WET THERMAL ACCUMULATION MODELING OF GERMINATION OF WESTERN U.S. RANGELAND SPECIES

by

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GRADUATE COMMITTEE APPROVAL

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ABSTRACT

WET THERMAL ACCUMULATION MODELING OF GERMINATION OF WESTERN U.S. RANGELAND SPECIES

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The key to stopping high-frequency or catastrophic wildfires in the western U.S. is the successful restoration of burned lands to native plant communities. Developing models of 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 incubated 10 revegetation species and 3 *Bromus tectorum* collections at constant temperatures to develop linear and curvilinear regression equations to estimate germination rates. Models were used to predict days to 10, 25, and 50% germination for each species, incubated at 3 spring temperature oscillations. Thermal accumulation models predicted the germination of most collections within 2 days of actual germination. Highest accuracy was seen for *Bromus tectorum*

populations (0.2 underestimated to 3.4 days overestimated). At lower temperatures models underestimated time to germination, possibly due to the stimulating effect of fluctuating temperatures on germination rate in some species ($P = 0.004$). Results suggest that thermal accumulation could be used to predict germination under dynamic temperature fluctuations of field seedbeds for non-dormant seeds of many species. Germination predictive accuracy of wet thermal accumulation models of 5 revegetation species and 2 populations of *Bromus tectorum* was tested at 2 field sites in central Utah. Parameters of base water potential thresholds and methods of thermal accumulation were compared for model accuracy. Model parameters of -1.5 MPa base water potential threshold and cumulative temperature accumulation for all wet periods best predicted field germination in seedbags. Model predictions were more accurate during the mid and late spring seasons than for fall and early spring. Model predictions were most accurate for species that germinated rapidly and had higher optimal germination temperatures. Overall, model predictions were accurate 75% of the time in predicting germination. These models may be used to determine species germination requirements and match them to the sites and weather conditions where they have the highest probability of germination.

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Chapter 1:

Wet Thermal Accumulation Model Development

1. Introduction

Every year, thousands of hectares in the western United States burn due to the increasing dominance of an invasive annual, *Bromus tectorum.* Efforts to restore burned lands to native plant communities by seeding native species are often unsuccessful. Temperature and moisture are the main abiotic factors that control plant establishment by supporting or restricting germination and growth (Bewley and Black, 1985; Bradford, 2002; Ogg and Dawson, 1984). This is especially true in western cold deserts where only short seasonal periods have adequate soil water and temperatures to produce germination and growth. Thermal accumulation models have been successfully used to predict the timing and rate of germination of invasive species in agricultural systems (Forcella et al., 2000; Vleeshouwers and Kropff, 2000). Thermal accumulation models have also been used to successfully model germination of several species adapted to temperature and water-limited ecosystems (Jordan and Haferkamp, 1989; Roundy and Biedenbender, 1996; Hardegree et al., 1999; Shrestha et al., 1999; Meyer et al., 2000; Hardegree 2003, 2006, 2007; Wang et al., 2006; Meyer and Allen, in review). If the establishment of potential weeds versus revegetation species were known for specific annual weather conditions on regional to site scales, the most potentially successful species could be selected for specific rehabilitation projects. Plant materials with the highest probability of establishment could be identified as an aid to planning rehabilitation seed mixes.

Modeling germination is the first step in developing seedling establishment models and predicting establishment success. In order to test the proposed models, germination requirements should be quantified in the lab and then verified in the field (Forcella et al., 2000; Mueller and Bowman, 1989).

After dormancy is lost, temperature and soil moisture availability determine germination rate (Bradford, 2002; Probert, 1992; Bewley and Black, 1985). Three temperatures characterize germination response to temperature: base (T_b, the temperature below which germination will not occur), optimum (T_o the temperature at which germination is most rapid), and maximum (T_m, the temperature above which germination will not occur) (Bradford, 2002). These cardinal temperatures are species and sometimes collection-specific (Bewley and Black, 1985). For non-dormant seeds of many species, germination rate is a function of degree days accumulated between T_b and T_m (Trudgill et al., 2005).

In this study we developed thermal accumulation models for several western U.S. rangeland species from constant temperature germination trials and then used the models to predict time to germination at oscillating temperatures in an incubator programmed to simulate field seedbed temperatures. We investigated the hypothesis that germination of these species under dynamic diurnal temperatures can be accurately estimated by thermal accumulation.

2. Methods and Materials

2.1. *Model development*

Thermal accumulation models were developed for 11 collections of plants commonly seeded or under consideration for fire rehabilitation seeding in the western U.S., as well as for 3 *Bromus tectorum* populations (Table 1)**.** Germination trials were conducted to determine time to 10, 25, and 50% subpopulations of total germinable seeds for each collection at 7 constant temperatures (5, 10, 15, 20, 25, 30, 35 °C**).** The rates to 10, 25, and 50% germination were modeled separately to maximize model accuracy because previous studies have found significant differences in cardinal temperatures and germination rates between these subpopulations within seedlots (Covell et al., 1986; Hardegree, 1999). Seeds of *Enceliopsis nudicaulis* and *Lupinus arbustus* were dusted with Captan fungicide wettable powder (N-trichloromethylthio-4-cyclohexene-1, 2-dicarboximide) at the beginning of each trial to control fungal growth. Thirty seeds of each seed collection were placed on moist blotter paper in a petri-dish. One petri-dish of each collection was placed in each of 4 plastic bags (replicates), which were randomly assigned to a shelf within an incubation chamber. Incubation chambers were programmed to 1 of the 7 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 to 3 days for 45 days or until germination ceased. Germination was recorded when the radical was 2mm in length. To obtain the germination percent relative to the maximum germinable seeds within a collection, daily totals were divided by the maximum number of seeds that germinated in the constant temperature trials for each collection (Covell et al., 1986).

The number of days required to reach or exceed the subpopulation germination percentage was determined by the following equation (Covell et al., 1986; Hardegree 1999; 2006; Roundy and Biedenbender, 1996):

$$T = \left[\left(\frac{t_a - t_b}{n_a - n_b}\right) * (N - n_b)\right] + t_b$$

T = time (days) to subpopulation germination percentage

t_a = incubation day when subpopulation germination percentage was reached

t_b = incubation day before subpopulation germination percentage was reached

n_a = number of germinated seeds on day that subpopulation germination percentage was reached

n_b = number of germinated seeds on day before subpopulation germination percentage was reached

N = number of germination seeds equal to 10, 25 or 50% of the total population

Table Curve® 2D was used to select linear and non-linear regression equations of best fit for germination rate of each subpopulation near T_b, T_m, and at T_o (Systat Software, Inc.; Hardegree, 2006; Roundy et al., 2007). T_b and germination rates below 5 °C were estimated using linear regression of the times to germination at 5 °C, 10 °C and sometimes 15 °C according to the procedure of Hardegree (2006), because germination rate at suboptimal temperatures is considered to be a linear function of incubation temperature (Hegarty, 1972). The minimum value for T_b was 0 °C, above which soil water would not be frozen and would be available for imbibition in field seedbeds. The exceptions were the 25 and 50% subpopulations of *Lupinus argentus*, where using the lower linear regressions that produced a T_b below 0 °C predicted germination much better than cutting off thermal accumulation at 0 °C. Our model assumed thermal accumulation

would only occur when water was available because moisture-dependent models have been shown to be more accurate than strictly thermal models (Forcella et al., 2000). Because of this, germination rates were assumed to be zero above a T_m of 42 °C because field seedbeds would not be expected to have available water above this temperature and also because the relationship between germination rate and temperature can become unstable at high temperatures. The model of the 50% subpopulation of *Achillea millefolium* L. (Eagle) did not converge to zero germination at T_m below 42 °C, so T_m was calculated using linear regression of the time to germination at 30 °C and 35 °C to better reflect its germination response at higher temperatures (Table 2). Non-linear and linear regressions with the lowest residuals and best coefficients of determination (R^2) values were selected (Tables 2 and 3). Progress toward germination was estimated for diurnal-fluctuating temperature regimes from each hourly temperature of incubation using the appropriate linear or curvilinear equation for that temperature range (Roundy and Biedenbender (1996).

2.2. *Spring temperature oscillations*

Diurnal field temperatures were simulated in incubation chambers to test model accuracy. Incubation chambers were programmed with 1 of 3 diurnal temperature oscillations (Fig. 1). Temperature oscillations were based on soil temperatures measured in sagebrush-dominated communities in Tintic Valley, Utah, during March 2003, April 2005, and May 2002 (Roundy et al., 2007). Spring temperature oscillations were used because in

revegetation projects most species are fall-seeded and germination that progresses to established seedlings occurs in the spring. Germination for late fall temperature oscillations could not be measured because incubation chambers were unable to sustain temperatures below 4 °C. Programmed temperature oscillations simulated fluctuating soil temperatures during cold, cool, or warm spring days when seedbeds are wet. The same methodology used in constant temperature trials was used in the fluctuating temperature trials. Time to germination during simulated spring temperatures was compared to model-predicted time to germination for each subpopulation.

2.3. *Statistical analysis*

Mixed model analysis (SAS Institute, Inc., 2001) and Tukey mean separation tests were conducted to determine significance of constant temperatures on germination time for the different collections. Fixed effects were temperature and collection; replication (petri-dish) was considered random for all analyses. Mixed model analysis was also used to compare collection germination time during the diurnal temperature oscillations. Germination model accuracy for each collection and subpopulation was evaluated for each temperature oscillation by subtracting model-predicted germination time from actual germination time and by conducting a mixed model analysis and Tukey mean separation test on the difference values. Significance was defined as $P < 0.05$.

3. Results

3.1. *Constant temperature trials*

The 10 and 25% subpopulations experienced higher T_o for maximum germination rates than the 50% subpopulation (Fig. 2). T_o for fastest germination was 25 °C except for the forbs *Enceliopsis nudicaulis* and *Lupinus arbustus* (15 °C), *A. millefolium* (Eagle), and *Linum lewisii* (20 °C), and 2 of the *Bromus tectorum* (20 °C) populations (Fig. 2)**.** Germination rates differed significantly among species. *Enceliopsis nudicaulis* and *Lupinus arbustus* had lower germination rates than the other species tested. *Bromus tectorum* populations tended to have higher germination rates than the other species tested, but this trend was not significant (Fig. 2). *Elymus elymoides* germination required the most time of any of the grasses at all constant temperatures (Fig. 2). Germination rates also differed among collections and *B. tectorum* populations. The Spanish Fork population of *B. tectorum* had the fastest germination of any collection.

3.2. *Model development*

Linear equation R^2 values ranged from 0.64 to 1.00 with 34 of 41 equations having an $R^2 > 0.85$ (Table 2). Model R^2 values for curvilinear equations ranged from 0.58 to 0.98, and 39 of the 46 total model regressions had an $R^2 > 0.80$ (Table 3).

3.3. *Spring temperature oscillations*

In most cases, the models overestimated time to germination. Overestimates ranged between 0.1 to 19.1 days with an average of 2.3 days. The 4% of model predictions that were underestimates ranged from 0.1 to 2.8 days (Figs. 4-6)**.** Models overestimated time to germination by 3.01 days (±0.29), 1.79 days (±0.29), and 1.97 days (±0.2) for the March, April, and May temperature oscillations, respectively (Figs. 4-6). Models were less accurate ($P = 0.004$) in predicting time to germination for March temperatures than for the warmer oscillating temperatures of April and May (Figs. 5 and 6)**.**

3.3.1. *Grasses*

Bromus tectorum reached subpopulation germination faster (3.6 to 6.5 days) at the March temperatures than other grass species (4.8 to 15.0 days) ($P < 0.0001$) (Fig. 4). *Agropyron desertorum* required less time than *A. cristatum x desertorum* to germinate in the March and April spring temperature oscillations (Figs. 5 and 6). *Elymus elymoides* consistently required the most time of any grass to reach the subpopulation germination percentages in all spring temperature oscillations except for the fastest 10% subpopulation incubated in May temperatures (Fig. 6). Models were the most accurate for predicting time to germination for the collections of *Bromus tectorum*.

3.3.2. *Forbs*

Forbs required noticeably more time than grasses for 10, 25, and 50% of their seeds to germinate under spring temperature oscillations (Figs. 4-6). *Linum perenne* germination was slightly faster at April and May temperatures than *Linum lewisii* (Figs. 5 and 6). The VNS White collection of *Achillea millefolium* required more time for 10% germination than the Eagle collection did in all spring oscillations. Models predicting the time to germination for *Achillea millefolium* (0.8 to 12.7 days) and *Enceliopias nudicaulis* (0.5 to 19.1 days) were least accurate (Figs. 4-6). Models of the VNS White collection of *A. millefolium* highly overestimated time to germination in the March temperature oscillation. The *E. nudicaulis* 50% germination model greatly overestimated time to germination for April (12.7 days) and May (19.1 days) temperatures.

4. Discussion

4.1.Constant temperature trials

Germination rates differed significantly among species and collections. *Enceliopsis nudicaulis* and *Lupinus arbustus* had lower germination rates than the other species tested. These 2 forbs have larger seeds which could require more time to imbibe water to germinate (Forcella, 2000).

Germination rates and T_o of *Elymus elymoides* and *Pseudoroegneria spicata* (Anatone) were similar to those reported previously by Hardegree (1999). The phenotypic plasticity in time to germination within each collection was exhibited through the skewed bell-shaped curve of the germination models at temperatures above 10 °C.

This plasticity has been shown in other models (Forcella, 2000). The 10 and 25% germination models indicated maximum germination rates at higher optimal temperatures than the 50% germination models (Figs. 2 and 3). This is consistent with other studies where the faster-germinating, smaller subpopulations had higher optimal temperatures for germination rate than larger subpopulations (Garcia-Huidobro et al., 1982a; Covell et al. 1986; Hardegree 1999).

4.2. Spring temperature oscillations

Models overestimated time to subpopulation germination during both cold and warm temperature oscillations. Oscillating temperatures decreased the time to germination but produced similar maximum germination as that in constant temperatures trials. This indicates that oscillating temperatures caused a gradual increase in germination rate rather than solely an increase in maximum germination and therefore dormancy loss or instantaneous response to temperature as found in other studies (Garcia Huidobro et al. 1982b, Benech Arnold et al., 1990; Ellis and Barrett, 1994; Roundy and Biedenbender, 1996; Hardegree 1999; Forcella, 2000; Vleeshouwers and Kropff, 2000). Model overestimation was slightly higher than reported in similar studies. When predicting time to 50% germination for 10 native and exotic southwestern grasses under simulated spring temperature oscillations, Roundy and Biendenbender (1996) found estimates were within 0.6 to 17 days with an average of 1.3 days.

The greater number of instances of significant model overestimation for the

March temperatures may indicate that there is more progress towards germination at lower temperatures than is reflected by the model (Hardegree 1999). This suggests that there is a non-linear response at lower temperatures, which has been observed in previous studies (Hardegree 1999; Hardegree 2006). Overestimation for both March and May temperatures may also be due to failure of the thermal accumulation model to account for germination stimulation at cooler and widely oscillating temperatures as has been noted for some species (Hegarty, 1975).

Bromus tectorum thermal accumulation models also reflected higher germination rates at cooler temperatures (Fig. 3). *Bromus tectorum* may outcompete native species for soil moisture in the fall or early spring by rapid germination at low temperatures (Wilson et al. 1974). Rapid development at lower temperatures indicates a low degree day requirement (Turdgill et al., 2005).

Forbs required more time than grasses to reach subpopulation germination in temperature oscillations, possibly because some seeds were still partially dormant. At March temperatures, *Enceliopsis nudicaulis* and *Lupinus arbustus,* and *Achillea millefolium,* required more germination time than the other species. Oscillating temperatures have been known to stimulate germination rates through dormancy loss by breaking down the seed coats of species adapted to warm ecosystems that frequently experience summer drought (Probert, 1992). *Enceliopsis nudicaulis* showed stimulation by the oscillating temperatures of germination rates beyond what the model-predicted, but *L. arbustus* did not. *Lupinus arbustus* lacks a hard seed coat and has limited seed dormancy compared to other lupines (personal communication Covey Jones, 2008). Enceliopsis nudicaulis requires 4-8 weeks of moist chilling to break dormancy. The

prechilling requirement would not have been met in the higher spring temperature oscillations. *Enceliopsis nudicaulis* will not germinate in cold temperatures (personal communication, Susan E. Meyer, 2008). Many *E. nudicaulis* seeds did not germinate at the lower constant temperatures trials used to create the model. This caused the model to overestimate time to initial germination at lower temperatures. All models of *A. millefolium* (VNS White) highly overestimated time to germination at March temperatures (8.1 to 12.6 days overestimation). This overestimation was not seen in the *A. millefolium* (Eagle) cultivar. Some seed sources of *A. millefolium* require 2 weeks of cool, moist stratification to break dormancy (Stevens et al., 1996). If *A. millefolium* (VNS White) had this requirement, the coolest temperature oscillation would have enhanced *A. millefolium* (VNS White) germination rates beyond rates predicted by the model. At least twice as much time was required to begin germination of VNS White than the Eagle cultivar of *A. millefolium* in all spring oscillations (Figs. 4-6). Also, the 10, 25, and 50% subpopulations of VNS White germinated almost concurrently at 16.0 days, 16.8 days, and 18.0 days respectively. This suggests that the VNS White cultivar had a greater requirement to break dormancy than the Eagle cultivar and that VNS White fulfilled this requirement after 16 days. We conclude that estimation of germination time using thermal accumulation is most accurate for non-dormant seed populations.

Our study indicates that thermal accumulation models can predict germination rate of non-dormant seeds using cardinal temperatures but may overestimate time required for germination. Model overestimation in our study was probably due to both an increase in dormancy loss for some seed populations and an increase in germination rate for less-dormant populations, both caused by the gradual fluctuation of temperatures.

Thermal accumulation models overestimated time to germination of forb species with specific dormancy loss requirements but produced very reasonable estimates for the more germinable grasses. Thermal model predictions within 2-4 days may be quite useful to predict and make relative comparisons for species under annual weather conditions of specific sites in fire rehabilitation projects. Thermal model predictions should be compared with actual field germination before these models are used to select species for restoration projects. Seedling establishment models require accurate prediction of both germination and seedling root growth in order to best predict seedling survival and establishment potential (Forcella, 2000; Vleeshouwers and Kropff, 2000).

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Chapter 2:

Wet Thermal Accumulation Model Field Testing

1. Introduction

The big sagebrush (*Artemisia tridentata*), ecosystem in the western United States is at risk due to wildfires caused by the increasing dominance of an invasive annual, *Bromus tectorum.* Fire rehabilitation projects seek to restore native plants in burned areas, but efforts are often unsuccessful. Predicting germination of native plants used in fire rehabilitation projects based on site abiotic conditions would enable the selection of species more likely to succeed in that area (Vleeshouwers and Kropff, 2000; Grundy, 2003). Predicting seedling establishment initially requires successfully predicting germination under the dynamic temperature and moisture conditions of field seedbeds.

Many laboratory studies have been able to predict different aspects of seedling development based on abiotic conditions, but there are few studies that have verified models with field observations (Forcella, 1993; Vleeshouwers, 1997; Roman et al., 2000; Vleeshouwers and Kropff, 2000; Forcella et al., 2000; Wang et al., 2006). Thermal accumulation germination models of *Kraschenninnikovia lanata* (Wang et al., 2006) and *Bromus tectorum* (Meyer and Allen, in review) have been field verified.

In this study, thermal accumulation models of several rangeland species previously demonstrated to predict germination at fluctuating temperatures were used to predict field germination (Rawlins et al., in preparation; Roundy et al., 2007). Models were based on the assumption that progress to germination was made within defined temperature and soil moisture thresholds. Wet thermal accumulation models presuppose

that seeds only make progress towards germination when water is available and seeds imbibe. These models have been more accurate in predicting germination than strictly thermal models (Finch-Savage and Phelps, 1993; Forcella et al., 2000). Although hydrothermal models can predict germination based on both temperature and water potential of the seed environment (Bradford, 2002), it is very difficult to measure water potential at the scale and depth of seeds in field seedbeds (Taylor et al., 2007). It is reasonable to expect that soils within 1–2 cm of the surface tend to be either wet or dry under warm fall or spring drying conditions in semi-arid areas. Simple, inexpensive sensors such as gypsum blocks can sense whether soils at 1-3 cm are wet (0 to -1.5 MPa water potential) (Taylor et al., 2007). For these reasons, wet thermal accumulation models that use moisture as a switch may provide sufficient accuracy to predict field germination without the need to precisely measure soil water potential and determine precise seed water potential thresholds required by hydrothermal models.

Two model parameters were tested to account for dynamic seedbed water potential conditions. The first parameter was a base water potential threshold, above which progress towards germination is expected. Model accuracy with 3 different base water potential thresholds (-0.5, -1.0, -1.5 MPa) was evaluated to determine the optimal base water potential threshold for predicting germination in each species. The second parameter accounted for the response of thermal accumulation to dry periods. Seeds may accumulate thermal progress towards germination either: (1) within a single wet period; or (2) cumulatively across intermittent wet periods. Our objective was to determine the best combination of base water potential threshold and thermal accumulation method for

most accurately predicting germination in field seedbeds using seed lot-specific wet thermal accumulation models.

2. Methods and Materials

Wet thermal accumulation germination models of the 10, 25, and 50% subpopulations of 6 species as developed by Rawlins et al. (In review) were tested for field accuracy (Table 4). The 2 populations of *Bromus tectorum* seed were collected from Skull Valley and Lookout Pass (Table 4).

Model accuracy was assessed by measuring field seedbed water potential and temperature to predict whether seeds would germinate or not within a seed burial period and comparing germination predictions with actual seed germination in seedbags buried during the same time periods.

2.1. Field Site description

Field testing of wet thermal accumulation models was conducted at 2 sites located in Tooele Co., Utah: Skull Valley and Lookout Pass. Skull Valley has a 1524 m elevation, average annual air temperatures and precipitation of 8-10 °C and 200-254 mm, and a Medburn fine sandy loam series of coarse-loamy, mixed (calcareous) mexic xeric Torriorthents (Trickler, 2001). Lookout Pass is located at a slightly higher elevation

(1676 m), and receives more precipitation (254-305 mm) and a greater range of 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 Wyoming big sagebrush and bunchgrass communities but are currently dominated by a monoculture of *Agropyron cristatum* that was planted in 1982 at Skull Valley and 1996 at Lookout Pass after wildfire.

2.2.Field study design

At each site, 4 blocks were established with 8.3 by 11 m areas designated for seedbag burial. Thermocouples measuring soil temperature and gypsum blocks (Delmhorst, Inc.) measuring soil water potential were buried at 1-3, 15-16 and 28-30 cm in 3 replicate plots within each of the 4 blocks. Sensors were read every minute and hourly averages calculated by Campell Scientific, Inc. (1983) CR-10X microloggers. Precipitation and air temperature were measured using an electronic tipping bucket rain gage and a thermister in a gill shield at each site. Prior to the first 2005 seedbag burial, the seedbag burial areas within each block were treated with glyphosate to fully control *A. cristatum*.

2.3.Seedbag retrievals

Enough seeds of each seed collection were placed in separate seedbags to provide a minimum of 25 germinable seeds/bag (Table 4). One seedbag of each species was buried 2-cm deep in each of 4 blocks for each of 19 installation and retrieval date combinations (Table 5). The Lookout Pass *B. tectorum* seed collection was seeded at Lookout Pass, while the Skull Valley collection was seeded at Skull Valley. Seedbag installations and retrievals included fall, and early, middle and late spring of 2005, 2006, and 2007 (Table 5). Seasons were defined according to the temperatures seeds experienced during the time between seedbag installation and retrieval.

2.4.Determination of model accuracy

Hourly averages of surface soil temperature and water potential from each block were used in thermal accumulation models to predict occurrence or non-occurrence of at least 10, 25, or 50% germination (Roundy et al. 2007) for each species and field incubation period. Accurate predictions were assigned a 1 and inaccurate predictions were assigned a 0. Mixed model analysis (SAS Proc Mixed, 2001) and Tukey mean separation tests were conducted with the binomial categorical assignments to determine whether model accuracy for each of the 3 subpopulations was significantly affected by year, season, site, collection, base water potential threshold, or thermal accumulation method. Block and block by site by year interactions were considered random effects in this analysis, while other effects were considered fixed. The percent accuracy of each species subpopulation model for a given season and combination of parameters was determined

by using mixed model and logistic regression analyses. First we performed mixed model analysis with the SAS GLIMMIX procedure (SAS Institute, Inc. 2006) on the binomial categorical data to determine categorical estimates for different combinations of model parameters. Base water potential threshold and thermal accumulation method were considered fixed effects and block was considered a random variable. We then used the categorical estimates from the SAS GLIMMIX analysis as coefficients in the logistic regression model. The logistic regression equation estimated the percent accuracy and standard error for each combination of model parameters.

3. Results

The categorical analysis indicated that the factors that most affected model accuracy were thermal accumulation method, base water potential, and season. Thermal accumulation method most affected model accuracy for the 10% and 25% germination models and was second to season in affecting accurate germination prediction of the 50% germination models ($P < 0.0001$). The base water potential threshold parameter had the third greatest influence on model accuracy across all subpopulation models ($P < 0.0001$). Cumulative thermal accumulation and a -1.5 MPa base water potential threshold yielded the most accurate germination prediction for all subpopulations ($P < 0.0001$) (Tables 6-9). The -1.5 MPa base water potential threshold and cumulative thermal accumulation models were over 80% accurate for most species, subpopulations, and seasons (Tables 6-9).

Accuracy was 79.4, 72.3, 83.4, 88.3, and 76.2% for *A. cristatum, Elymus elymoides, Pseudoregneria spicata , B. tectorum,* and *Linum perenne,* respectively (Tables 6-9).

Season of seedbag incubation had the greatest influence on the accuracy of the 50% germination models and the second greatest influence on the accuracy of the 10% and 25% germination models ($P < 0.0001$) (Tables 6-9). Retrievals for seeds incubated in the fall and early spring had lower model accuracy than those retrieved in the mid and late spring seasons (Tables 8 and 9). The ability of any model to predict germination differed among species ($P < 0.0001$). Models for *Bromus tectorum* populations were the most accurate (Tables 6-9). Little *Achillea millefolium* germination occurred in seedbags for all retrievals. A lab experiment verified that *A. millefolium* has a light requirement that was not fulfilled in the mesh seedbags. For this reason, *Achillea millefolium* data were not included in the analysis.

Year was significant for all subpopulations: 10 ($P = 0.0105$), 25 ($P = 0.0114$), 50% ($P = 0.0235$). During mid and late spring and for the Lookout Pass site, models were less accurate in 2007 than in 2006. In 2007, Lookout Pass had fewer days of available water and higher temperatures than during 2006. Site was not significant for all subpopulations: 10 ($P = 0.6099$), 25 ($P = 0.4597$), 50% ($P = 0.9462$).

4. Discussion

4.1.Model parameters

Wet thermal accumulation models were most accurate for all field incubation periods when using cumulative thermal accumulation and a more inclusive water threshold (-1.5 MPa). Similar results were reported by Roundy and Biedenbender (1996), where germination of 15 collections of 10 native and exotic semi-arid grasses was best predicted by cumulative thermal accumulation. The thermal accumulation method parameter had more influence on how closely the model predicted actual germination than did the base water potential model parameter. This suggests that soil temperature dynamics should also be considered when selecting species to seed for a rehabilitation site and not merely drought tolerance or response to water availability.

4.2.Season

Model accuracy was lower for all species subpopulations during fall and early spring than mid and late spring seasons. Models underestimated germination, possibly due to the exclusion of temperatures below 4 °C in model development because incubation chambers were unable to maintain temperatures below 4 °C (Rawlins et al., in preparation). Another explanation is that soil water potential sensors recorded that the soil was dry when water in them was frozen and therefore did not account for possible thermal accumulation when seeds were wet and actually above 0 °C for some periods. Also, seeds experienced higher temperature fluctuations during the fall and early spring than in the other seasons. Models were less accurate in predicting germination above certain thresholds incubated under high temperature fluctuations during laboratory

experiments (Rawlins et al., in preparation). The highest overall accuracy was observed with a -1.5 MPa base water potential threshold and cumulative thermal accumulation. The difference in accuracy between this and the other model types was more pronounced during the fall and early spring seasons, when seeds experienced cooler temperatures and less heat accumulation. Some thermal accumulation in those seasons may not have been accounted for by other parameter combinations because other combinations were less sensitive to thermal accumulation at soil temperatures below 4 °C. Model accuracy was greater than 90% for all species and subpopulations during the late spring season (Table 9). This is significant, because if the -1.5 MPa water threshold and cumulative thermal accumulation models are used to predict final spring germination of these fall-seeded species, managers can expect over 90% accuracy for all species 10, 25, and 50% subpopulations (Table 9).

4.3.Site

Sites varied in soil water availability, but this did not affect model accuracy. In Skull Valley during the fall the various parameter combinations did not differ significantly from each other in predictive accuracy. This is probably due to the fact that most of the retrievals done for the fall season at this site were done in 2006 when the soil was wet when installed. It follows that when the soil is near field capacity thermal accumulation determines germination because the soil water potential is greater than any of the base water potential thresholds. However, under the drier conditions observed in Lookout Pass

for this season, using a -1.5 MPa water threshold produced much higher model accuracy than the other water potential thresholds.

4.4.Species

Model accuracy was highest for the Lookout Pass population of *Bromus tectorum* during the fall and early spring. The Lookout Pass population of *Bromus tectorum* had the highest germination percentage. This population also had the highest germination rates of any species tested (Rawlins et al., in preparation). This suggests that simple thermal accumulation models will be more accurate for species that respond quickly to temperature and are less sensitive to high temperatures. Model accuracy was lowest for *Elymus elymoides* in the early, mid, and late spring. In the fall and the early spring, *Elymus elymoides* models were second in accuracy to *Bromus tectorum* models. In the mid and late spring *Elymus elymoides* had the lowest optimal temperatures for germination and for germination rates of any grass species. This indicates that the germination of *E. elymoides* responds more readily to temperature increases in the cooler months and was less tolerant of the higher temperatures that occurred during the later spring than other species (Meyer et al., 2000). In our laboratory experiments (Rawlins et al., in preparation), seeds experiencing supraoptimal temperatures often had unpredictable responses to heat accumulation even when temperatures returned to optimal or suboptimal temperatures. This may be due to biochemical changes that damage germination processes within seeds exposed to supraoptimal temperatures

(Bewley and Black, 1985). The *Pseudoregneria spicata* and *Agropyron cristatum* models had comparable accuracy during all seasons (Tables 6-9). Models for both these species were more accurate during the warmer seasons than during the cooler seasons. The model curves of these species mirror each other in shape and often overlap (Rawlins et al., in preparation). Models of *Linum perenne* had the best prediction for early spring compared to all other species but the worst prediction during the fall season (Tables 6 and 7). Possibly the thicker seed coat of *Linum* may have reduced fall compared to spring germination for this species.

4.5.Model accuracy

In the final analysis, wet thermal accumulation models were accurate in predicting fall germination of *B. tectorum* and in predicting late spring germination of all species with the exception of *E. elymoides.* Over 90% of inaccurate predictions were underestimates of germination. These same results occurred during model laboratory test at fluctuating temperatures (Rawlins et al., in preparation). Although models were accurate in predicting *Elymus elymoides* germination during the fall and early spring, approximately half (49%) of the underestimates of germination in all seasons were for *E. elymoides*. Accuracy of these models may be improved for fall predictions by conducting constant temperature germination trials at temperatures lower than 4°C and incorporating the trends seen at those temperatures into the models. Our results suggest that wet thermal accumulation models may be used to predict actual germination of non-dormant seeds of

species of concern in weed control and fire rehabilitation programs. Based on soil water potentials and seedbed temperatures measured across an array of sites and for a range of annual weather conditions, these models could be used to predict the potential germination of modeled species and rank them for potential success. These models could also be used to predict fall or spring germination of *B. tectorum* to time weed control treatments.

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APPENDIX A

CHAPTER 1

TABLES AND FIGURES

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

Species	Common Name/Cultivar	Source	Year Collected
Achillea millefolium	'Eagle' yarrow	Eastern WA	2003
Achillea millefolium	'VNS white' yarrow	UDWR-Lot# 31053,WA	2003
Enceliopsis nudicaulis	'B1-04' 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	'U1-04' 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	Skull Valley, UT	2005
Bromus tectorum	cheatgrass	Spanish Fork, UT	2002
Bromus tectorum	cheatgrass	Lookout Pass, UT	2005
Elymus elymoides	'Sanpete' bottlebrush squirreltail	UDWR-Sanpete Co., UT	2003
P. spicata spp. spicata	'Anatone' bluebunch wheatgrass	UDWR-Lot# LHSID3-445	2003
Psuedoroegneria spicata	'Secar' bluebunch wheatgrass	UDWR- Lot# 31932, WA	2003

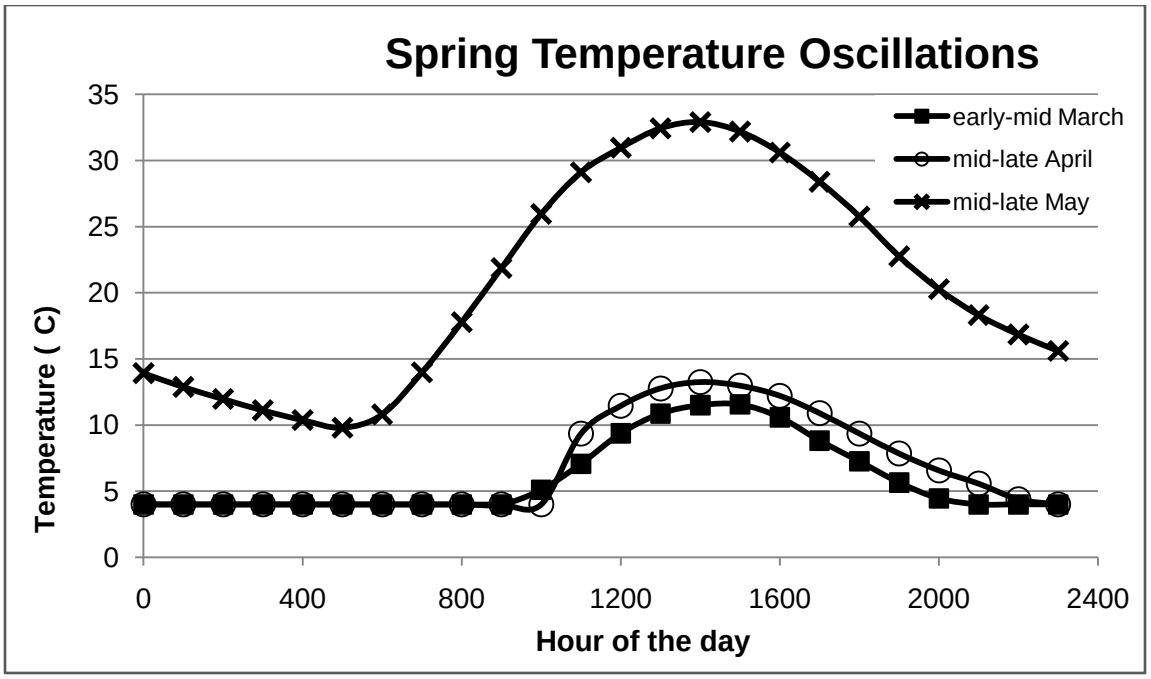

Figure 3: Incubation chamber temperature oscillations based on field soil temperatures for a cold, cool, or warm spring day (24-hour) from soil temperatures recorded in sagebrush-dominated communities in Tintic Valley, Utah during March, April, and May when the seedbed was wet (Roundy et. al. 2007).

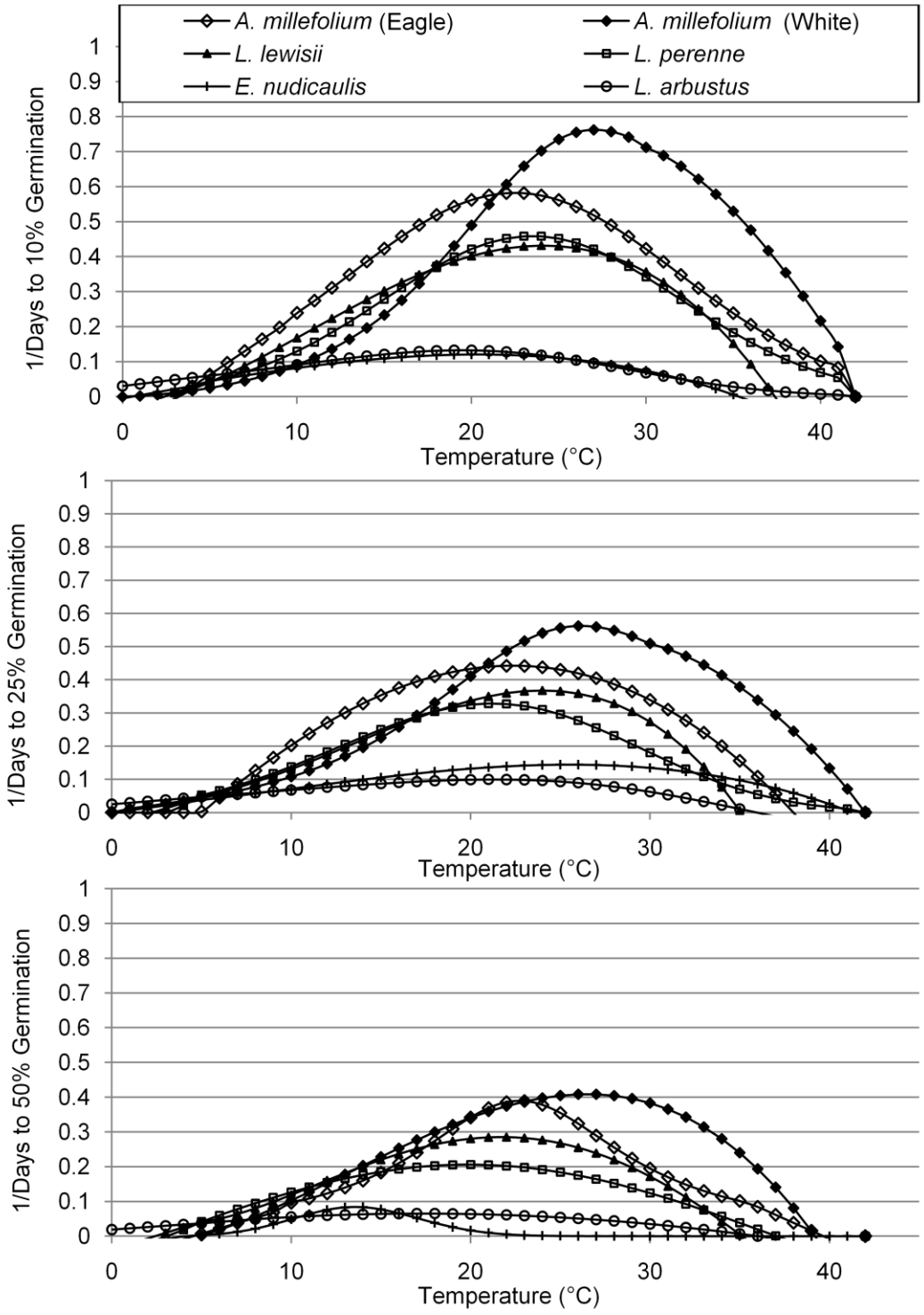

Figure 2: Combined linear and curvilinear regression equations fit to 1/days to 10, 25, or 50% germination data for each forb species (10, 25, or 50% subpopulation) and selected for thermal accumulation modeling.

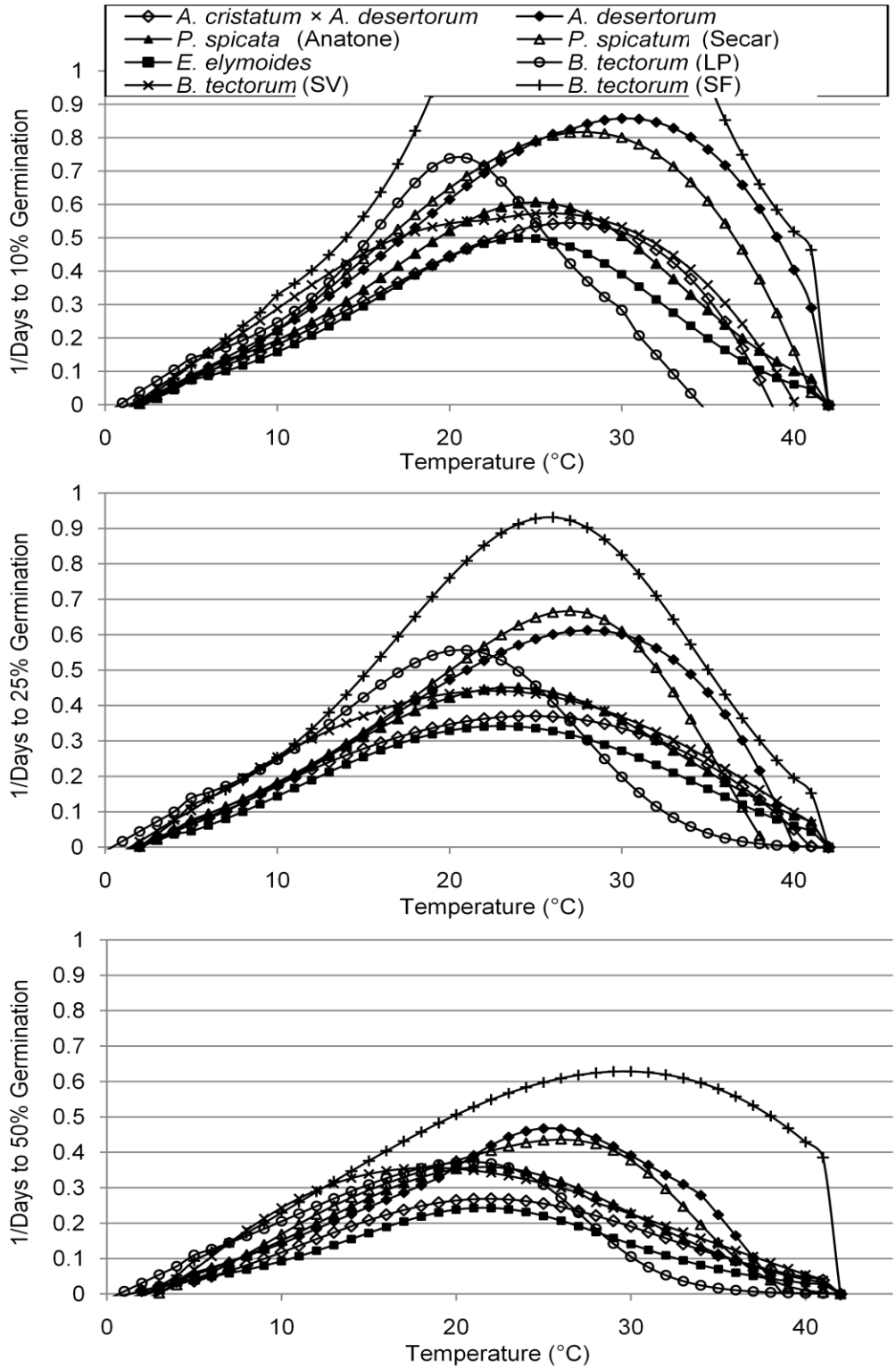

Figure 3: Combined linear and curvilinear regression equations fit to 1/days to 10, 25, or 50% germination data for each grass species (10, 25, or 50% subpopulation) and selected for thermal accumulation modeling. The Spanish Fork (SF) collection of *B. tectorum* 10% subpopulation had a much higher germination rate than all other species; germination rate peaked for this population at 2.03 (1/days to 10% germination) at 27°C.

Table 3: Linear 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.

Species	Sub-pop. (%)	Linear Regressions Range (°C)	ddf[i]	R^2	SE[ii]	F-stat	*P*-value
Achillea millefolium (Eagle)	10	0 --10	2	0.996	0.008	462	0.0022
	25	0--5	4	0.888	0.022	31.6	0.0049
	50	0--10	4	0.878	0.044	21.6	0.0188
		35--41	4	0.924	0.021	36.4	0.0091
Achillea millefolium (VNS White)	25	0--5	3	0.962	0.02	75.5	0.0032
	50	0--5	7	0.701	0.102	16.4	0.0048
Enceliopsis nudicaulis	10	0--5	3	0.784	0.012	10.9	0.0459
	50	0--5	6	0.644	0.017	10.9	0.0165
Linum lewisii	10	0--5	6	0.978	0.008	266	0
	25	0--5	6	0.969	0.009	190	<0.0001
	50	0--5	6	0.956	0.01	130	<0.0001
Linum perenne	10	0--5	6	0.999	0.002	8456	0
	25	0--5	6	0.997	0.004	2194	0
	50	0--5	6	0.994	0.004	977	0
Lupinus arbustus	10	0--5	6	0.707	0.011	14.5	0.0089
	25	0--5	6	0.863	0.005	37.7	0.0009
	50	0--5	5	0.871	0.004	33.6	0.0022
Agropyron cristatum × *A. desertorum*	10	0--7	6	0.969	0.012	189	<0.0001
	25	0--7	6	0.987	0.007	447	0
	50	0--7	6	0.854	0.015	35.1	0.001
Agropyron desertorum	10	0--10	6	0.942	0.021	97.1	<0.0001
	25	0--5	6	0.957	0.014	134	<0.0001
	50	0--10	6	0.970	0.01	193	<0.0001
Bromus tectorum (Spanish Fork)	10	0--10	6	0.961	0.018	254	0
	25	0--5	6	0.955	0.019	206	<0.0001
	50	0--5	6	0.974	0.03	68.2	0.0002
Bromus tectorum (Skull Valley)	10	0--5	6	0.969	0.048	29	0.0017
	25	0--5	6	0.906	0.015	226	0
	50	0--5	6	0.802	0.029	72.4	0.0001
Bromus tectorum (Lookout Pass)	10	0--5	6	0.969	0.017	187	<0.0001
	25	0--5	6	0.906	0.026	58	0.0003
	50	0--5	6	0.802	0.034	24.2	0.0027
Elymus elymoides	10	0--5	6	0.965	0.012	164	<0.0001
	25	0--5	6	0.946	0.012	104	<0.0001
	50	0--5	5	0.749	0.016	15	0.0118
Psuedoroegneria spicata (Anatone)	10	0--7	6	0.978	0.012	272	0
	25	0--5	6	0.979	0.010	278	0
	50	0--5	66	0.986	0.007	436	0
Psuedoroegneria spicata (Secar)	10	0--5	66	0.961	0.017	149	<0.0001
	25	0--5	6	0.955	0.016	127	<0.0001
	50	0--5	6	0.974	0.011	221	<0.0001

[i] Denominator degrees of freedom [ii] Standard Error

Table 3: 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.

Species	Sub-pop. (%)	Curvilinear Range (°C)	ndf[i]	ddf[ii]	R^2	SE[iii]	F-stat	*P*-value
Achillea millefolium (Eagle)	10	10—41	2	13	0.656	0.088	12.4	0.001
	25	5--41	2	23	0.809	0.079	48.6	0
	50	10--35	2	10	0.826	0.046	23.7	0.0002
Achillea millefolium (VNS White)	10	0--30	2	19	0.941	0.061	150	0
		30--41	3	18	0.945	0.06	103	0
	25	5--35	2	14	0.875	0.036	48.8	0
		35--41	2	14	0.848	0.04	39	0
	50	5--41	2	13	0.832	0.032	32.1	<0.0001
Enceliopsis nudicaulis	10	5--41	2	12	0.586	0.029	8.5	0.0050
	25	0--41	2	11	0.749	0.017	16.4	0.0005
	50	5--41	3	15	0.847	0.014	27.7	0
Linum lewisii	10	5--41	2	23	0.965	0.029	318	0
	25	5--41	2	25	0.963	0.027	329	0
	50	5--41	3	23	0.952	0.025	153	0
Linum perenne	10	5--41	2	24	0.824	0.067	56.1	0
	25	5--41	2	22	0.905	0.035	105	0
	50	5--41	2	19	0.809	0.036	40.2	0
Lupinus arbustus	10	5--41	4	13	0.880	0.014	23.9	<0.0001
	25	5--41	4	13	0.948	0.007	58.9	0
	50	5--41	3	10	0.859	0.008	20.3	0.0001
Agropyron cristatum × *A. desertorum*	10	7--41	2	21	0.846	0.077	57.9	0
	25	7--41	2	21	0.879	0.045	76.6	0
	50	7--41	2	21	0.81	0.04	44.8	0
Agropyron desertorum	10	10--27	2	24	0.976	0.046	479	0
		27--41	2	24	0.973	0.049	429	0
	25	5--41	2	20	0.983	0.028	580	0
	50	10--19.5	5	20	0.923	0.041	48	0
		20--33.5	2	22	0.891	0.046	59.9	0
		33.5--41	4	21	0.880	0.05	38.4	0
Bromus tectorum (Spanish Fork)	10	10--41	2	25	0.596	0.552	18.5	<0.0001
	25	5--41	2	20	0.928	0.087	129	0
	50	5--41	2	25	0.949	0.047	232	0
Bromus tectorum (Skull Valley)	10	5--22.5	2	23	0.647	0.112	21.1	<0.0001
		22.5-41	2	23	0.587	0.121	16.3	<0.0001
	25	5--41	3	22	0.722	0.076	19.1	0
	50	5--27	2	22	0.768	0.053	36.5	0
Bromus tectorum (Lookout Pass)	10	5--41	2	21	0.899	0.07	93	0
	25	5--41	2	21	0.873	0.059	72.4	0
	50	5--41	2	19	0.818	0.056	42.6	0
Elymus elymoides	10	5--30	2	23	0.935	0.041	166	0
		30--41	1	6	0.789	0.086	22.5	0.0032
	25	5--41	2	25	0.832	0.046	62.1	0
	50	5--41	2	18	0.798	0.038	35.5	0
Psuedoroegneria spicata (Anatone)	10	7--41	2	21	0.905	0.061	100	0
	25	5--41	2	21	0.970	0.025	340	0
	50	5--41	2	21	0.932	0.029	144	0
Psuedoroegneria spicata (Secar)	10	5--41	2	25	0.959	0.056	294	0
	25	5--41	4	23	0.92	0.06	66.3	0
	50	5--41	4	23	0.879	0.052	41.6	0

[i] Numerator degrees of freedom [ii] Denominator degrees of freedom [iii] Standard Error

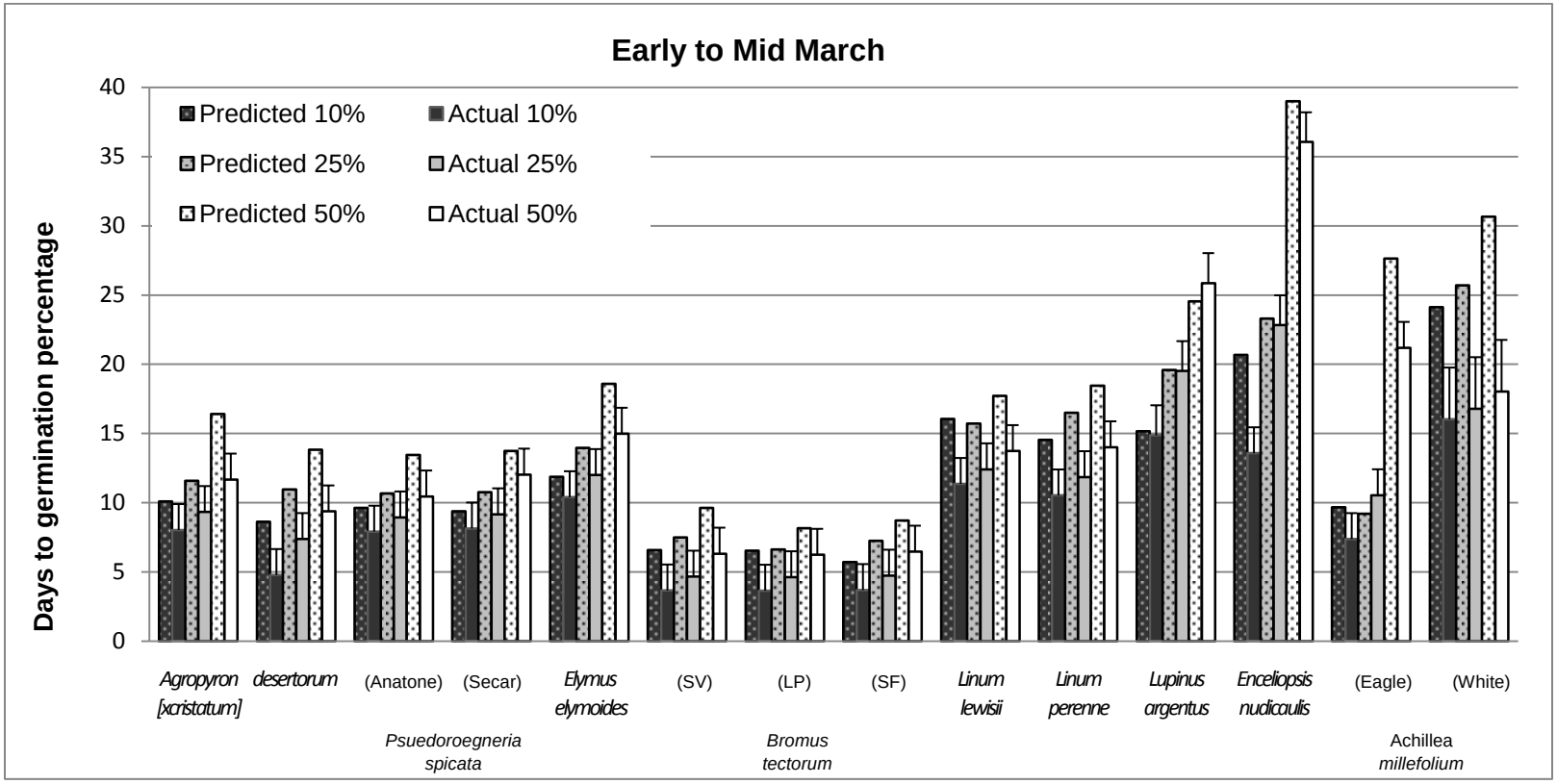

Figure 4: Measured versus predicted days required for 10, 25, and 50% subpopulation germination under the March spring temperature oscillation using a thermal accumulation model. SV, LP, and SF refer to the Skull Valley, Lookout Pass, and Spanish Fork collections of *Bromus tectorum*.

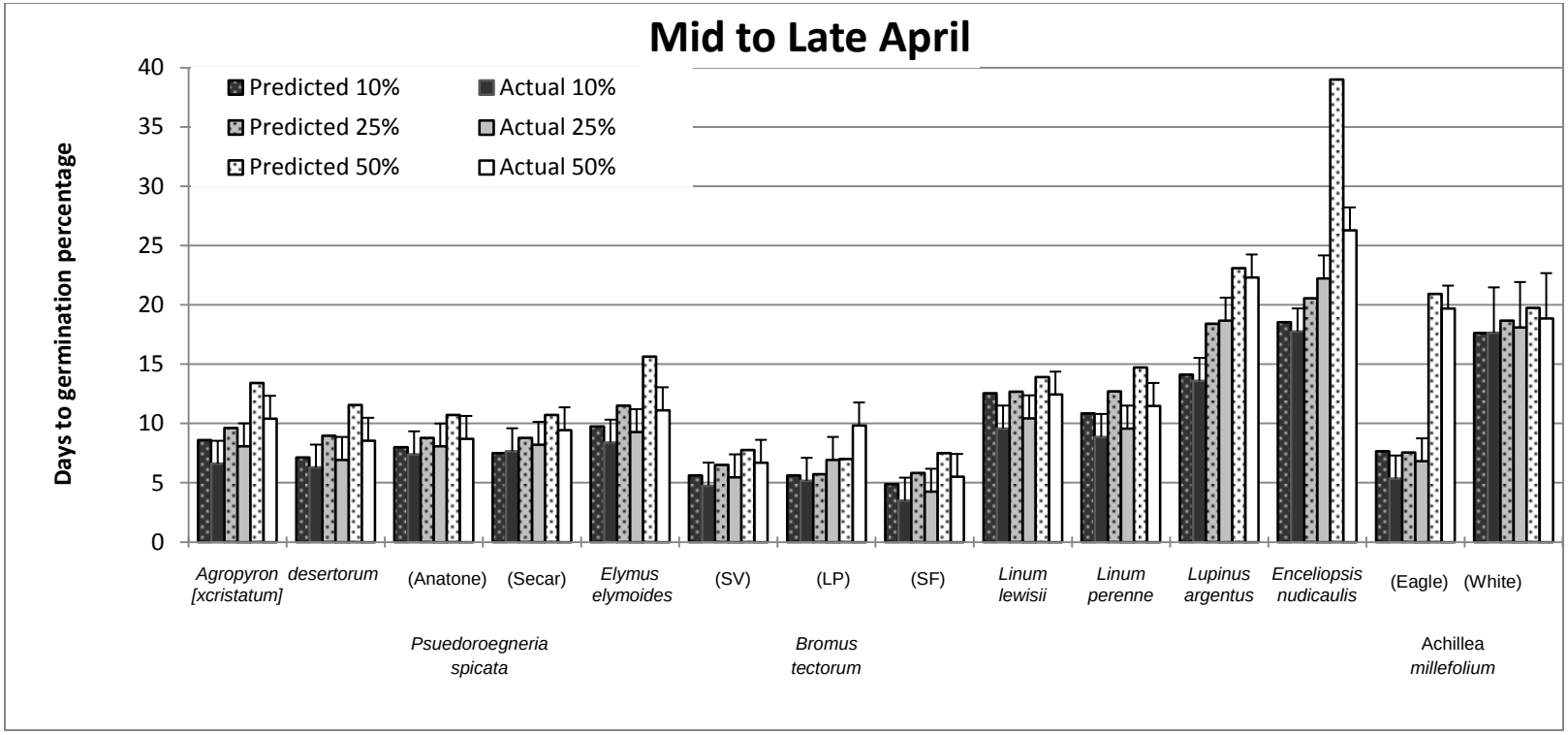

Figure 5: Measured versus predicted days required for 10, 25, and 50% subpopulation germination under the April spring temperature oscillation using a thermal accumulation model. SV, LP, and SF refer to the Skull Valley, Lookout Pass, and Spanish Fork collections of *Bromus tectorum.*

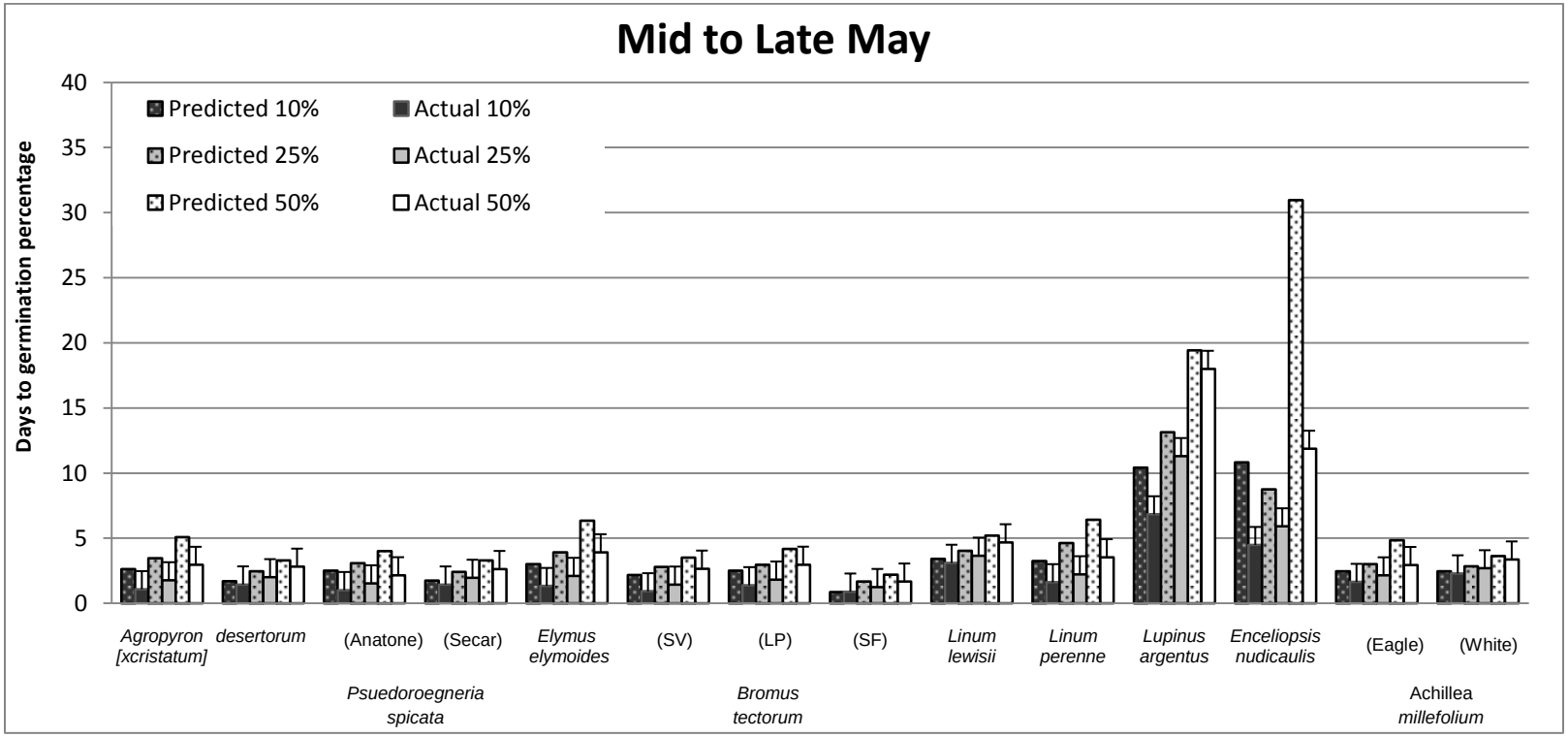

Figure 6: Measured versus predicted days required for 10, 25, and 50% subpopulation germination under the May spring temperature oscillation using a thermal accumulation model. SV, LP, and SF refer to the Skull Valley, Lookout Pass, and Spanish Fork collections of *Bromus tectorum.*

APPENDIX B

CHAPTER 2

TABLES

Table 4: Species, cultivar or population seed source, collection date, and number of seeds used per bag (replication) to provide a minimum of 25 germinable seeds/bag.

Species	Common Name/Cultivar	Source	Year Collected	Seeds/ Seedbag
Achillea millefolium	'Eagle' yarrow	Eastern WA	2003	37
Linum perenne	'Appar' blue flax	UDWR-Lot# LHSIGNIA-245-1R	2003	28
Agropyron cristatum x A. desertorum	'Hycrest' crested wheatgrass	UDWR-Lot# 1377-9-127223	2003	27
Elymus elymoides	'Sanpete' bottlebrush squirreltail	Sanpete Co., UT	2003	35
Pseudoroegneria spicata spp. spicata	'Anatone' bluebunch wheatgrass	UDWR-Lot# LHSID3-445	2003	26
Bromus tectorum	cheatgrass	Skull Valley, UT	2005	30
Bromus tectorum	cheatgrass	Lookout Pass, UT	2005	30

Table 5: Installation and retrieval dates and number of days in the ground for 19 seedbag burials during fall, early, mid, and late spring of 2005, 2006, and 2007.

	2005-2006			2006-2007		
	Installation	Retrieval	# of days	Installation	Retrieval	# of days
Fall-Winter				24-Oct	9-Nov	16
				24-Oct	16-Nov	23
	15-Oct	6-Dec	52	24-Oct	30-Nov	37
Early Spring	15-Oct	19-Jan	96	24-Oct	21-Feb	120
	27-Feb	16-Mar	17	21-Feb	8-Mar	15
Mid Spring	27-Feb	28-Mar	29	21-Feb	20-Mar	27
	28-Mar	11-Apr	14	20-Mar	5-Apr	16
Late Spring	27-Feb	11-Apr	43	21-Feb	5-Apr	43
	27-Feb	25-Apr	57	21-Feb	18-Apr	56
	11-Apr	25-Apr	14	5-Apr	18-Apr	13
	27-Feb	10-May	72			

Table 6: Model accuracy percentages and standard errors with 2 model parameters of base water potential threshold (-0.5, -1.0, and -1.5 MPa) and either an intermittent or cumulative wet thermal accumulation method across wet and dry seedbed conditions for 10, 25 and 50% seed germination subpopulations for fall.

Sub-population (%)	Fall	Intermittent			Cumulative		
		Water potential threshold (-MPa)			Water potential threshold (-MPa)		
	Species	0.5	1	1.5	0.5	1	1.5
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

Table 7: Model accuracy percentages and standard errors with 2 model parameters of base water potential threshold (-0.5, -1.0, and -1.5 MPa) and either an intermittent or cumulative wet thermal accumulation method across wet and dry seedbed conditions for 10, 25 and 50% seed germination subpopulations for the early spring season.

Sub-population (%)	Early Spring	Intermittent			Cumulative		
		Water potential threshold (-MPa)			Water potential threshold (-MPa)		
	Species	0.5	1	1.5	0.5	1	1.5
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

Table 8: Model accuracy percentages and standard errors with 2 model parameters of base water potential threshold (-0.5, -1.0, and -1.5 MPa) and either an intermittent or cumulative wet thermal accumulation method across wet and dry seedbed conditions for 10, 25 and 50% seed germination subpopulations for the mid spring season.

Sub-population (%)	Mid Spring	Intermittent			Cumulative		
		Water potential threshold (-MPa)			Water potential threshold (-MPa)		
	Species	0.5	1	1.5	0.5	1	1.5
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

Table 9: Model accuracy percentages and standard errors with 2 model parameters of base water potential threshold (-0.5, -1.0, and -1.5 MPa) and either an intermittent or cumulative wet thermal accumulation method across wet and dry seedbed conditions for 10, 25 and 50% seed germination subpopulations for the late spring season.

Sub-population (%)	Late Spring	Intermittent			Cumulative		
		Water potential threshold (-MPa)			Water potential threshold (-MPa)		
	Species	0.5	1	1.5	0.5	1	1.5
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