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## Predicting Germination Response to Temperature. II. Three-dimensional Regression, Statistical Gridding and Iterative-probit Optimization Using Measured and Interpolated-subpopulation Data

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• **Background and Aims** Most current thermal-germination models are parameterized with subpopulation-specific rate data, interpolated from cumulative-germination-response curves. The purpose of this study was to evaluate the relative accuracy of three-dimensional models for predicting cumulative germination response to temperature. Three-dimensional models are relatively more efficient to implement than two-dimensional models and can be parameterized directly with measured data.

• **Methods** Seeds of four rangeland grass species were germinated over the constant-temperature range of 3 to 38 °C and monitored for subpopulation variability in germination-rate response. Models for estimating subpopulation germination rate were generated as a function of temperature using three-dimensional regression, statistical gridding and iterative-probit optimization using both measured and interpolated-subpopulation data as model inputs.

• **Key Results** Statistical gridding is more accurate than three-dimensional regression and iterative-probit optimization for modelling germination rate and germination time as a function of temperature and subpopulation. Optimization of the iterative-probit model lowers base-temperature estimates, relative to two-dimensional cardinal-temperature models, and results in an inability to resolve optimal-temperature coefficients as a function of subpopulation. Residual model error for the three-dimensional model was extremely high when parameterized with measured-subpopulation data. Use of measured data for model evaluation provided a more realistic estimate of predictive error than did evaluation of the larger set of interpolated-subpopulation data.

• **Conclusions** Statistical-gridding techniques may provide a relatively efficient method for estimating germination response in situations where the primary objective is to estimate germination time. This methodology allows for direct use of germination data for model parameterization and automates the significant computational requirements of a two-dimensional piece-wise-linear model, previously shown to produce the most accurate estimates of germination time.

**Key words:** Thermal, germination, model, *Elymus elymoides*, *Elymus lanceolatus*, *Poa secunda*, *Pseudoroegneria spicata*.

### INTRODUCTION

The most common models for estimating thermal and hydrothermal-germination response are based on subpopulation-specific regression of germination rate, calculation of cardinal temperatures, and the distribution of regression coefficients across subpopulations using the probit distribution (Garcia-Huidobro *et al.*, 1982; Covell *et al.*, 1986; Ellis *et al.*, 1986, 1987; Gummerson, 1986; Ellis and Butcher, 1988; Murdoch *et al.*, 1989; Dahal and Bradford, 1990; Dahal *et al.*, 1990; Ellis and Barrett, 1994; Jacobsen and Bach, 1998; Cheng and Bradford, 1999; Kebreab and Murdoch, 1999; Roman *et al.*, 1999; Shrestha *et al.*, 1999; Grundy *et al.*, 2000; Meyer *et al.*, 2000; Steinmaus *et al.*, 2000; Alvarado and Bradford, 2002; Rowse and Finch-Savage, 2003; Bradford and Alvarado, 2005). These models can be used to predict cumulative germination response, but they also yield cardinal temperatures and model coefficients for comparing seedlots and screening germplasm (Covell *et al.*, 1986; Ellis *et al.*, 1986, 1987; Ellis and Butcher, 1988; Craufurd *et al.*, 1996; Fidanza *et al.*, 1996; Holshauser *et al.*, 1996; Steinmaus *et al.*, 2000; Phartyal *et al.*, 2003).

There are several base assumptions inherent to all thermal-germination models: (a) instantaneous-germination rate is independent of temperature pattern; (b) instantaneous-germination rate is unaffected by thermal history; and (c) subpopulations maintain their relative-germination rate regardless of the thermal environment to which they are subjected (Garcia-Huidobro *et al.*, 1982; Hardegree *et al.*, 1999). These assumptions may not be valid for species that require fluctuating-temperatures to release dormancy (Thompson, 1974; Thompson and Grime, 1983; Murdoch *et al.*, 1989; Benech Arnold *et al.*, 1990) or for high- and low-temperature conditions that cause physiological damage to the germinating seed (Bewley and Black, 1994; Ellis and Barrett, 1994). Hardegree (2006) tested three cardinal-temperature thermal-germination models, non-linear regression and a piece-wise linear regression procedure, and determined that predictive accuracy of germination rate and germination time could be improved by using empirical models that contained fewer *a priori* shape assumptions. Elimination of *a priori* shape assumptions allows one to distinguish between predictive errors that are inherent to a given model and those errors that are caused by violations of base assumptions associated with dormancy, hysteresis

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in temperature response, and seed damage at extreme temperatures (Hardegree *et al.*, 1999).

The purpose of this study was to evaluate three-dimensional regression, statistical gridding and iterative-probit optimization for estimating cumulative-germination response to temperature. Specific objectives were to test whether these models could be parameterized directly from untransformed germination data, and to evaluate their efficiency and accuracy relative to the previous two-dimensional, subpopulation-specific model formulations tested by Hardegree (2006).

## MATERIALS AND METHODS

The experimental design for generating the germination-response data in this study is described in more detail by Hardegree (2006). Thickspike wheatgrass [*Elymus lanceolatus* (Scribn. and J.G. Smith) Gould], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], Sandberg bluegrass [*Poa secunda* Vasey] and bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey] seedlots used in the current study were the same as those used in previous studies by Hardegree (1994a, b; 1996, 2006), Hardegree *et al.* (1999) and Hardegree and Van Vactor (1999, 2000).

Cumulative-germination response was evaluated at 21 constant temperatures, in 1.75 °C increments, between 3 and 38 °C as described by Hardegree (2006). Each temperature treatment was replicated three times in different environmental chambers. In the previous study (Hardegree, 2006), days required to achieve 5–90 % germination were calculated for each species and temperature-treatment by linear interpolation between daily germination percentiles from the cumulative germination curves (Covell *et al.*, 1986). These interpolated data (I data) were also used in the current study as a means of direct comparison with the two-dimensional model formulations described by Hardegree (2006). Two additional datasets were derived for model parameterization in the current study. One of these datasets was derived directly from the measured data (M data). On any day in which new germination was observed, a single data-point was recorded establishing germination time, germination rate, temperature, and cumulative-germination percentage (subpopulation). A combined dataset of both I and M data (IM data) was also compiled for each seedlot.

### Optimized three-dimensional regression (3DR) model

The TableCurve® 3D curve fitting program (Systat Software, Inc.) was used for equation discovery to evaluate alternative regression models for predicting germination rate ( $R$ ) as a function of temperature ( $T$ ) and subpopulation ( $G$ ). Alternative equations were ranked based on maximization of the coefficient of determination ( $r^2$ ). Consistently good model fit was obtained for a rational equation (ratio of polynomial expressions;

TableCurve equation 1106) of the following form:

$$R = \frac{a + bG + cG^2 + dG^3 + eT + fT^2}{1 + gG + hT + iT^2} \quad (1)$$

where  $a - i$  are equation-specific model-fit coefficients. This model was optimized for all seedlots using the I data ( $r^2$  range of 0.85–0.94), M data ( $r^2$  range of 0.17–0.70) and IM data ( $r^2$  range of 0.80–0.92).

### Spatial-gridding (SG) model

The SG model was parameterized with data from the constant-temperature treatments by computing a three-dimensional surface map of germination rate as a function of subpopulation and temperature using the Surfer® 8 program (Golden Software, Inc.). Of the available gridding options, triangulation with linear interpolation was selected. This method is an exact interpolator and creates triangles by drawing lines between data-points in such a way that no triangle edges are intersected by other triangles (Lee and Schachter, 1980; Guibas and Stolfi, 1985). This method is the three-dimensional equivalent of the PWL model described by Hardegree (2006) except that it is automatically derived upon importation of the input-data file. As the  $X(G)$  and  $Y(T)$  co-ordinates for these data have different numerical ranges, the data were anisotropic. In the triangulation procedure, points closer to a grid node are given more weight than points further away, potentially weighting the estimate of the  $Z(R)$  co-ordinate by the variable with the closer-numeric interval. A gridding option was selected that corrected for this effect by using a seedlot-specific anisotropy ratio ( $X$  range/ $Y$  range) of approx. 3.

An SG model was developed for each species and input dataset (I, M and IM). Residual errors in the prediction of germination rate were derived from these models by submitting  $X$ - and  $Y$ -co-ordinate data with a dummy-variable for the  $Z$  co-ordinate equal to zero. The gridding software automatically computed residual error between the model and the submitted data, which in the case of  $Z = 0$  produced an error estimate equal to  $-Z(-R)$ . Other statistical-gridding techniques, such as Kriging, were evaluated but the triangulation method yielded relatively accurate estimates of germination rate and did not require additional data-transformation to compensate for the use of different measurement units along the  $X$ - and  $Y$ -axes.

### Iterative-probit-optimization cardinal-temperature (IPO) model

The IPO model used in this study was similar to the probit cardinal-temperature (PCT) model described by Hardegree (2006) except that thermal-time coefficients were estimated by iterative optimization of the relationship between  $G$  and  $\theta$  (Covell *et al.*, 1986; Ellis *et al.*, 1986, 1987). In the present procedure, subpopulation-rate data were split into sub-optimal and supra-optimal temperature ranges using the same procedure described

by Hardegree (2006). Sub-optimal and supra-optimal estimates of thermal time were calculated for each value of  $G$  using the following formulas:

$$\theta_1 = (T - T_b)/R \quad (2)$$

$$\theta_2 = (T_m - T)/R \quad (3)$$

where  $\theta_1$  is sub-optimal thermal time,  $\theta_2$  is supra-optimal thermal time,  $T_b$  is base temperature and  $T_m$  is maximum or ceiling temperature. Subpopulation values were converted to probits (Finney, 1971) and linear regression used to iteratively estimate probit ( $G$ ) as a function of  $\ln\theta$  for each thermal range using different values of  $T_b$  and  $T_m$ . Optimal values of  $\theta_1$ ,  $\theta_2$ ,  $T_b$  and  $T_m$  were selected from the regression models that exhibited the lowest standard error in the estimation of probit ( $G$ ).  $T_b$  and  $T_m$  values were varied in 0.1 °C increments over a 5 °C temperature range relative to average values previously established for these parameters by Hardegree (2006). This procedure was repeated for each species using I, M and IM data.

## RESULTS

Two-dimensional representations of 3DR-, SG- and IPO-model shapes are shown in Fig. 1 for models parameterized with I data. The SG model essentially interpolates between data-points and, therefore, most closely represents the actual data distribution used to parameterize the other models shown in Fig. 1.

Residual-model error in germination-rate prediction of interpolated subpopulations is shown in Fig. 2 for models parameterized with I data. These data can be directly compared with the data presented by Hardegree (2006) for two-dimensional model formulations. Of the models tested in the current study, residual errors associated with the SG model were relatively low and randomly distributed across all temperatures (Fig. 2). All models showed relatively greater variability in residual errors in the supra-optimal temperature range (Fig. 2). Residual model error for the SG model was lower than the model error of all but one of the two-dimensional models tested by Hardegree (2006). The PWL model (Hardegree, 2006) was the only two-dimensional model formulation that was superior to the SG model for estimating interpolated-subpopulation germination rate.

Small model errors in germination rate produced relatively large errors in germination time in the lowest-temperature treatment (Fig. 3). 3DR-model formulations underestimated germination time by 2–5 d, SG models overestimated germination time by 0.5–2 d, and IPO models overestimated germination time by 4–8 d at 3 °C (Fig. 3). Predictive errors in germination time for the IPO model at 3 °C were much less than for the CT-type models tested by Hardegree (2006). Unlike the previously tested CT models, however, the IPO model also tended to underestimate germination time in the 5–10 °C temperature range (Fig. 3). 3DR-model errors (Fig. 3) were similar

in magnitude to the two-dimensional, non-linear regression (NLR) models described by Hardegree (2006). SG-model errors in the prediction of germination time were relatively low across all but the highest temperature treatments (Fig. 3).

The three-dimensional model formulations tested in this study differ from those tested by Hardegree (2006) in that they can be directly parameterized with measured-subpopulation data. Figure 4 shows the mean and standard deviation of predicted-rate errors of measured subpopulations for models parameterized with M data. General patterns of residual model error did not change, but variability in error estimates was increased, for SG and IPO models when parameterized with M data (Figs 2 and 4). 3DR models parameterized with M data had relatively large systematic errors (Fig. 4). Variability in residual model error was reduced for all models parameterized with IM data (Fig. 5). Equivalent residual-errors for predictions of germination time are shown in Fig. 6 for models parameterized with M and IM datasets. Residual errors in the prediction of germination-time were very large for 3DR models parameterized with M data and could not be plotted at the scale shown in Fig. 6 (data not shown).

## DISCUSSION

The most common method for predicting thermal-germination response is to partition seed populations into subpopulations ( $G$ ) based on relative germination rate (Garcia-Huidobro *et al.*, 1982). Subpopulation-rate response is then assumed to be linear at sub- and supra-optimal temperature between the following cardinal temperatures: base temperature ( $T_b$ ), optimal temperature ( $T_o$ ) and maximum or ceiling temperature ( $T_m$ ). The inverse-slope of rate response defines the sub-optimal and supra-optimal thermal time ( $\theta_1$ ,  $\theta_2$ ) for a given subpopulation. Additional assumptions are often made regarding the distribution of these variables across subpopulations. The most common assumptions are that  $T_b$  is constant for the entire population, and that the relationship between  $\theta_1$ , or  $\ln\theta_1$  and  $G$  can be described using a probit function (Covell *et al.*, 1986; Ellis *et al.*, 1986; Ellis and Butcher, 1988; Roberts, 1988; Benech Arnold *et al.*, 1990; Probert, 1992; Ellis and Barrett, 1994; Shrestha *et al.*, 1999; Steinmaus *et al.*, 2000; Alvarado and Bradford, 2002). Supra-optimal shape assumptions vary for different studies, some of which have produced better model fit by assuming commonality of  $\theta_2$  and a normal or log-normal distribution of  $T_m$  (Covell *et al.*, 1986; Ellis *et al.*, 1986). Hardegree (2006) determined that, for the same data used in the current study, supra-optimal CT-model fit was highest under the assumption of a common value for  $T_m$  and a log-normal distribution of  $\theta_2$ .

Hardegree (2006) and McDonald (2002) tested several CT-type models, non-linear regression and piece-wise linear regression, and determined that model-shape assumptions reduced the accuracy of germination-rate and germination-time predictions. This conclusion was reinforced in the current study as the model with no  $a$



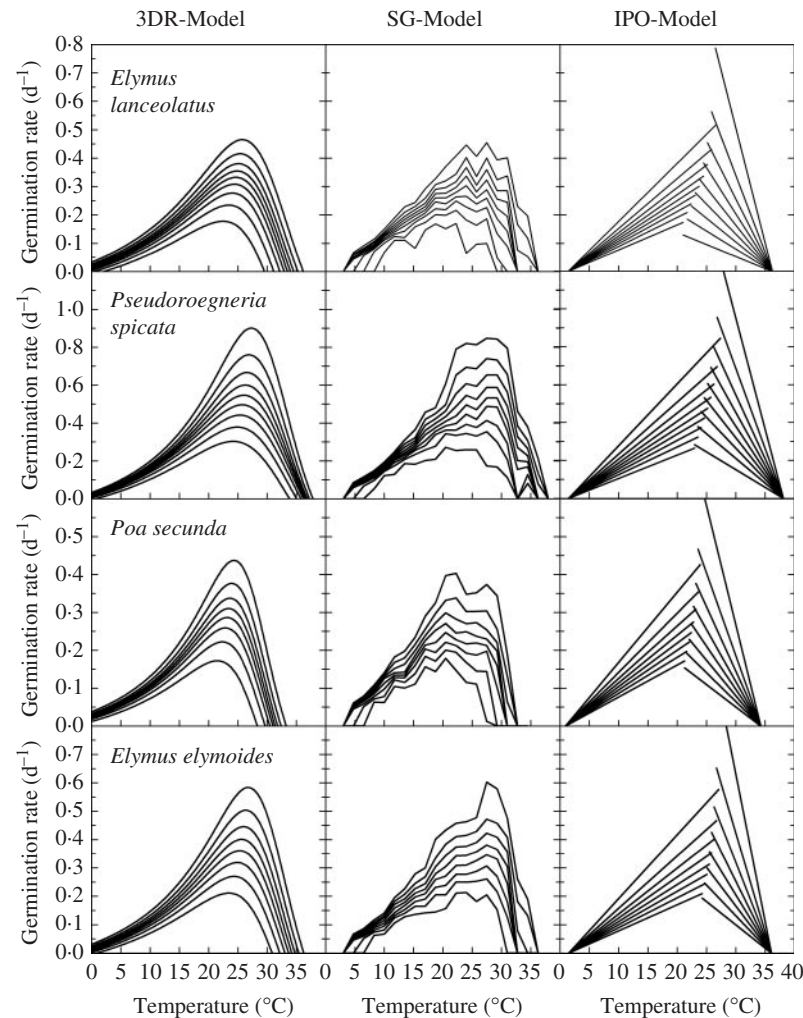


FIG. 1. Two-dimensional representations of model shape for the 3DR, SG and IPO models for predicting germination rate as a function of subpopulation and temperature. Models shown here were derived from interpolated subpopulation data. Uppermost lines represent the 10 % subpopulation. Subpopulation data are shown in 10 % increments for clarity.

*priori* shape assumptions (SG model) produced the most-accurate and least-variable predictions of both germination rate and germination time (Figs 2 and 3). The only model in either study that produced better model fit was the two-dimensional, subpopulation-specific, PWL model (Hardegree, 2006). The PWL model, however, was the least computationally efficient of all models tested as it required development and utilization of as many as 20 separate regression equations for every interpolated subpopulation (Hardegree and Van Vactor, 1999; McDonald, 2002; Hardegree, 2006).

Relative model fit can be overestimated when models are derived from, and residual errors evaluated for, interpolated-subpopulation data (Ellis *et al.*, 1986). Subpopulation datasets interpolated from measured data can be internally correlated, especially for temperature treatments that exhibit rapid germination within a single-day interval. As such, residual errors associated with models parameterized from M data (Fig. 4) are a more realistic representation of true model fit. The 3DR model

is an exception in that models derived from measured-subpopulation data tended to systematically underestimate germination rate over the entire temperature range (Fig. 4). This is attributed to the regression-optimization procedure. In the intermediate-temperature range, daily changes in  $G$  were relatively large, therefore, the number of data-points in the M dataset were relatively small. The relative paucity of data at intermediate temperatures biased regression fit toward the larger amount of data representing slower-germinating seeds in low-temperature treatments, and slower-germinating subpopulations across all treatments. Relative accuracy in germination-rate predictions of measured-subpopulations was restored for the 3DR model when parameterized with the IM dataset (Fig. 5).

The IM-data parameterization did not greatly improve estimates of germination rate and time for either the SG model or the IPO model (Figs 4–6). SG-model optimization is obtained by triangulation between adjacent data-points in a three-dimensional data-field.

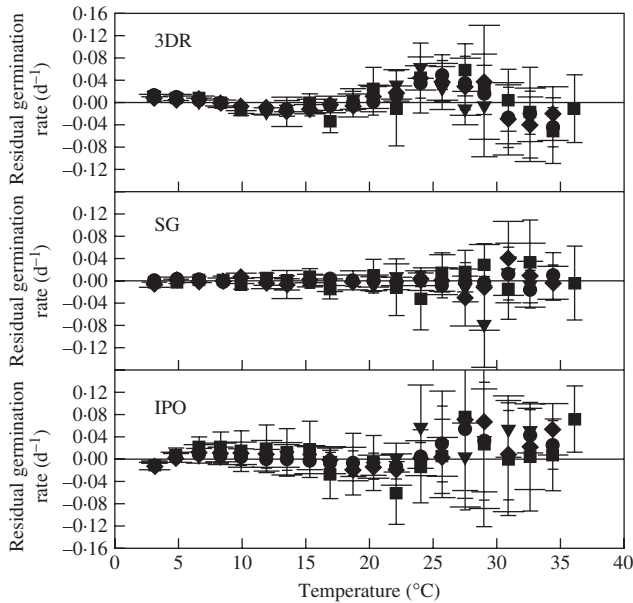


FIG. 2. Residual-model error in germination rate as a function of temperature and model for *E. lanceolatus* (●, small error bars), *P. spicata* (■, medium-small error bars), *P. secunda* (▼, medium-large error bars) and *E. elymoides* (◆, large error bars). Error bars represent  $\pm 1$  s.d. from the mean. These data were derived from models parameterized with I data.

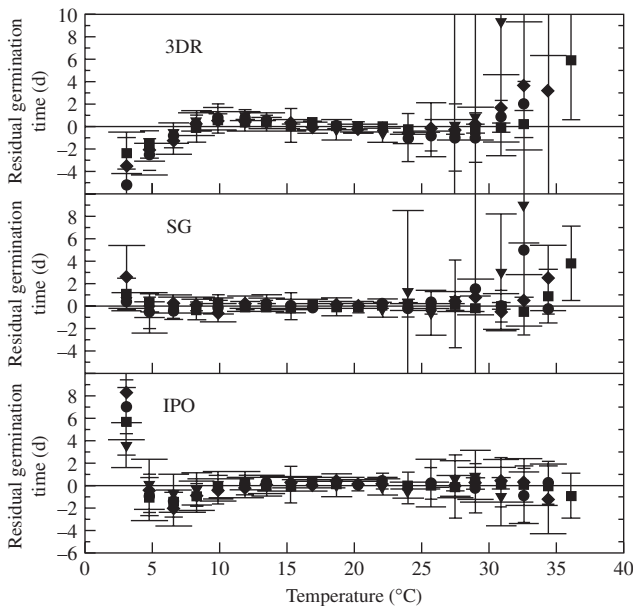


FIG. 3. Residual-model error in germination time as a function of temperature and model for *E. lanceolatus* (●, small error bars), *P. spicata* (■, medium-small error bars), *P. secunda* (▼, medium-large error bars) and *E. elymoides* (◆, large error bars). Error bars represent  $\pm 1$  s.d. from the mean. These data were derived from models parameterized with I data.

This procedure automatically interpolated between measured data, therefore, did not greatly benefit from inclusion of additional data-points interpolated from the cumulative germination curves. The IPO model was pre-constrained

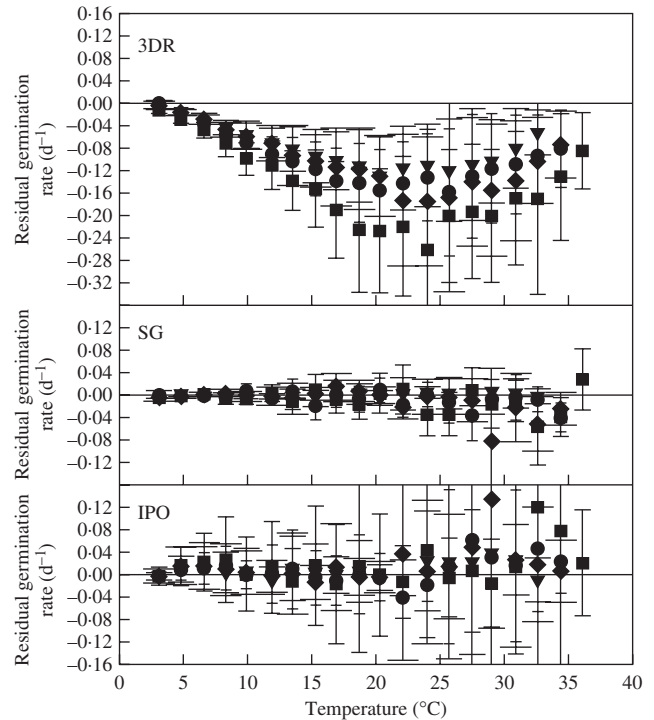


FIG. 4. Residual-model error in germination rate as a function of temperature and model for *E. lanceolatus* (●, small error bars), *P. spicata* (■, medium-small error bars), *P. secunda* (▼, medium-large error bars) and *E. elymoides* (◆, large error bars). Error bars represent  $\pm 1$  s.d. from the mean. These data were derived from models parameterized with M data.

to linear interpolation between temperatures, and a probit distribution of  $\ln\theta$ . This also reduced any benefit from inclusion of interpolated data for IPO-model parameterization.

Direct parameterization with measured-subpopulation data is only possible with three-dimensional model formulations of the type tested in the current study. The PCT and SCT models tested by Hardegree (2006) required parameterization with interpolated-subpopulation data but could subsequently be used to estimate germination rate as a continuous function of subpopulation. PCT and SCT models, however, produced low model fit relative to NLR and PWL-model formulations, especially in the lowest-temperature treatment.

The 3DR and SG models tested here, and the NLR and PWL models tested by Hardegree (2006) are entirely empirical. It has been suggested by Alvarado and Bradford (2002) and Allen (2003) that CT-type probit models are superior to empirical models because CT-model coefficients can be linked to specific physiological mechanisms that determine thermal-rate response. Physiological relevance must be justified, however, by an acceptable level of conformance between measured and predicted germination response. Several authors have had to introduce some degree of empiricism to these models to compensate for poor model fit (Dahal and Bradford, 1994; Finch-Savage *et al.*, 1998; Kebreab and Murdoch, 1999; Grundy *et al.*, 2000; Alvarado and Bradford 2002) and

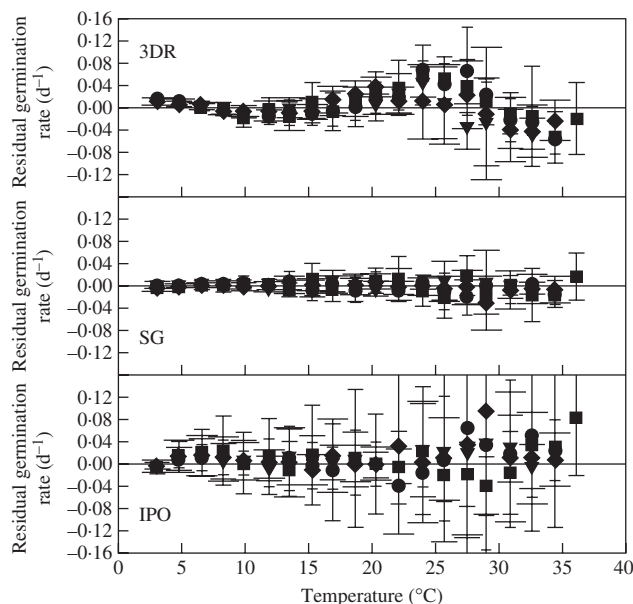


FIG. 5. Residual-model error in germination rate as a function of temperature and model for *E. lanceolatus* (●, small error bars), *P. spicata* (■, medium-small error bars), *P. secunda* (▼, medium-large error bars) and *E. elymoides* (◆, large error bars). Error bars represent  $\pm 1$  s.d. from the mean. These data were derived from models parameterized with IM data but residual error was only calculated for M-data values.

practical application may value predictive accuracy over physiological relevance (Finch-Savage *et al.*, 1993, 1998; Phelps and Finch-Savage, 1997; Forcella *et al.*, 2000).

The IPO model tested in the current study incorporated several CT-type model assumptions, but the physiological relevance of this model may have been degraded by the optimization procedure. In the IPO procedure, values for  $\theta_1$ ,  $\theta_2$  were optimized for maximum model fit based on iterative testing of alternative values of  $T_b$  and  $T_m$ . The resulting models retained the shape assumptions of a linear-temperature response, and a log-normal distribution of  $\theta$ , but at the expense of converting cardinal-temperature values to empirical coefficients. In the case of  $T_b$ , IPO-model estimates were systematically lower than the average estimate of  $T_b$  derived for any seedlot of the CT models described by Hardegree (2006). IPO estimates of  $T_b$  were also lower than all estimates extrapolated by the unconstrained cardinal temperature (UCT) model for any individual subpopulation for all species except *P. secunda*. In addition, separate optimization procedures at sub- and supra-optimal temperatures made it impossible to resolve a single value of  $T_o$  for individual subpopulations (Fig. 1). The most likely cause of low CT-model fit at 3 °C, however, appears to be curvilinearity in rate response at low temperature (Hardegree, 2006). The IPO model was more accurate than the PCT-, SCT- and UCT-model formulations at 3 °C (Hardegree, 2006) but this was an artefact of the optimization procedure which simultaneously resulted in overestimation of the germination rate between 5 and 10 °C (Figs 2 and 3).

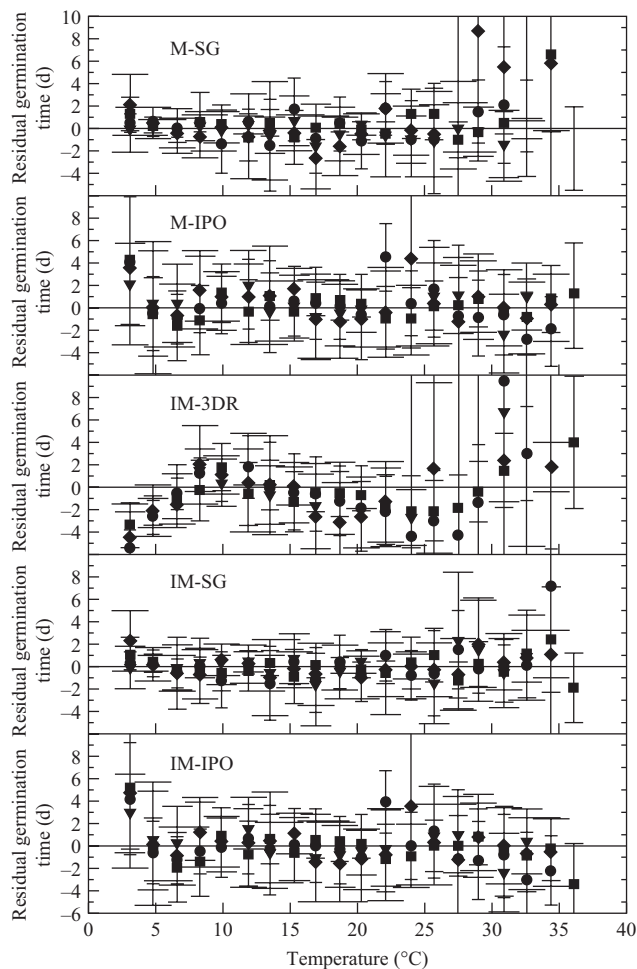


FIG. 6. Residual-model error in germination time as a function of temperature, input-parameter dataset (M, IM) and model (3DR, SG, IPO) for *E. lanceolatus* (●, small error bars), *P. spicata* (■, medium-small error bars), *P. secunda* (▼, medium-large error bars) and *E. elymoides* (◆, large error bars). Error bars represent  $\pm 1$  s.d. from the mean. Residual errors for models parameterized with IM data were only calculated for M-data values.

One clear advantage of CT-type models is that they produce coefficients that can be used directly for seedlot comparison or for screening germplasm (Covell *et al.*, 1986; Ellis *et al.*, 1986, 1987; Ellis and Butcher, 1988; Jordan and Haferkamp, 1989; Craufurd *et al.*, 1996; Fidanza *et al.*, 1996; Holshauser *et al.*, 1996; Steinmaus *et al.*, 2000; Phartyal *et al.*, 2003). Hardegree *et al.* (2003) suggested an alternative method of comparing seedlots for empirical models that do not yield comparable model coefficients. Hardegree *et al.* (2003) used an empirical model to estimate hydrothermal-germination response as a function of planting date for a 38-year simulation of seedbed microclimate. This approach yields comparative statistics for evaluating ecological responsiveness under a wide range of potential microclimatic conditions in the field. Long-term ecological simulations of this type benefit greatly from the computational efficiency obtained with the more empirical, three-dimensional model formulations.

It is concluded that the SG model had the best combination of efficiency and accuracy of the models tested here and by Hardegree (2006) for predicting thermal-germination response. The PWL model was slightly more accurate than the SG model at extreme temperatures (Hardegree, 2006) but this was most apparent in the supra-optimal temperature range which may be of little practical importance given the early-spring emergence syndrome for these species (Hardegree *et al.*, 2003). The SG-model formulation was the most efficient of all models tested in both the procedure used to parameterize the model and the procedure used to estimate germination rate and germination time.

## CONCLUSIONS

Subpopulation-specific regression has been used previously to estimate cumulative-germination response to temperature (Hardegree, 2006). The most accurate model of this type, previously tested by McDonald (2002) and Hardegree (2006), was relatively inefficient and could only be used to estimate germination rate for the specific subpopulations used in model development. Cardinal-temperature germination models can be used to estimate germination rate as a continuous function of subpopulation, but require adoption of a number of *a priori* shape assumptions that cause relatively large predictive errors in germination rate and germination time, especially at low temperature. The most accurate models for predicting germination rate and germination time appear to be those models that contain the fewest *a priori* assumptions about model shape. Of these, the statistical gridding technique was both the most accurate and efficient. This model has significant advantages over some previous models for estimation of cumulative germination time.

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