be summed across intermittent wet periods or within singular wet periods (Roundy et al., 2007). Wet periods may be defined by any reasonable water potential above which seeds are expected to imbibe sufficiently to progress toward germination. The accuracy of field germination predictions for this wet-thermal model depends on whether water potential inputs from sensors (Taylor et al., 2007) or simulations (Hardegree et al., 2010) are similar to actual seed water potentials in seedbeds.

Most water potential sensors are much larger than seeds and may lag seeds in both wetting and drying (Taylor et al., 2007). Seasonal seedbed water and temperature conditions may affect how well sensors track the water potential of seeds. Sensors would be expected to lag wetting of seeds with the onset of fall or winter rains, but to lag seed drying in spring. In winter, resistance sensors may indicate that the soil is dry when water in the sensors is frozen while seeds near the surface may be unfrozen and accumulating thermal-time progress toward germination on sunny days. There has been limited characterization of wildland field seedbeds or field-testing of hydrothermal or wet-thermal models (Meyer and Allen, 2009; Wang et al., 2006). Our objectives were to: (1) characterize the seasonal soil temperature and moisture environments of *Artemisia* zone seedbeds, (2) determine the accuracy of wet thermal-time models for predicting germination during different seasonal field incubation periods, and (3) determine the most accurate combination of calculating thermal progress toward germination (singular or within a continuously wet period, or cumulative, across multiple wet periods) and wet period threshold (−0.5, −1.0, or −1.5 MPa water potential).

2. Methods and materials

We tested the accuracy of predicting time of germination in the field for thermal-time germination models of 10, 25, and 50% subpopulations for six species as developed by Rawlins et al. (2011). The two populations of *Bromus tectorum* L. seed were collected from Skull Valley and Lookout Pass, Utah. We assessed model accuracy by measuring field seedbed water potentials and temperatures to predict whether seeds would germinate or not and comparing germination predictions with actual seed germination in seedbags buried during 19 incubation periods.

2.1. Site descriptions

We conducted field testing at two sites located in Tooele Co., Utah. The Skull Valley site has an elevation of 1524 m, an average annual air temperature of 8–10 °C, and annual precipitation of 200–254 mm. Soils are Medburn fine sandy loam series of coarse-loamy, mixed (calcareous) mesic xeric Torriorthents (Trickler, 2001). The Lookout Pass site is located at a slightly higher elevation (1676 m), receives more precipitation (254–305 mm), and has a wider range of annual temperatures (7–11 °C) than the Skull Valley site. Soils are Taylorsflat loamy series of fine-loamy, mixed, mesic xerolic Calciorthids (Trickler, 2001). Both sites were originally occupied by *A. tridentata* Nutt. ssp. *wyominesis* Beetle and Young and bunchgrass communities. The sites are currently dominated by *Agropyron cristatum* (L.) Gaertn. that was planted in 1982 at Skull Valley and 1996 at Lookout Pass after wildfire.

2.2. Field study

We buried thermocouples to measure soil temperature and gypsum blocks (Delmhorst, Inc.) to measure water potential. We buried sensors at 1–3 cm in three replicate plots adjacent to each of four blocks at each field site. CR-10 X microloggers (Campbell Scientific, Inc.) read sensors every minute and calculated hourly averages. We converted gypsum block resistance to MPa of water potential using standard calibration curves (Campbell Scientific Inc., 1983). Although some error may be introduced by not individually calibrating each gypsum block, blocks calibrated with standard equations were relatively consistent and sensitive to surface soil drying conditions in a growth chamber study (Taylor et al., 2007). Precipitation and air temperature were measured using an electronic tipping bucket rain gage (Texas Electronics, Inc.) and a Campbell Scientific, Inc. model 107 temperature probe (thermistor) in a gill shield at each site. Prior to the first 2005 seedbag burial, we treated the seedbag burial areas within each block with glyphosate to fully control *A. cristatum*.

We buried seedbags in four 8.3 by 11 m blocks at each site. We placed enough seeds of each seed collection in separate nylon mesh bags (Meyer and Allen, 2009) approximately 5 cm^2 to provide a minimum of 25 germinable seeds/bag as determined by previous germination tests (Rawlins et al., 2011). We buried one seedbag of each species 2-cm deep in each of the four blocks for each of 19 incubation periods. We seeded the Lookout Pass *B. tectorum* seed collection at Lookout Pass and the Skull Valley collection at Skull Valley. We chose seedbag installation and retrieval dates to represent a range of thermal and moisture conditions from fall through spring of 2005 to 2007. We assigned incubation periods to one of four seasons based on planting and retrieval dates (Table 1). On a retrieval date, we placed collected seedbags on ice until we counted the number of germinated seeds in each bag.

2.3. Analysis

We calculated a number of variables to characterize seedbed water potential and temperature conditions for each season (Table 2). We used mixed model analysis of variance (Littell et al., 1996) and Tukey's mean separation test ($P < 0.05$) to determine significant differences among seasons.

We estimated germination date for the fastest 10, 25, and 50% of seeds for a species, block, and incubation period using two summation methods and three different water-potential thresholds to define a wet period, according to the methods of Roundy et al. (2007). We input hourly soil temperature as the independent variable into thermal-time equations developed by Rawlins et al. (2011) to estimate hourly progress toward a germination percentage. These equations estimate 1/days to a germination percentage, which, when divided by 24 equals the hourly progress toward germination for an hour at that soil temperature. The wet thermal-time model sums progress toward germination only for hours when the soil water potential is above the given threshold. The two summation methods were designated as singular (when progress toward germination had to sum to 1 within at least one continuously wet period) and cumulative (germination predicted when progress toward germination summed to 1 across all intermittent wet periods). In addition, we tested the effects of water potential (wet period) thresholds of −0.5, −1.0, and −1.5 MPa on model accuracy.

Because we could not retrieve bags on an hourly or daily basis, our data consist of whether a subpopulation was predicted to germinate or not by a retrieval date, and actual number of seeds germinated in a seedbag by the retrieval date. There were four possible outcomes for each model combination of water potential threshold and summation method for each species at a site for each incubation period: (1) subpopulation predicted to germinate and did germinate, (2) subpopulation predicted to not germinate and did not germinate, (3) subpopulation predicted to not germinate and did germinate, and (4) subpopulation predicted to germinate and did not germinate. Counts and percentages of the last two outcomes were used to determine model overestimation (outcome 3) or underestimation (outcome 4) of germination time.

To analyze prediction accuracy, we assigned model prediction outcomes 1 and 2 above a value of 1 (accurate predictions) and outcomes 3 and 4 a value of 0 (inaccurate predictions). We conducted mixed model logistic regression analysis (Wolfinger and O'Connel, 1993; Littell et al., 1996) on the binomial data to determine effects of season, species, water potential threshold, and thermal summation method on prediction accuracy. We considered the block within-site interaction as random and all other effects as fixed. The percent accuracy of each species and subpopulation model for a given season, water potential threshold, summation method or any combination of these was calculated according to Littell et al. (1996) by:

$$P = \frac{e^{\mathrm{LME}}}{1 + e^{\mathrm{LME}}}$$

where P is the predicted probability or percentage of the time that the model is correct, and LME is the logistic model estimate for that combination of season, species, water potential threshold, and summation method.

The standard error for the accuracy of each combination was calculated according to Littell et al. (1996) using the Delta method of Bishop et al. (1975).

3. Results

All seedbed characterizing variables varied significantly ($P < 0.001$) among seasons. Seasonal differences in the seedbed environment were greater for variables related to soil water potential than those related to soil temperature (Table 2). The fall-early winter season was drier than the other seasons with fewer or shorter wet periods and a lower percentage of time when the seedbed was wet compared to the other seasons. Soil temperatures, percentage of frost-free days, and air temperatures were generally lower for fall-late winter than for the other seasons. Wet seedbeds were relatively cold (between 0 and 5 °C) for at least 20% of the incubation time for all seasons. Wet seedbeds were practically never warmer than 25 °C. Wet degree days or the summation of hourly soil temperatures above 0 °C when the soil is wet increased substantially from late winter into mid-spring. The differences in percentage time that the seedbed was above different water potential thresholds decreased as seedbeds were warmed into mid-spring.

Across all seasons, species, threshold water potentials and summation methods thermal-time models correctly predicted germination or no germination in seedbags for 67, 65, and 61% of the 3492 total observations for the 10, 25, and 50% subpopulations. Failure to predict germination when germination was observed in seedbags occurred for 95, 95, and 91% of the incorrect predictions for the 10, 25, and 50% subpopulations. This indicates that incorrect predictions were almost always due to over-estimation of time to germination.

The logistic regression analysis ranked in order of greatest effect on model accuracy summation method, season, water potential threshold, and species. This order is based on the magnitude of the associated F-statistic, where this relative order was consistent and $P < 0.0002$ for all listed effects for all subpopulations. Cumulative summation was 22–33% more accurate than singular summation, depending on the subpopulation. A water potential threshold of −1.5 MPa was 8–12% more accurate than −1.0 MPa, and 19–27% more accurate than −0.5 MPa, depending on the subpopulation. Accuracy of predictions for seasons ranked late winter–mid-spring > late winter–early spring > fall-late winter > fall-early winter. Model accuracy was generally highest for *B. tectorum* and lowest for *Linum perenne* 'Appar'. Cumulative thermal summation and a −1.5 MPa wet-soil threshold yielded the most accurate germination prediction for all species and subpopulations ($P < 0.0001$) (Table 3). The interaction of season with seedlot and with summation method was significant ($P < 0.001$) for all subpopulations, while the 3-way interaction of season, summation method, and water potential threshold varied in significance with the subpopulation (10% and 25% subpopulations, $P < 0.08$; 50% subpopulation, $P < 0.04$). Using the most accurate model, accuracy was 82, 78.8, and 71.5% for the 10, 25, and 50% subpopulations averaged across all seasons and species. With this model, germination predictions for fall-early winter had the lowest accuracy while the late winter–mid-spring season had the highest. Predictions for fall-early winter averaged 70.8, 59.8, and 49.6% while those for the other seasons averaged 85.8, 85.1, and 78.8% for the 10, 25, and 50% subpopulations. Predictions for *Elymus elymoides* and *L. perenne* had the lowest accuracy, especially in fall-early winter and late winter–mid-spring. *A. cristatum* X *A.* desertorum 'Hycrest' and *Pseudoroegneria spicata* spp *spicata* had 36% lower prediction accuracy for the 50% than the 10% subpopulation in fall-early winter. All species and subpopulations had at least 90% accuracy in late winter–early spring, except *E. elymoides*.

4. Discussion

Overall, wet-thermal model predictions were accurate enough to predict whether or not germination would occur for all of these species by mid-spring. Lowest prediction accuracy was for seeds buried from fall to early-winter. The seedbed during this season

Table 2
Site air temperature and precipitation and soil temperature and available water data for *Artemisia* zone seedbeds during seedbag incubation over four seasonal periods.

Variable	Range	Fall-early winter	Fall-mid or late winter	Late winter–early spring	Late winter–mid-spring
Incubation periods (no.)		4	2	6	7
Dates		15 October–6 December	15 October-8 March	21 February–28 March	21 February–10 May
Total days		16–52	15–120	14–29	14–72
Precipitation (mm)		0.8–17.4	3.6–36.5	2.8–17.1	1.6–48.8
Wet days	≥−0.5 MPa	4.9 C[a]	17.3 B	12.7 B	22.9 A
	≥−1.0 MPa	8.0 D	23.3 B	15.6 C	30.3 A
	≥−1.5 MPa	12.5 C	27.9 B	17.3 C	33.6 A
Wet days (% of time)	≥−0.5 MPa	16.7 C	43.3 B	60.6 A	55.6 A
	≥−1.0 MPa	27.9 C	54.4 B	72.0 A	66.8 A
	≥−1.5 MPa	44.0 C	61.6 B	80.0 A	74.4 A
Number of wet periods	≥−1.5 MPa	5.6 B	11.1 A	2.6 C	4.4 BC
Average wet period (days)	≥−1.5 MPa	3.0 B	5.0 B	10.6 A	13.2 A
Wet degree days	≥−1.5 MPa	72.6 B	81.4 B	96.4 B	239.5 A
Soil temperature (°C)	Maximum	21.3 B	19.0 C	21.8 B	25.9 A
	Minimum	−4.6 B	−5.6 B	−0.90 A	−1.5 A
	Mean	5.6 A	2.4 D	6.7 B	8.5 A
Dry and wet soil degree days		188.7 B	186.9 B	132.5 C	339.4 A
Soil frost-free days (% of time)		86.7 B	66.7 C	93.9 A	95.5 A
Air temperature (°C)	Maximum	21.3	18.7	22.1	26.5
	Minimum	−4.6	−5.5	−0.9	−1.3
	Mean	5.6	2.3	6.8	9.1
Wet days (≥−1.5 MPa)	<0 °C	0.8 C	6.3 A	1.3 BC	1.9 B
	>0 ≤ 5 °C	5.5 C	15.3 A	8.3 B	13.1 A
	>5 ≤ 10 °C	3.6 B	4.2 B	4.2 B	8.8 A
	>10 ≤ 25 °C	2.5 B	2.0 B	3.4 B	9.6 A
	>5 ≤ 25 °C	6.1 B	6.2 B	7.6 B	18.4 A
	>25 ≤ 30 °C	0.0 B	0.0 B	0.0 B	0.2 A
Wet days (% of time)	<0 °C	2.5 C	12.2 A	4.9 B	3.7 BC
	>0 ≤ 5 °C	19.8 C	35.6 A	35.7 A	26.2 B
	>5 ≤ 10 °C	12.9 B	9.3 B	21.3 A	20.2 A
	>10 ≤ 25 °C	8.8 C	4.3 D	17.9 B	23.9 A
	>5 ≤ 25 °C	21.7 B	13.6 C	39.2 A	44.1 A
	>25 ≤ 30 °C	0.0 B	0.0 B	0.0 B	0.3 A

[a] Values with different letters within a row are significantly different ($P < 0.05$) by the Tukey test.

was not very different from the other seasons in soil-temperature and temperature-related variables (Table 2). However, the seedbed during this season had fewer wet days, shorter wet periods (mean = 3 days), and fewer wet days when the soil temperature (>5–25 °C) was favorable for germination. During the fall, soil temperatures are warm enough for germination, but soil moisture is lacking due to limited precipitation. Overestimation of germination time for this season may be related to differences in soil moisture sensor and seed response to fall rains. Fall rains occurred in both 2005 and 2006 both before and after seedbag burial. Gypsum blocks are 2-cm diameter by 2-cm long and would be expected to lag behind seeds in water uptake after rainfall. Seeds exposed to fall rains may have imbibed water and accumulated thermal time toward germination when gypsum blocks were still indicating that the seedbed was dry. However, an examination of hourly rainfall and soil water potential data for fall 2005 and 2006 indicated that gypsum blocks measured the surface soil as wet within 1–3 h after onset of most fall rains. We also observed that blocks generally dried out within the same hour or within a few hours of each other.

Seeds sown for fire rehabilitation and other revegetation purposes are often sown in late fall or even winter with the expectation that they will not emerge as seedlings until spring. From a practical standpoint for post-fire seeding, the lower percentage accuracy for fall-early winter germination may not be a problem because the model had high accuracy for predicting germination by mid-spring, by which time emergence is essential for establishment. On the other hand, the use of germination prediction for weed control of fall-germinated *B. tectorum* requires accurate fall-early winter accuracy. The best model had 87.9, 90.5, and 76.1% accuracy for the 10, 25, and 50% subpopulations of *B. tectorum* during this season. This accuracy is high enough to assess probability of *B. tectorum* fall germination using soil temperature and moisture sensors across a range of sites and years (Roundy et al., 2007).

One concern for using thermal models for predicting germination is that it is difficult to quantify rate of germination at temperatures between 0 and 5 °C because the cooling apparatus of incubators often freeze at these low temperatures (Rawlins et al., 2011). This has led to concerns that thermal models may underestimate progress toward germination and overestimate time to germination at these low temperatures (Rawlins et al., 2011). Interestingly, wet seedbeds in our study were in this low temperature range 20–30% of the incubation period time (Table 2). Possible underestimation of germination progress for 20% or more of the incubation period time may help explain why 90% of incorrect germination predictions were failure to predict that germination would occur when it had already occurred. Gypsum blocks record high resistance when frozen and may have indicated soils were dry during some hours when the seeds were actually unfrozen and progressing toward germination. Differences between actual and predicted germination times were greatest in cooler March and March–April field-simulated temperature regimes in the laboratory for these models (Rawlins et al., 2011). More research on germination progress at low temperatures is warranted. However, the model was highly accurate for seasons that had up to 36% of the wet seedbed incubation time between 0 and 5 °C (Table 3).

The most accurate model included a summation of progress toward germination across all wet periods and a water potential threshold for thermal summation of −1.5 MPa. We expected this model to underestimate, rather than overestimate time to germination because we expected that seeds would not continue additive progress toward germination after drying and rewetting. We also expected that, especially in spring, seeds would dry out faster than soil moisture sensors (Taylor et al., 2007). Our results agree with those of Meyer and Allen (2009) who found that cumulative thermal summation across intermittent wet periods most accurately predicted field germination of *B. tectorum.* Hardegree

Table 3
Accuracy percentages and standard errors for prediction of field germination using thermal summation across singular and cumulative wet periods and three wet period water potential thresholds for 10, 25 and 50% seed germination subpopulations for four seasonal periods.

Sub-population (%)	Species	Singular wet period Water potential threshold (−MPa)			Cumulative wet periods Water potential threshold (−MPa)		
		0.5	1	1.5	0.5	1	1.5
Fall-early winter							
10	*Linum perenne*	6.0 ± 4.7	9.2 ± 5.7	12.3 ± 6.4	12.3 ± 6.4	15.5 ± 7.1	46.0 ± 9.8
	Agropyron cristatum	13.8 ± 6.8	20.2 ± 7.9	30.9 ± 9.1	23.7 ± 8.3	42.5 ± 9.7	70.5 ± 8.9
	Elymus elymoides	15.2 ± 6.8	18.3 ± 7.3	27.7 ± 8.5	21.4 ± 7.7	30.8 ± 8.7	75.5 ± 8.1
	Bromus tectorum	13.6 ± 6.7	30.9 ± 9.1	66.4 ± 9.3	54.6 ± 9.8	84.6 ± 7.1	87.9 ± 6.4
	Pseudoroegneria spicata	11.6 ± 6.3	14.6 ± 6.9	27.7 ± 8.8	17.8 ± 7.5	48.8 ± 9.8	74.0 ± 8.6
25	*Linum perenne*	8.5 ± 5.5	8.5 ± 5.5	8.5 ± 5.5	11.5 ± 6.3	17.9 ± 7.5	38.8 ± 9.6
	Agropyron cristatum	21.9 ± 8.1	25.3 ± 8.5	21.9 ± 8.1	28.8 ± 8.9	32.3 ± 9.2	57.7 ± 9.7
	Elymus elymoides	36.0 ± 9.1	36.0 ± 9.1	36.0 ± 9.1	39.3 ± 9.2	46.2 ± 9.4	56.5 ± 9.4
	Bromus tectorum	11.3 ± 7.9	24.6 ± 10.8	50.6 ± 12.5	50.6 ± 12.5	76.7 ± 10.6	90.5 ± 7.3
	Pseudoroegneria spicata	13.7 ± 10.9	19.9 ± 12.6	23.2 ± 13.3	23.2 ± 13.3	40.7 ± 15.5	55.7 ± 15.7
50	*Linum perenne*	25.4 ± 8.5	25.4 ± 8.5	25.4 ± 8.5	28.8 ± 8.9	25.4 ± 8.5	28.8 ± 8.9
	Agropyron cristatum	18.9 ± 7.7	18.9 ± 7.7	18.9 ± 7.7	22.3 ± 8.2	25.8 ± 8.6	33.2 ± 9.2
	Elymus elymoides	68.9 ± 8.7	68.9 ± 8.7	68.9 ± 8.7	68.9 ± 8.7	72.1 ± 8.5	72.1 ± 8.5
	Bromus tectorum	12.8 ± 8.4	16.1 ± 9.2	40.4 ± 12.3	22.9 ± 10.5	51.1 ± 12.5	76.1 ± 10.7
	Pseudoroegneria spicata	13.8 ± 10.9	13.8 ± 10.9	13.8 ± 10.9	17.0 ± 11.9	23.6 ± 13.4	37.8 ± 15.3
Fall-late winter							
10	*Linum perenne*	22.9 ± 8.6	26.5 ± 9.0	26.5 ± 9.0	42.5 ± 10.1	81.0 ± 8.0	85.7 ± 7.1
	Agropyron cristatum	9.8 ± 6.0	15.5 ± 7.2	21.8 ± 8.3	48.3 ± 10.0	66.0 ± 9.5	66.0 ± 9.5
	Elymus elymoides	17.9 ± 8.0	21.3 ± 8.5	21.3 ± 8.5	53.4 ± 10.4	77.6 ± 8.7	83.6 ± 7.7
	Bromus tectorum	7.1 ± 5.3	16.7 ± 7.8	51.8 ± 10.4	72.0 ± 9.4	77.0 ± 8.8	77.0 ± 8.8
	Pseudoroegneria spicata	19.4 ± 8.2	22.9 ± 8.8	34.7 ± 9.9	58.1 ± 10.3	63.1 ± 10.1	63.1 ± 10.1
25	*Linum perenne*	23.9 ± 8.7	23.9 ± 8.7	27.6 ± 9.1	31.4 ± 9.5	62.1 ± 9.9	85.2 ± 7.2
	Agropyron cristatum	9.7 ± 5.9	12.5 ± 6.6	12.5 ± 6.6	40.3 ± 9.8	62.0 ± 9.7	66.6 ± 9.4
	Elymus elymoides	26.7 ± 9.2	26.7 ± 9.2	30.8 ± 9.6	39.5 ± 10.2	73.5 ± 9.2	73.5 ± 9.2
	Bromus tectorum	6.8 ± 5.2	12.3 ± 6.8	46.0 ± 10.4	70.0 ± 9.6	80.7 ± 8.2	85.5 ± 7.3
	Pseudoroegneria spicata	22.5 ± 8.7	26.3 ± 9.2	34.6 ± 9.9	48.5 ± 10.4	74.7 ± 9.1	74.7 ± 9.1
50	*Linum perenne*	31.5 ± 9.5	31.5 ± 9.5	35.3 ± 9.8	35.3 ± 9.8	43.1 ± 10.1	82.9 ± 7.7
	Agropyron cristatum	24.5 ± 8.6	24.5 ± 8.6	28.0 ± 9.0	28.0 ± 9.0	54.8 ± 10.0	71.2 ± 9.1
	Elymus elymoides	52.7 ± 10.4	52.7 ± 10.4	52.7 ± 10.4	57.7 ± 10.3	62.9 ± 10.1	73.4 ± 9.2
	Bromus tectorum	16.1 ± 7.7	22.9 ± 8.8	34.5 ± 9.9	47.8 ± 10.4	73.4 ± 9.2	83.8 ± 7.7
	Pseudoroegneria spicata	25.2 ± 9.0	25.2 ± 9.0	28.9 ± 9.5	37.2 ± 10.1	73.1 ± 9.2	84.1 ± 7.6
Late winter–early spring							
10	*Linum perenne*	33.6 ± 9.1	50.4 ± 9.6	78.7 ± 7.9	64.2 ± 9.2	92.4 ± 5.1	88.2 ± 6.2
	Agropyron cristatum	34.8 ± 9.2	58.1 ± 9.5	90.2 ± 5.7	80.8 ± 7.6	95.7 ± 3.9	95.7 ± 3.9
	Elymus elymoides	46.9 ± 9.8	37.6 ± 9.5	56.6 ± 9.7	61.5 ± 9.5	66.4 ± 9.3	61.5 ± 9.5
	Bromus tectorum	49.0 ± 9.4	69.4 ± 8.7	83.5 ± 7.0	83.5 ± 7.0	95.5 ± 3.9	95.5 ± 3.9
	Pseudoroegneria spicata	42.6 ± 9.7	67.2 ± 9.2	90.1 ± 5.9	93.3 ± 4.9	95.8 ± 3.9	93.3 ± 4.9
25	*Linum perenne*	27.0 ± 8.5	44.3 ± 9.6	52.0 ± 9.6	44.3 ± 9.6	68.4 ± 8.9	76.9 ± 8.1
	Agropyron cristatum	43.4 ± 9.5	56.3 ± 9.5	90.3 ± 5.7	75.5 ± 8.3	96.6 ± 3.5	93.8 ± 4.6
	Elymus elymoides	55.1 ± 9.8	55.1 ± 9.8	69.0 ± 9.1	59.7 ± 9.6	59.7 ± 9.6	55.1 ± 9.8
	Bromus tectorum	49.4 ± 9.4	76.1 ± 8.1	89.2 ± 5.9	89.2 ± 5.9	85.2 ± 6.7	92.8 ± 4.9
	Pseudoroegneria spicata	41.3 ± 9.7	61.5 ± 9.5	89.9 ± 5.9	80.5 ± 7.8	96.4 ± 3.7	96.4 ± 3.7
50	*Linum perenne*	26.6 ± 8.5	26.6 ± 8.5	33.2 ± 9.1	36.6 ± 9.3	40.1 ± 9.4	58.2 ± 9.5
	Agropyron cristatum	20.6 ± 7.8	27.0 ± 8.5	41.5 ± 9.5	30.5 ± 8.9	53.5 ± 9.6	70.4 ± 8.8
	Elymus elymoides	64.1 ± 9.4	64.1 ± 9.4	59.4 ± 9.6	59.4 ± 9.6	68.8 ± 9.1	50.2 ± 9.8
	Bromus tectorum	36.7 ± 9.1	54.4 ± 9.4	72.7 ± 8.4	72.7 ± 8.4	81.5 ± 7.3	77.1 ± 7.9
	Pseudoroegneria spicata	28.2 ± 8.8	42.4 ± 9.7	81.6 ± 7.6	65.0 ± 9.4	94.4 ± 4.5	90.8 ± 5.7
Late winter–mid-spring							
10	*Linum perenne*	61.3 ± 7.3	71.5 ± 6.8	93.2 ± 3.8	93.2 ± 3.8	97.4 ± 2.4	94.9 ± 3.3
	Agropyron cristatum	73.0 ± 6.5	87.5 ± 4.9	96.8 ± 2.6	97.6 ± 2.2	97.6 ± 2.2	97.6 ± 2.2
	Elymus elymoides	69.2 ± 6.7	66.5 ± 6.9	88.6 ± 4.6	90.5 ± 4.3	94.0 ± 3.5	92.3 ± 3.9
	Bromus tectorum	81.7 ± 5.7	94.7 ± 3.3	92.9 ± 3.8	96.2 ± 2.8	92.9 ± 3.8	92.9 ± 3.8
	Pseudoroegneria spicata	81.8 ± 6.0	95.3 ± 3.3	99.4 ± 1.2	99.4 ± 1.2	99.7 ± 0.9	99.7 ± 0.9
25	*Linum perenne*	43.0 ± 7.5	70.3 ± 6.9	83.1 ± 5.7	92.8 ± 3.9	97.2 ± 2.5	96.1 ± 2.9
	Agropyron cristatum	75.1 ± 6.4	71.6 ± 6.7	94.8 ± 3.3	95.9 ± 2.9	98.3 ± 1.9	97.6 ± 2.2
	Elymus elymoides	65.0 ± 7.0	67.6 ± 6.8	82.3 ± 5.6	86.5 ± 5.0	92.1 ± 3.9	90.3 ± 4.3
	Bromus tectorum	81.9 ± 5.7	94.7 ± 3.3	93.0 ± 3.8	94.7 ± 3.3	93.0 ± 3.8	93.0 ± 3.8
	Pseudoroegneria spicata	81.6 ± 6.0	90.4 ± 4.5	99.4 ± 1.2	99.4 ± 1.2	99.6 ± 0.9	99.6 ± 0.9
50	*Linum perenne*	38.1 ± 7.3	48.7 ± 7.5	71.9 ± 6.8	74.8 ± 6.5	93.5 ± 3.7	91.8 ± 4.1
	Agropyron cristatum	39.5 ± 7.2	57.2 ± 7.3	72.1 ± 6.6	82.5 ± 5.6	95.4 ± 3.1	94.1 ± 3.5
	Elymus elymoides	51.4 ± 7.3	57.8 ± 7.2	62.1 ± 7.1	64.2 ± 7.0	64.2 ± 7.0	62.1 ± 7.1
	Bromus tectorum	70.9 ± 6.7	83.6 ± 5.5	95.5 ± 3.0	96.7 ± 2.6	96.7 ± 2.6	95.5 ± 3.0
	Pseudoroegneria spicata	62.9 ± 7.5	73.1 ± 6.8	93.0 ± 3.9	93.0 ± 3.9	97.1 ± 2.6	97.1 ± 2.6

(1996) and Hardegree and Van Vactor (2000) found that grass seeds germinated more rapidly at cooler temperatures when hydrated or primed to certain water potentials and air-dried after priming. Overestimation of germination time in our study may have been associated with more rapid germination of seeds from natural priming during intermittent wet and dry periods in the field.

Our results suggest that wet thermal-time models may be used to predict actual germination of non-dormant seeds of species of concern in weed control and revegetation programs. Because we determined accuracy of germination by a given retrieval date, we are not able to judge whether such modeling is accurate enough to predict germination on specific dates, as would be needed for more exact modeling of seedling establishment. Additional detailed research with frequent regularly spaced planting and retrieval dates would better assess ability of these models to predict germination at finer time-scales. Using a wet-thermal germination model with a water potential threshold of −1.0 MPa and 12 simulated planting dates, Hardegree et al. (2010) showed that potential germination of numerous seedlots was lowest in winter, higher in fall, and highest in spring. Germination potential was limited by low water potentials in fall and low temperatures in winter. Germination potential was highest in spring, increasing as temperatures warmed, and then decreasing as soils dried out.

Based on soil water potentials and seedbed temperatures measured across an array of sites and for a range of annual weather conditions, wet-thermal models could be used to predict the potential germination by mid-spring of revegetation species. Advantages of the wet thermal summation model over more complex hydrothermal models for predicting germination timing include: (1) germination response to constant temperatures, rather than temperatures and water potentials can be used to develop the models, and (2) relatively coarse seedbed water potential measurements using inexpensive gypsum blocks may be accurate enough to preclude the need for highly accurate, expensive, and challenging measurements of soil water potential under the dynamic conditions of field seedbeds and at the scale of a seed. Germination models will need to be coupled with models which predict root growth and seedling survival under field conditions to best predict field seedling establishment.

5. Conclusion

Wet-thermal prediction of germination time in field seedbeds was most accurate for seeds incubated in spring when soil water was available for longer periods than in fall. Summation of progress toward germination for intermittent wet periods and use of a −1.5 MPa soil water potential threshold to define wet periods produced the highest accuracy. Although germination timing was predicted more accurately for some species than others, prediction was accurate enough to use wet-thermal models as a tool to evaluate potential germination by mid-spring. Predictions could be made for numerous plant materials for a range of sites and years where soil temperature and water potential are available (Hardegree et al., 2010). Such evaluations may help choose plant materials with higher probability of establishment in fire rehabilitation and other direct-seeding projects to restore ecosystem function on semiarid lands.

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