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RESEARCH

Hydrothermal Germination Models: Assessment of the Wet-Thermal Approximation of Potential Field Response

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ABSTRACT

Hydrothermal (HT) models can be used to characterize seed germination response to field-variable conditions of temperature (*T*) and water potential (Ψ). Hydrothermal response data are relatively difficult to generate, which limits their utility for large-scale comparisons of inter- and intraspecies germination response. Previous studies have hypothesized that HT germination response can be estimated using a simple model for thermal-time accumulation above a fixed threshold of environmental Ψ (wet-thermal [WT] model). The purpose of this study was to test this hypothesis by explicitly comparing HT and WT germination rates and estimated cumulative germination response of 13 rangeland grass seedlots under simulated conditions of field-variable *T* and Ψ. We used a 44-yr weather record to parameterize a seedbed-microclimate model for estimation of hourly *T* and Ψ at seeding depth for a sandy loam soil type at the Orchard field test site in southwestern Ada County, Idaho. Hydrothermal and WT germination responses for each hour of the simulation were estimated for 13 range grass seedlots. We found that overestimation of germination rate by thermal accumulation at low Ψ contributed relatively little to WT model error rates, and that >95% of the variability in predicted germination response could be explained by WT germination response above a Ψ threshold of −0.3 to −0.5 MPa. Given the pulse-like nature of favorable germination conditions in the field, this modeling approach may have immediate and wide potential application, as there are a relatively large number of thermal-germination datasets currently available for rangeland plant species.

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Abbreviations: HT, hydrothermal; Ψ, water potential; SHAW, Simultaneous Heat and Water; *T*, temperature; WPT, water potential threshold; WT, wet-thermal.

Seedbed microclimate in the Great Basin and Intermountain West of the United States is highly variable in both space and time (Rajagopalan and Lall, 1998; Hardegree et al., 2003; Roundy et al., 2007). Understanding the impact of this variability on seed germination, emergence, and plant establishment has been the focus of numerous studies in the rangeland literature (Hardegree et al., 2011). Historically, however, the majority of seed germination studies of rangeland plants have evaluated only a limited number of environmental conditions, with subsequent analyses constrained to simple treatment comparisons of germination rate and total germination (Wester, 1991). Subsequent to Garcia-Huidobro et al. (1982a, 1982b) and Gummerson (1986), thermal and hydrothermal (HT) modeling have been available for a more rigorous evaluation of population-level germination response of many rangeland species and seedlots (Jordan and Haferkamp, 1989; Allen et al., 2000; Meyer et al., 2000; Hardegree, 2006; Roundy et al., 2007; Hardegree et al., 2008, 2010, 2015; Meyer and Allen, 2009). Hydrothermal modeling can provide detailed information about potential seed germination response over a wide range of temperature (*T*) and water potential (Ψ) conditions, but generation of full-range

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HT model data is very time consuming, which can limit the utility of these models for screening multiple species and seedlots (Hardegree et al., 2017).

Roundy et al. (2007) suggested that field germination of cheatgrass (*Bromus tectorum* L.) could be adequately described by a wet-thermal (WT) model that accumulated thermal time above a fixed Ψ threshold (WPT). Rawlins et al. (2012a, 2012b) tested WT models for cheatgrass and several other species in the field and found that a WPT of −1.5 MPa produced relatively accurate estimates of field germination response. Theoretically, one would expect that thermal accumulation models would overestimate germination rate in the environmental range where water stress reduced, but did not completely suppress, germination response. Rawlins et al. (2012a, 2012b), however, found that WT germination models with a WPT of −1.5 MPa underestimated germination rate in the field for some species and environmental conditions. A more rigorous assessment of HT vs. WT germination models is necessary to determine the magnitude of potential errors in WT rate estimation, and the degree to which these errors might contribute to field estimates of germination and emergence. Should WT models prove to be sufficiently accurate under realistic field-variable conditions of *T* and Ψ, they would provide a relatively efficient methodology for comparison of intra- and interspecific germination response, as thermal-germination data are widely available for many rangeland grass species (Jordan and Haferkamp, 1989; Roundy et al., 2007; Hardegree et al., 2008, 2010).

The purpose of this study was to conduct an explicit comparison of HT and WT germination rates using detailed *T* and Ψ response estimates previously developed for 13 range grass seedlots (Hardegree et al., 2013, 2015). Specific objectives were to compare seasonal HT and WT germination rate accumulation, to estimate the degree to which WT-rate accumulation can explain predicted HT germination response, and to determine the most effective WPT for estimating germination time under realistic variable-*T* and variable-Ψ conditions in the field.

MATERIALS AND METHODS

The Simultaneous Heat and Water (SHAW) model is a process-based model that estimates a time series of soil *T* and Ψ as a function of depth using meteorological inputs of precipitation, solar radiation, wind speed, humidity, and air *T* (Flerchinger and Saxton, 1989a, 1989b). The SHAW model was previously calibrated by Flerchinger et al. (2012) to optimize soil microclimatic estimates at 2-cm depth for a Tindahay sandy-loam soil (sandy, mixed mesic, Xeric Torriorthent) from the Orchard field site in southern Ada County, Idaho. We used the SHAW model to estimate hourly *T* and Ψ for the period of 1 Oct. 1961 through 30 Sept. 2005 using hourly meteorological inputs derived from the Boise Airport. This soil type and weather scenario is representative of the 300-mm yr^{-1} precipitation zone characterizing sagebrush–bunchgrass rangelands in the Snake River Plain in southwestern Idaho (Flerchinger and Hardegree, 2004).

Hydrothermal germination data were developed for two seedlots of cheatgrass (Kuna and Orchard accessions), four seedlots of bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve, MOPX and P4 accessions and two commercial seedlots], three seedlots of bottlebrush squirreltail [*Elymus elymoides* (Raf) Swezey, GV accession and two commercial seedlots], one seedlot of big squirreltail [*Elymus multisetus* (J.G. Smith) M.E. Jones, SH accession], and one commercial seedlot each of Sandberg bluegrass (*Poa secunda* J. Presl.), thickspike wheatgrass [*Elymus lanceolatus* (Scribn. and J.G. Smith) Gould], and Idaho fescue (*Festuca idahoensis* Elmer). Although some of these species have been shown to have short-term seed after-ripening requirements (Allen et al., 1995; Goodwin et al., 1995), there is little evidence that any of these species had any significant seed dormancy issues (Hardegree et al., 1999; Young et al., 2003).

Cumulative germination response for these seedlots was measured over the *T* range of 3 to 36°C and the Ψ range of 0 to −2.5 MPa using the thermal- and Ψ-control system described by Hardegree et al. (2003). Water potential treatments for each seedlot were replicated two to four times within each thermal-control environment, and *T* treatments were replicated in three separate chambers for each experiment. Protocols for randomization of treatment vials, detection and removal of germinated seeds, fungicide application, and data evaluation were as described by Hardegree et al. (2003).

Germination counts for treatment vials within an environmental chamber were pooled, and the chamber values were used as replicate samples for development of the HT models. Each seed population was divided into 19 subpopulations, based on relative germination rate between 5 and 95% germination (Garcia-Huidobro et al., 1982a; Benech Arnold et al., 1990). Germination time and germination rate for each subpopulation were determined by interpolation from cumulative germination curves under each combination of *T* and Ψ (Covell et al., 1986). The number of inverse days required for a given subpopulation to germinate was considered to equal the per-day germination rate. Daily germination rates were divided by 24 to obtain hourly rate estimates for each combination of *T* and Ψ (Hardegree and Van Vactor, 2000).

The statistical gridding procedure described by Hardegree et al. (2015) was used to model subpopulation germination rate for each hour of the field simulation. This procedure plots germination rate as a function of *T* and Ψ and uses a topographic mapping program to produce a response surface that allows for triangulation of rate estimates as a direct interpolation from treatment data (Hardegree and Winstral, 2006; Hardegree et al., 2013). Statistical gridding is an empirical procedure that does not introduce any model shape assumptions that can induce systematic bias in germination rate estimates. Hardegree et al. (2015) demonstrated for these same seedlots that statistical gridding models have lower residual model error across the full range of HT conditions when compared with probit and regression model formulations.

Hydrothermal germination rate was first estimated for every subpopulation of every seedlot for every hour of the 44-yr microclimatic simulation as a function of *T* and Ψ from the SHAW simulation. Thermal germination rate for each hour was then estimated using the same HT models, but after first setting all input values of soil Ψ to zero. Hourly WT germination rate was then estimated for each seedlot and subpopulation for each of the following WPT values: −0.05, −0.1, −0.2, −0.3, −0.4, −0.5, −0.6, −0.7, −0.8, −0.9, −1.0, −1.1, −1.2, −1.3, −1.4, −1.5, −1.6, −1.7, −1.8, −1.9, and −2.0 MPa. Wet-thermal germination rate was considered to equal the thermal germination rate for Ψ values less negative than a given WPT. Wet-thermal germination rates were considered to be zero for all Ψ values more negative than the WPT.

Rate sums are considered to be an estimate of the relative favorability of the seedbed during a given aggregation interval and are highly responsive to seasonal patterns of T and water availability (Hardegree et al., 2016). Hourly HT and WT rate estimates were aggregated into rate sums for each month and hydrologic year of the simulation as a function of WPT. Mean HT and WT rate sum estimates for a given time period were plotted as a function of WPT and the optimal WPT determined to be the Ψ at which the mean HT and WT rate sum estimates were equal.

A second procedure for comparing HT and WT models was to estimate germination time for each seedlot–subpopulation as a function of five alternative planting dates for every year of the simulation. We used five planting dates (1, 15, and 29 October, 12 and 26 November) to represent the most common seasonal planting scenarios for rangeland grass species in the Great Basin. Hourly rate estimates for each seedlot and subpopulation were calculated using both the full HT model formulation and all WT models as a function of WPT. Germination rates of a given subpopulation were estimated to occur when the sum of hourly rate estimates subsequent to planting (rate sum) became equal to one (Roundy and Biedenbender, 1996). Germination times for WT and HT models were compared using correlation analysis and derivation of regression slope and R^2 values as a function of seedlot–subpopulation and WPT.

RESULTS

We considered that there could be two sources of residual error when comparing WT and HT germination rate estimates. First, the WT model would overestimate germination rate at all Ψ values between zero and the WPT that were in the germinable thermal range (Fig. 1). Second, the WT model would underestimate germination rate for conditions below the WPT that still exhibited a positive HT rate (Fig. 1). Figure 1 shows that the relative magnitude of these errors is dependent on the WPT. The

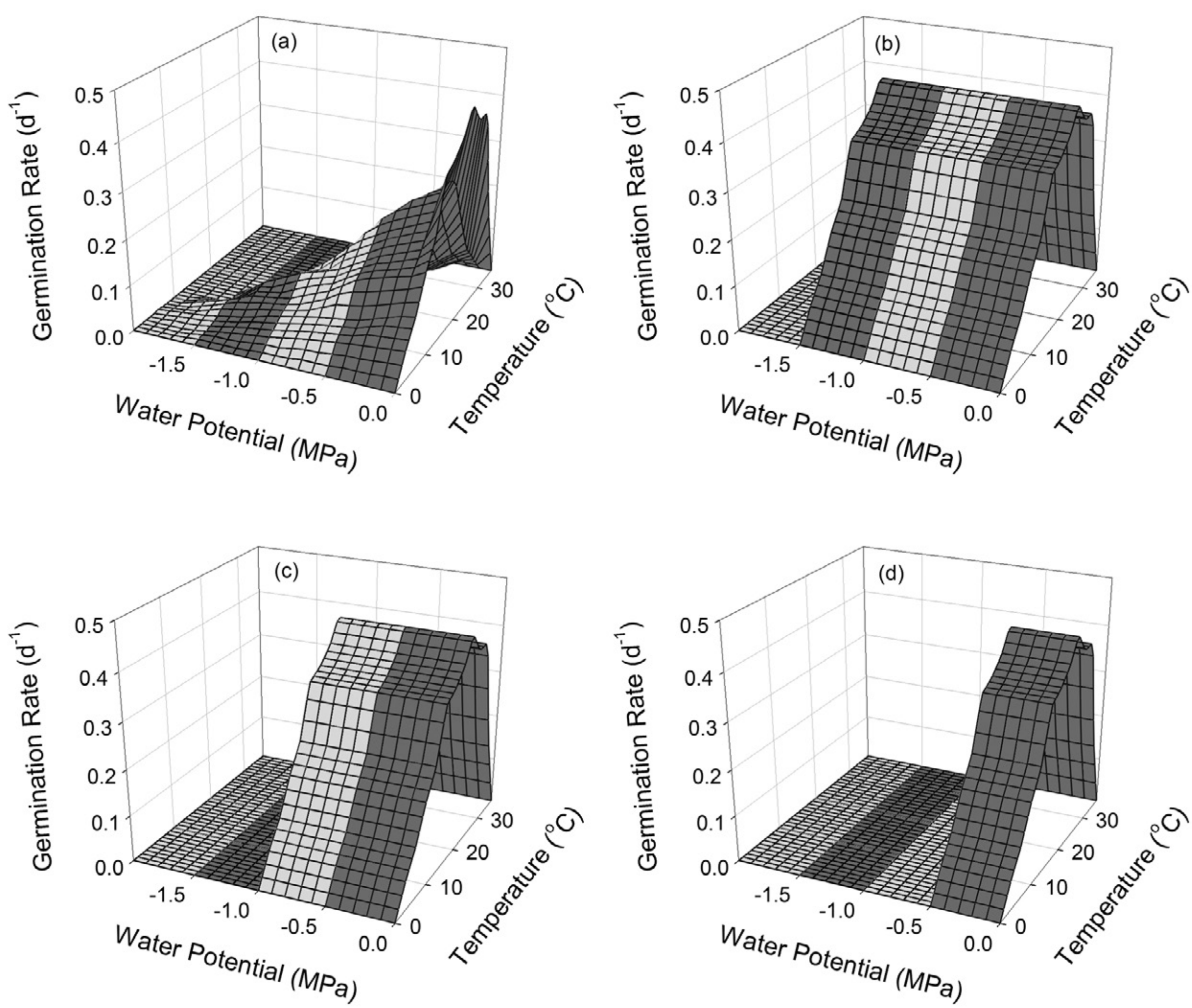

Fig. 1. Comparison of the (a) full hydrothermal germination rate response model and wet-thermal germination response models for the 50% subpopulation of *Elymus elymoides* GV using a water potential threshold of (b) −1.5, (c) −1.0, and (d) −0.5 MPa.

relative degree to which these model errors express themselves in the field, however, depends on both the absolute model error during a given hour (Fig. 1), and the number of hours spent under those conditions after sowing and before germination (Hardegree et al., 2017). We show an example of these relative model errors as a function of WPT for the rate sums of the 50% subpopulation of *F. idahoensis*, *E. elymoides* GV, and *B. tectorum* Kuna as aggregated over all hours in the 44-yr simulation (Fig. 2). For these scenarios, the optimal WPT was between −0.1 and −0.4 MPa, so in general, germination rate of these subpopulations would have potentially been overestimated for models based on the −0.5, −1.0 and −1.5 WPT values previously used by Roundy et al. (2007) and Rawlins et al. (2012a, 2012b).

Optimal WPT estimates varied by seedlot, subpopulation, and season but mean values across all seedlots and time periods were generally less negative than −0.5 MPa (Fig. 3). Some seedlots and subpopulations, however, had a mean optimal WPT of between −1.2 and −1.3 MPa for some periods of the year (Fig. 3).

The relative accuracy of WT models as a function of WPT is, perhaps, most relevantly assessed by comparing HT and WT estimates of germination time under realistic field-variable planting scenarios (Fig. 4). Figure 4 model output was generated using a WT WPT of −1.0 MPa, but we found that, in general, >95% of HT germination response was explained by any WT model with a WPT between −0.5 and −1.5 MPa, and that residual model error was relatively consistent over this WPT range (Fig. 4 and 5).

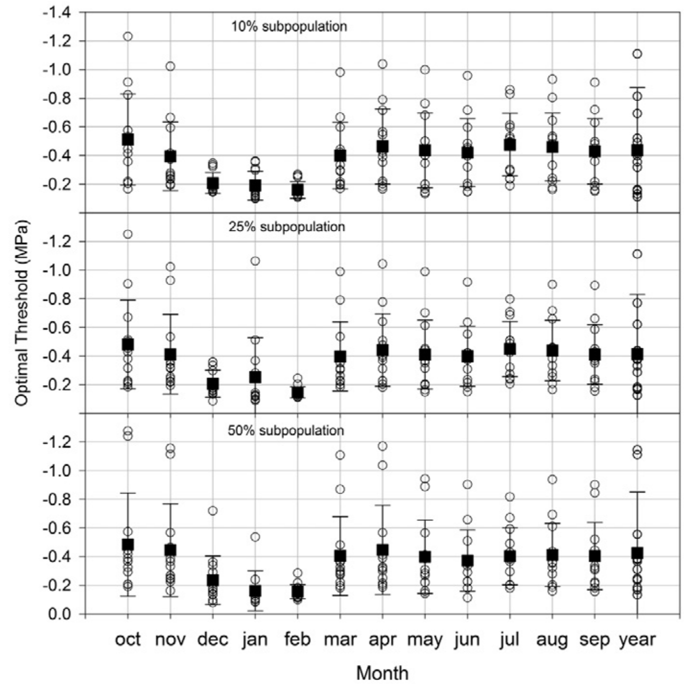

Fig 3. Optimal water potential threshold values for individual seedlots (circles) and three subpopulations (10, 25, and 50%) based on the mean rate sum estimates averaged across all years of the simulation for different months, and as a function of hydrologic year. Error bars represent 1 SD around the mean (squares) across all seedlots.

DISCUSSION

Hydrothermal germination models have been used to generate model coefficients to compare and rank relative seed quality, to explore the underlying physiological mechanisms of seedlot response to *T* and water stress, and to

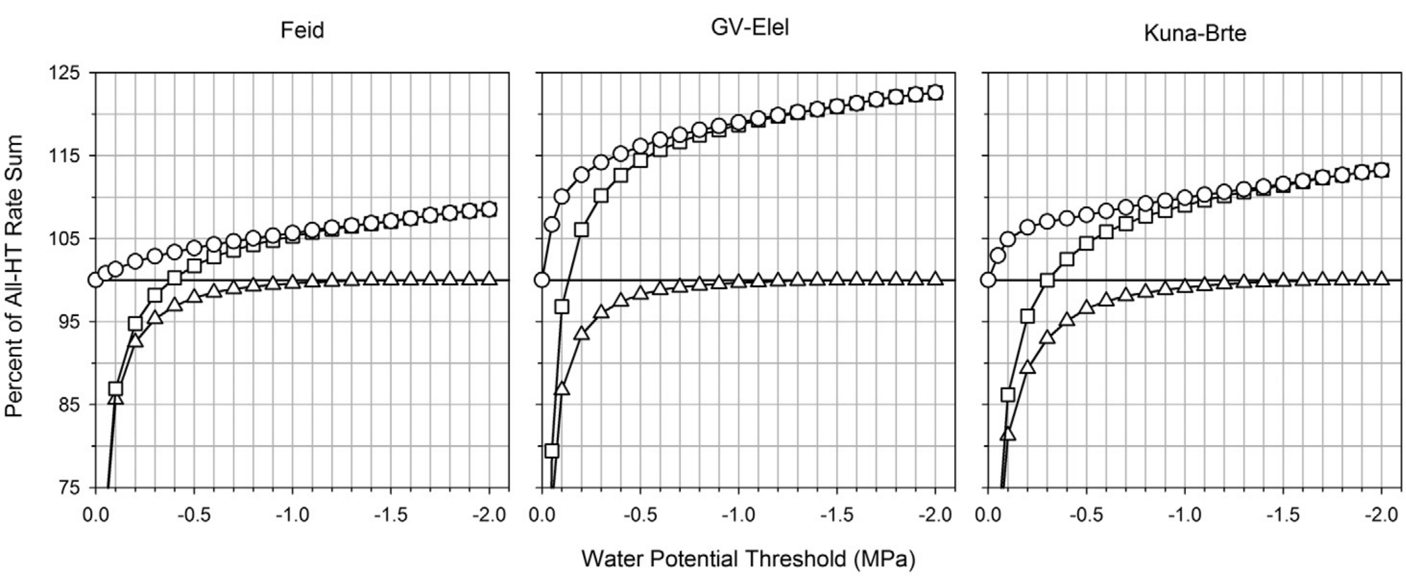

Fig. 2. Hydrothermal (HT) model error (triangles), wet-thermal model error (squares), and thermal-only model error (circles) of the average annual rate sum value of the 50% subpopulations of *Festuca idahoensis* (Feid), *Elymus elymoides* accession GV (GV-Elel), and *Bromus tectorum* accession Kuna (Kuna-Brte) as a function of water potential threshold value. Model error is expressed as a percentage of the full hydrothermal estimate of the mean yearly rate sum value averaged across all years of the simulation.

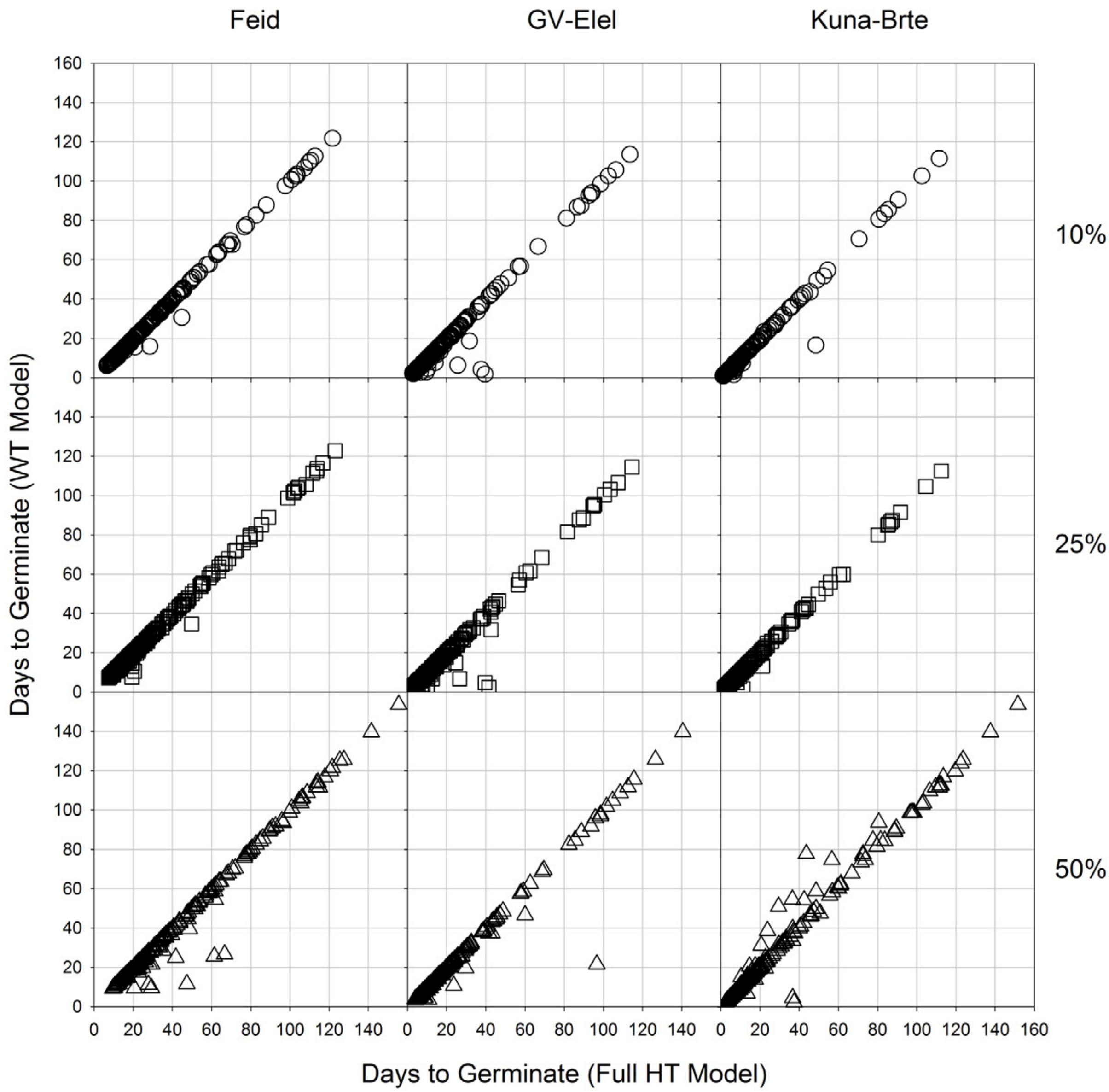

Fig. 4. Comparison of hydrothermal (HT) and wet-thermal (WT) germination time estimates for the 10, 25, and 50% subpopulations of seedlots representing relatively slow native seedlot germination (*Festuca idahoensis* [Feid]), relatively rapid native seedlot germination (*Elymus elymoides* accession GV [GV-Elel]), and extremely rapid annual weed germination (*Bromus tectorum* accession Kuna [Kuna-Brte]). Data in this figure include germination time estimates for all years (44) and all fall planting dates (5) of the simulation. These specific WT data were estimated using a water potential threshold of –1.0 MPa.

predict seed population response in the field (Finch-Savage et al., 1998; Allen et al., 2000; Allen, 2003; Hardegree et al., 2013). Regardless of the application, however, characterization of germination response across all possible conditions of T and Ψ is sufficiently time consuming that most studies on the subject are limited to relatively few seedlots (Gummerson, 1986; Dahal and Bradford, 1994; Alvarado and Bradford, 2002; Rowse and Finch-Savage 2003; Bloomberg et al., 2009; Hardegree et al., 2015). To increase the efficiency of larger scale HT assessments, various authors have either made simplifying assumptions that reduce the data necessary for model parameterization, or they have used methods employing surrogate estimates of main model parameters (Allen and Meyer, 1998; Allen et al., 2000; Köchy and Tielbörger, 2007). For applications where the primary objective is to estimate germination time in the field, an accurate WT model would take significantly less effort to develop and parameterize than a full-range HT model. For rangeland seeding applications in particular, there are several orders of magnitude more data currently available for thermal model parameterization than exist for HT assessment (Jordan and Haferkamp, 1989; Roundy et al., 2007; Hardegree et al., 2008, 2010).

Field studies suggest that WT models generally provide relatively accurate estimates of germination response (Rawlins et al., 2012a, 2012b) despite the fact that WT models would be expected to overestimate germination rate for all conditions where soil Ψ was between

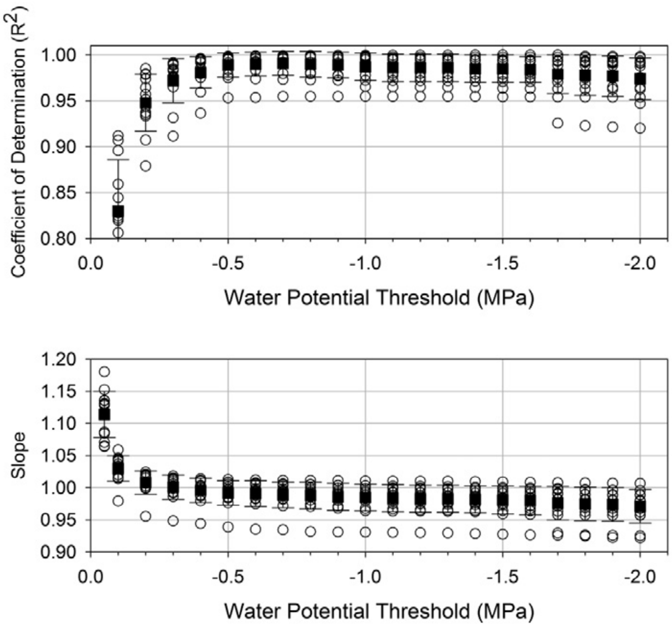

Fig. 5. Coefficient of determination (R^2) and slope estimates for correlation analysis of hydrothermal vs. wet-thermal germination time predictions for the 25% subpopulation of all seedlots (circles) as a function of water potential threshold. Regression intercepts were constrained to pass through the origin. Error bars represent 1 SD around the mean (squares) across all seedlots.

0 MPa and the WPT, and that this error would be exacerbated for seedlots and subpopulations that had a lower WPT (Fig. 1 and 3). The relatively few instances noted by Rawlins et al. (2012a, 2012b) of WT models underestimating germination rate in the field could be due to other abiotic or physiological factors other than WT or HT germination response. In particular, seed equilibration at subgermination Ψ in the field could possibly have induced natural seed priming that might increase the subsequent germination rate of some seeds (Hardegree and Van Vactor, 2000). The model simulations in the current study, however, suggest that any discrepancies in modeled and predicted germination rate in the field were probably not caused by inherent differences in WT and HT model estimates, per se, as regression comparisons of germination time were highly correlated and relatively linear over a wide range of potential WPT values for all seedlots and subpopulations (Fig. 4 and 5). Hardegree et al. (2017) provided some insight into the relative accuracy of these WT field predictions by demonstrating that the bulk of environmental conditions contributing to field germination may occur at Ψ less negative than −0.5 MPa, and often in the 0 to −0.2 MPa range for planting dates later in the fall. This would minimize the magnitude of thermal overestimation of germination rate, as relatively little germination time would be spent in the range where the underlying models had the highest degree of potential error (Fig. 1).

As Fig. 2 demonstrates, overestimation by the thermal model component in the 0 to −0.5 MPa Ψ range is offset by underestimation of the underlying HT response below a given WPT. This generally resulted in an average optimal WPT value less negative than −0.5 MPa for most seedlots and subpopulations across all years of the simulation (Fig. 3). Roundy et al. (2007) and Rawlins et al. (2012a, 2012b), however, noted that reliable germination predictions could be obtained using WPT values of −1.0 and −1.5. We attribute this to a relative insensitivity of residual model error between HT and WT estimates of germination rate in the WPT range of −0.5 to −1.5 MPa, because relatively little rate sum accumulation occurs in this Ψ range (Fig. 5).

Figure 4 also shows a number of outliers, both positive and negative, in the regression of HT and WT model estimates of germination time. These outliers are infrequent, however, and the high degree of relative data conformity is obscured by overlap of the majority of data points along the regression axis (Fig. 4). Most of the outliers in Fig. 4 can be attributed to relatively small differences in WT and HT model estimates of germination time that occurred either shortly before or shortly after the onset of cold winter conditions. A relatively small discrepancy in germination time prediction in early December could sometimes result in a relatively large difference in germination time for predictions that fell just before and just after a subsequent period of prolonged soil freezing. The presence of these outliers was greatly reduced for early- and late-fall seeding dates where the majority of germination was predicted to occur either before or after the onset of winter (data not shown).

In conclusion, there are two principal theoretical errors associated with WT models: a general overestimation of germination rate under conditions of suboptimal Ψ, and an offsetting underestimation of germination rate at suboptimal Ψ values that fall below the WPT (Fig. 1). These errors, however, are minimized given the pattern of actual Ψ and T in the field under the most common planting date scenarios, and the relatively high germination rates expected at Ψ greater than −0.5 MPa (Hardegree et al., 2017). This results in a high correlation between HT and WT predictions of germination time regardless of seedlot, subpopulation, planting date, and arbitrarily selected WPT value as long as it is more negative than the optimal WPT. Wet-thermal and HT estimates need to be evaluated more broadly to expand these inferences to additional species groups and agricultural applications. This approach appears promising, however, for expanding practical applications of germination response prediction to diverse field scenarios for non-dormant agricultural and native plant species.

Conflict of Interest

The authors declare that there is no conflict of interest.

Acknowledgments

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