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Using thermal time models to predict seedling emergence of orchardgrass (*Dactylis glomerata* L.) under alternating temperature regimes

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Abstract

The effects of alternating temperatures on seed dormancy changes, germination and seedling emergence were investigated in 'Arctic' and 'Lineta' orchardgrass (*Dactylis glomerata* L.). Thermal time models were successfully developed for 0, 5, 10 and 15°C temperature amplitudes, using 28 constant and alternating temperature regimes. These models were then modified by linking seed germination in Petri dishes and seedling emergence in soil. A field experiment was conducted with four seeding dates over 2 years to validate the modified thermal time models. Temperature regimes with a 5–15°C amplitude enhanced seed germination percentages of orchardgrass, indicating that the conditional dormancy was released by these temperature regimes. Base temperatures decreased with increasing temperature amplitude. Seeds germinated more rapidly under alternating temperatures than under constant temperatures. The dual effects of temperature for dormancy breaking and germination were accounted for by thermal time models based on alternating temperature regimes, which accurately predicted the timing and percentage of 'Arctic' and 'Lineta' orchardgrass seedlings emerging in the field ($R^2 \geq 0.88$).

Keywords: alternating temperature, *Dactylis glomerata*, dormancy, seed germination, thermal time model

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Introduction

Seedling emergence of conditionally dormant seeds in the field is the combined result of dormancy release, seed germination and seedling growth. Among environmental factors in the field, soil temperature is most important in regulating seedling emergence when water is not limiting (Vleeshouwers and Kropff, 2000), but temperature is highly variable in the field, especially at the soil surface. Temperatures in the field regulate germination of seeds with dormancy in two ways: breaking dormancy by fluctuating temperatures (Benech Arnold *et al.*, 1988) and determining the germination rate of seeds after dormancy has been released (Garcia-Huidobro *et al.*, 1982a).

Changes in seed dormancy and germination can be influenced by the components of the alternating temperature regimes, including mean temperature, maximum and minimum temperatures, amplitude and thermoperiod (Roberts and Totterdell, 1981; Murdoch *et al.*, 1989). At suboptimal temperatures, the maximum percentage of germination (Murdoch *et al.*, 1989) and germination rate (Garcia-Huidobro *et al.*, 1982b) increase with increasing amplitude of alternating temperatures. A study of 34 *Carex* species revealed that alternating temperatures enhanced germination percentages, and an increase in the temperature amplitude increased germination (Schutz, 2000). In contrast, the percentage germination of four *Orobanche* species at a given mean temperature was higher at constant than at alternating temperatures (Kebreab and Murdoch, 1999a). These authors suggested that alternating temperatures with certain amplitude can be inhibitory, and the prolonged time that seeds spent at the maximum temperature can also reduce germination.

Thermal time has been widely used to model dormancy changes (Pritchard *et al.*, 1996; del Monte and Tarquis, 1997; Bauer *et al.*, 1998; Pritchard *et al.*, 1999; Steadman, 2004) and seed germination

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(Garcia-Huidobro *et al.*, 1982a; Ellis *et al.*, 1986; Wang *et al.*, 2004). For seeds with dormancy, models were usually constructed after dormancy release treatments (Welbaum and Bradford, 1991; Pritchard *et al.*, 1999). However, the effects of temperature on dormancy change and germination occur simultaneously under field conditions, and it is impossible to separate the germination of seeds released from dormancy by field temperature conditions from that of non-dormant seeds. The dual functions of temperature in dormancy change and germination make it difficult to predict quantitatively seedling emergence in the field using thermal time models. Thermal time models that are based on seed germination after dormancy release treatments do not truly reflect the effect of alternating temperatures on seedling emergence in the field. Therefore, the dual roles of the temperature must be considered for seeds with dormancy, if thermal time models are to predict accurately seedling emergence in the field (Finch-Savage and Phelps, 1993; del Monte and Tarquis, 1997; Grundy *et al.*, 2000). It is also possible that alternating temperature regimes may modify thermal time requirements of seeds for germination, compared to constant temperatures, because of the effect of alternating temperature on dormancy release. Given the complexity of seedling emergence as affected by pre- and post-germination events in the field, it is necessary to modify germination-based thermal time models.

Orchardgrass (*Dactylis glomerata* L.) was chosen to quantify the effects of temperature on changes in seed dormancy and germination using a thermal time model, because of the variable dormancy levels within seed populations and among cultivars in this species. Seed dormancy of this species can be broken by alternating temperatures (Pannangpetch and Bean, 1984; Probert *et al.*, 1985a, b). According to Benech-Arnold *et al.* (2000), seeds that can germinate over a wider range of conditions have less dormancy. It was hypothesized that: (1) the base temperature for seed germination can be modified by alternating temperatures; (2) the dual roles of temperature on dormancy and germination of orchardgrass can be described by a thermal time model; and (3) a thermal time model constructed using germination at alternating temperatures can be used to predict seedling emergence of orchardgrass in the field.

Materials and methods

Seed sources

Certified seeds of two cultivars of orchardgrass, 'Arctic' and 'Lineta', were used in this experiment. Seeds were cleaned using a seed blower by controlling airflow at a fixed speed for 1.5 min. Light seeds blown into the upper container of the blower were discarded, and the heavy seeds left in the lower container were saved. The dry weight of the seeds used for experimentation averaged 0.91 ± 0.06 (mean $\pm$ SE) and 0.94 ± 0.03 mg seed^{-1} for 'Arctic' and 'Lineta', respectively. Cleaned seeds were stored in darkness at -18°C until use.

Seed germination tests for model construction

Germination tests were conducted at 28 constant and alternating temperature regimes (12/12 h) in growth chambers (Sanyo Versatile Environment Chamber MLR-350H, Sanyo Scientific, USA). Constant temperatures in 5°C increments between 0 and 35°C and alternating temperatures with amplitudes from 5 to 20°C were used (Table 1). A randomized complete block design (RCBD) with five replicates was used, and replicates were put into growth chambers at weekly intervals. Designated temperatures were randomly allocated to each growth chamber (one chamber for each temperature treatment). For each replicate, a unit of 50 seeds was imbibed on two layers of filter paper (Whatman No. 1) in 9 cm plastic Petri dishes. The filter paper was moistened with 5 ml of distilled water, and seeds were then carefully spread on the filter paper. Ten Petri dishes (two cultivars × five replicates) were randomized within each chamber in darkness. Petri dishes were enclosed and sealed in clear plastic bags to reduce water evaporation. Seeds were sprayed with 0.05% benomyl solution at the beginning of the tests and whenever there was visible microbial growth during incubation.

Germinated seeds were counted and removed at 24-h intervals. Seeds with coleoptiles greater than 3 mm were considered germinated. Distilled water was added when necessary to keep the filter paper wet. Germination tests were terminated when no seeds had germinated for 14 consecutive days.

Table 1. Treatment design of constant and alternating temperatures with temperature amplitudes from 0 to 20°C and 5°C increments

Mean temperature (°C)	Temperature amplitude (°C)				
	0	5	10	15	20
0	0/0				
5	5/5	2.5/7.5	0/10		
10	10/10	7.5/12.5	5/15	2.5/17.5	0/20
15	15/15	12.5/17.5	10/20	7.5/22.5	5/25
20	20/20	17.5/22.5	15/25	12.5/27.5	10/30
25	25/25	22.5/27.5	20/30	17.5/32.5	15/35
30	30/30	27.5/32.5	25/35		
35	35/35				

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Linking seed germination to seedling emergence

A growth chamber experiment was designed to establish the relationship of thermal time for seed germination in darkness in Petri dishes and seedling emergence from soil. A RCBD with five replicates was used, and replicates were put into growth chambers at weekly intervals. Four treatments (two cultivars × two germination media) were applied to two temperature regimes (5/15 and 15/25°C). Field-collected soil was air dried, passed through a 5-mm sieve and placed in seeding trays, before water was added to bring the soil water potential to −0.03 MPa. Fifty seeds were spread on the soil surface and covered with 1 cm of soil. Petri dishes and trays containing soil were placed randomly in growth chambers. Seeds with coleoptiles greater than 3 mm in Petri dishes and seedlings visible at the soil surface were considered germinated or emerged, respectively. Seed germination and seedling emergence were recorded daily, and the experiment was terminated after no new seeds germinated or seedlings emerged for 14 consecutive days. Germinated seeds or emerged seedlings were removed after each counting, and water was added to Petri dishes or soil when necessary.

Statistical analysis and model development

For modelling purposes, a seed population was considered to be composed of subpopulations because of differences in their relative germination rate (Garcia-Huidobro *et al.*, 1982b). The germination rates for different subpopulations g [$GR_{(g)}$] were calculated as the reciprocal of germination time ($1/t_g$). The germination time for each subpopulation was calculated based on the Chapman–Richards function, and used to calculate the germination rate for the construction of a thermal time model. The Chapman–Richards growth function (Richards, 1959) takes the following form:

$$g = m\{1 - \exp[-nt_{(g)}]\}^p \quad (1)$$

where g = germination percentage, $t_{(g)}$ = time, m = the asymptote, n = the rate parameter and p = the shape parameter. The three parameters, m, n and p, are constants. A sigmoidal growth form has an asymptote (parameter m) for the maximum germination percentage. The n and p parameters together define the shape of the curve.

A non-linear regression procedure with the Levenberg–Marquardt algorithm method (Marquardt, 1963; PROC NLIN, SAS/STAT software Version 8.2 for Windows, SAS Institute, Cary, North Carolina, USA) was used to estimate germination time (t_g) for the 10, 20, 30, 40, 50, 60, 70, 80 and 90% subpopulations wherever available. The Levenberg–Marquardt (LM) algorithm is an iterative procedure that locates a local minimum of a function (the Chapman–Richards function, in this case) that is expressed as the sum of squares of non-linear functions. Multiple starting values for parameters were provided to ensure that the non-linear least square solution was a global minimum, rather than a local minimum (Schabenberger and Pierce, 2002).

The base temperature (T_b) and thermal time of different subpopulations at constant and alternating temperatures were estimated using extrapolation (graphical) methods (Garcia-Huidobro *et al.*, 1982a, b; Kebreab and Murdoch, 1999b; Steinmaus *et al.*, 2000). The intercept of the linear regression line is T_b, and the slope of the regression line is the thermal time [$\theta_{(g)}$]:

$$\overline{T} = T_b + \theta_{(g)}GR_{(g)} = T_b + \theta_{(g)}/t_{(g)} \quad (2)$$

A sum of squares reduction test (Schabenberger and Pierce, 2002) was used to assess if there was a common T_b among the subpopulations. The full model was composed of different T_b and $\theta_{(g)}$ values for subpopulations. The reduced model was composed of a common T_b, but different slopes, for the subpopulations. The following equation was used for the sum of squares (SS) reduction test:

$$F = \{[SS_{(Residual)}\text{Reduced} - SS_{(Residual)}\text{Full}]/ [df_{(Residual)}\text{Reduced} - df_{(Residual)}\text{Full}]\}/ \text{MSError}_{(Full)} \quad (3)$$

If this test showed that the full and reduced models were not significantly different ($P \leq 0.05$), a common T_b was used for all subpopulations, and slopes of subpopulations based on the common T_b were $\theta_{(g)}$.

Thermal time models for seed germination were constructed for each temperature amplitude and cultivar, using the Chapman–Richards growth function. The model takes the following form:

$$g = a\{1 - \exp[-b\theta_{(g)}]\}^c \quad (4)$$

where g = germination percentage, $\theta_{(g)}$ = thermal time for subpopulation g, a = the asymptote, b = the rate parameter and c = the shape parameter. The three parameters, a, b and c, are constants.

Thermal time models for seed germination developed under controlled conditions must be modified before being applied to seedling emergence. The germination/seedling emergence time (t_g) for different subpopulations in Petri dishes and seedling emergence in the soil were estimated with non-linear regression using the Levenberg–Marquardt algorithm method (Marquardt, 1963; PROC NLIN, SAS/STAT software Version 8.2 for Windows). Thermal time for seed germination and seedling emergence was

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calculated from equation (5):

$$y = (\overline{T} - T_b)t_{(g)} \quad (5)$$

where y = the thermal time for seed germination in the Petri dish, or the thermal time for seedling emergence in soil, $\overline{T}$ = average temperature, T_b = base temperature [obtained from equation (2)], and $t_{(g)}$ = the germination/seedling emergence time for certain subpopulations of seeds germinated in Petri dishes or seedlings emerged in the soil.

The required thermal time for the corresponding subpopulations between seed germination in the Petri dish and seedling emergence in soil was expressed better by the Chapman–Richards function, compared to linear and other exponential functions in this study. The Chapman–Richards function has the following form:

$$y = \alpha(1 - \exp(-\beta x))^{\gamma} \quad (6)$$

where y = the thermal time for seed germination in the Petri dish, α = the asymptote, β = the rate parameter and γ = the shape parameter, and x = the thermal time for seedling emergence in soil.

According to equation (4), the final function of thermal time model for seedling emergence in the field was modified as equation (7):

$$\text{seedling emergence}\,(\%) = a(1 - \exp(-by))^{c} \quad (7)$$

where all constants (a, b and c) were from the thermal time models constructed using equation (5) (Table 2), and y = the relative thermal time for germination in the Petri dish in equation (6).

Model validation

Field trials were conducted at the field experimental station of Agriculture and Agri-Food Canada, Saskatoon Research Centre, Saskatoon, Canada. Four seeding dates were conducted in 2003 and 2004. Seeds were sown on 3 May, 15 May, 27 May and 8 June 2003; and 7 May, 19 May, 31 May and 10 June 2004. A RCBD with five replicates was used, and the plot size was 1.0 × 1.0 m. Eight treatments (two cultivars × four seeding dates) were randomly allocated to plots in each block within a year. Within each plot, 200 seeds were hand-sown at a 1-cm depth in four rows in each plot. Irrigation (10 litres plot^{-1}) was provided once a day to bring the top 2 cm of the soil to field capacity, unless there was a precipitation event > 5 mm in the previous 24 h, and the soil was near its field capacity.

Soil temperatures at the 1-cm sowing depth were recorded every hour using dataloggers (21X, Campbell Scientific Inc., Logan, Utah, USA). The average, maximum and minimum daily soil temperatures were used for thermal time model assessment. Seedling emergence in the field was monitored at 2-d intervals. Seedlings were counted as emerged when coleoptiles were visible from the soil surface, and seedlings were removed after each counting. The experiment was terminated after no new seedlings emerged for 14 consecutive days.

Modified thermal time models were used to predict seedling emergence in the field. The ability of the modified model to predict seedling emergence was determined by the coefficient of determination (R^2) of the linear regression analysis of the predicted against the observed seedling emergence. RMSE (root mean square error), SRES (sum of residuals) and SARES (sum of absolute residuals) between the predicted and observed seedling emergence were also calculated for each cultivar on each seeding date, to estimate the variation and accuracy of thermal time models (Oryokot *et al.*, 1997). A small RMSE indicates that predicted emergence is similar to the actual emergence (McMaster *et al.*, 1992). The SRES and SARES assess bias as follows: (1) if the SRES is smaller than the SARES, any errors tend to cancel one another; (2) when the SRES and SARES are large and the SARES is positive, the model underestimates seedling emergence; and (c) if the

Table 2. The estimated parameters (means ± SE) of thermal time models for 'Arctic' and 'Lineta' orchardgrass at different temperature amplitudes: T_b = base temperature; a = the asymptote; b = the rate parameter; and c = the shape parameter

Variety	Temperature amplitude (°C)	T_b (°C)	a	b	c
'Arctic'	0	3.6 ± 0.8	67.4 ± 7.0	0.024 ± 0.003	12.8 ± 3.0
	5	1.4 ± 0.3	87.2 ± 2.4	0.025 ± 0.001	16.9 ± 1.9
	10	−1.9 ± 0.7	84.7 ± 0.9	0.019 ± 0.000	18.9 ± 1.0
'Lineta'	0	0.9 ± 0.1	79.4 ± 0.5	0.034 ± 0.000	38.6 ± 1.2
	5	0.7 ± 0.1	93.9 ± 0.3	0.047 ± 0.004	91.5 ± 3.5
	10	−0.1 ± 0.2	89.2 ± 0.1	0.058 ± 0.000	305.4 ± 4.0
	15	−1.9 ± 0.4	91.6 ± 0.1	0.033 ± 0.000	42.8 ± 0.4

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SRES is negative and larger than the SARES, the model overestimates seedling emergence (McMaster *et al.*, 1992).

Results

Effects of temperature on germination percentage

Total germination of orchardgrass seeds varied among temperatures, and the range of temperatures for high germination varied between cultivars. Total germination showed bell-shaped responses to temperature (Fig. 1). Respectively, total germination of 'Arctic' and 'Lineta' orchardgrass averaged about 77 and 83% at 20°C, the optimal constant temperature.

Total germination for both cultivars was higher under alternating than under constant temperature regimes with the same mean temperature (Fig. 1). Germination increased by 10–60% in 'Arctic' orchardgrass and by 10–30% in 'Lineta' orchardgrass under alternating temperatures, as compared to constant temperatures. In both cultivars, alternating temperature regimes with mean temperatures between 10 and 25°C were optimal for total germination, and dormancy breaking by alternating temperatures was dependent on the mean temperature and the amplitude of temperature fluctuation among cultivars. A 5–10°C temperature amplitude broke dormancy in these cultivars, and further increasing the temperature amplitude did not increase germination.

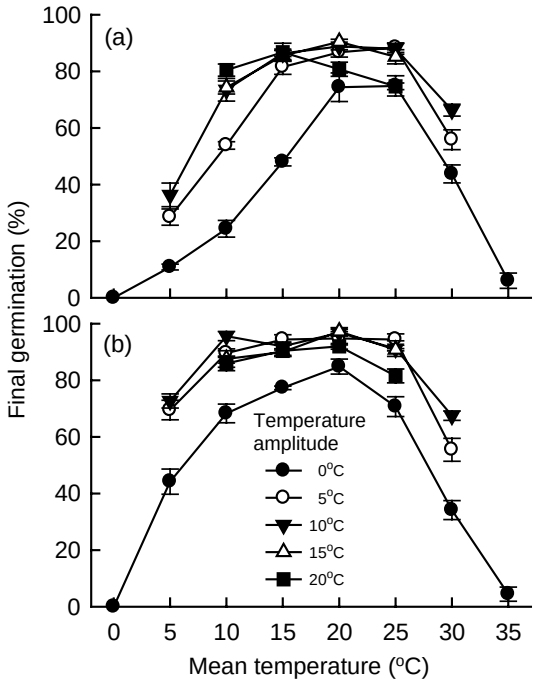


Figure 1. Total germination of (a) 'Arctic' and (b) 'Lineta' orchardgrass under temperature regimes with different temperature amplitudes. Data are means ± SE ($n = 5$).

Modelling seed dormancy change and seed germination as affected by temperature

The sum of squares reduction test showed that there were common T_b values among subpopulations at 0, 5 and 10°C amplitudes for 'Arctic' orchardgrass and at 0, 5, 10 and 15°C amplitudes for 'Lineta' orchardgrass. Therefore, reduced models were used to estimate T_b for the two cultivars at those temperature amplitudes (Figs 2 and 3). There were not sufficient data points to do regression analyses for 'Arctic' orchardgrass with the 15°C amplitude (Fig. 2d). Seed germination was limited in both cultivars when the temperature amplitude was 20°C; thus, T_b could not be estimated (data not shown).

The T_b of 'Arctic' orchardgrass differed significantly among temperatures with 0 (constant temperature), 5 and 10°C amplitudes; T_b decreased as the temperature amplitude increased (Table 2). The T_b of 'Lineta' orchardgrass also varied among 0, 5, 10 and 15°C amplitudes, declining as the amplitude increased.

Thermal times to germination for different subpopulations, based on the estimated T_b, were affected by temperature amplitude at the same mean temperature. Thus, thermal time models were constructed separately for each cultivar and temperature amplitude, using the Chapman–Richards growth function, and those models explained more than 95% of the variation in germination timing.

Modification of the thermal time model for seedling emergence

The temperature amplitude at the 1 cm depth in the soil, for each 36-d period of seedling emergence, averaged 11.7, 10.8, 11.1 and 11.5°C in 2003 and 11.1, 9.4, 10.3 and 11.6°C in 2004 for the four seeding dates, respectively (Fig. 4). Mean soil temperatures at the 1-cm depth were 14.0, 15.7, 17.6 and 17.8°C in 2003 and 9.4, 12.7, 14.4 and 16.2°C in 2004, respectively. Therefore, thermal time models based on the 10°C amplitude were judged most relevant to seedling emergence in the field.

The base temperature for seedling emergence of each cultivar was adopted from parameters in Table 2. The thermal times required for seedling emergence and seed germination corresponding to the same subpopulations were well correlated, with an exponential relationship using equation (6), for 'Arctic' ($R^2 = 0.62$) and 'Lineta' orchardgrass ($R^2 = 0.93$) (Fig. 5).

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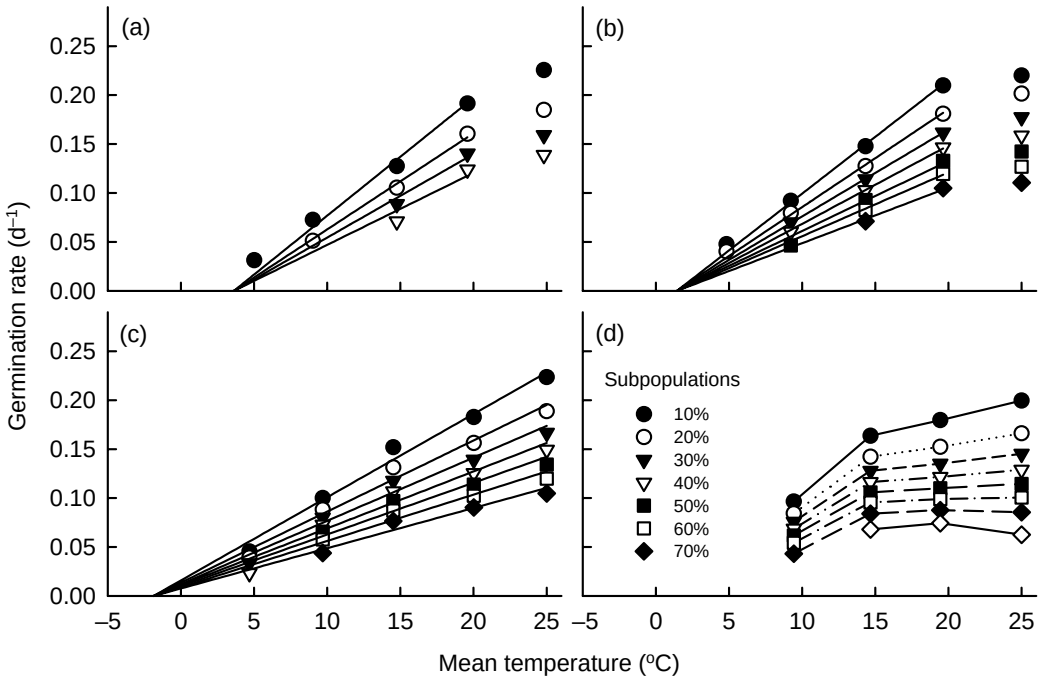


Figure 2. Germination rate (GR) of 'Arctic' orchardgrass within the range of suboptimal temperatures, as a function of temperature and subpopulation, with temperature amplitudes of (a) 0°C, (b) 5°C, (c) 10°C and (d) 15°C.

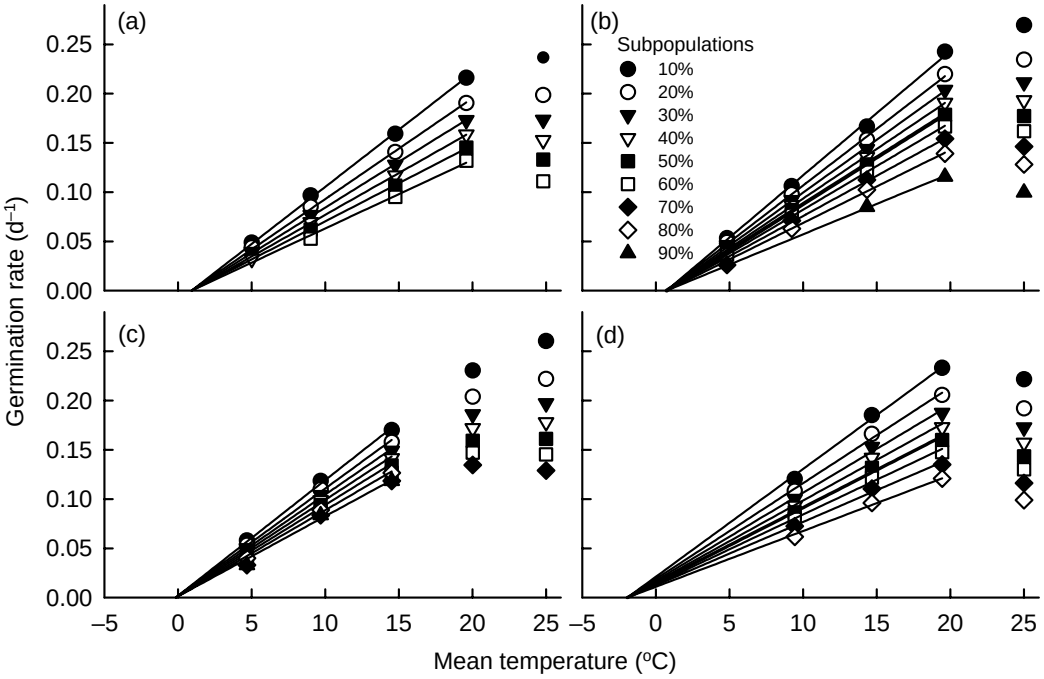


Figure 3. Germination rate (GR) of 'Lineta' orchardgrass within the range of suboptimal temperatures, as a function of temperature and subpopulation, with temperature amplitudes of (a) 0°C, (b) 5°C, (c) 10°C and (d) 15°C.

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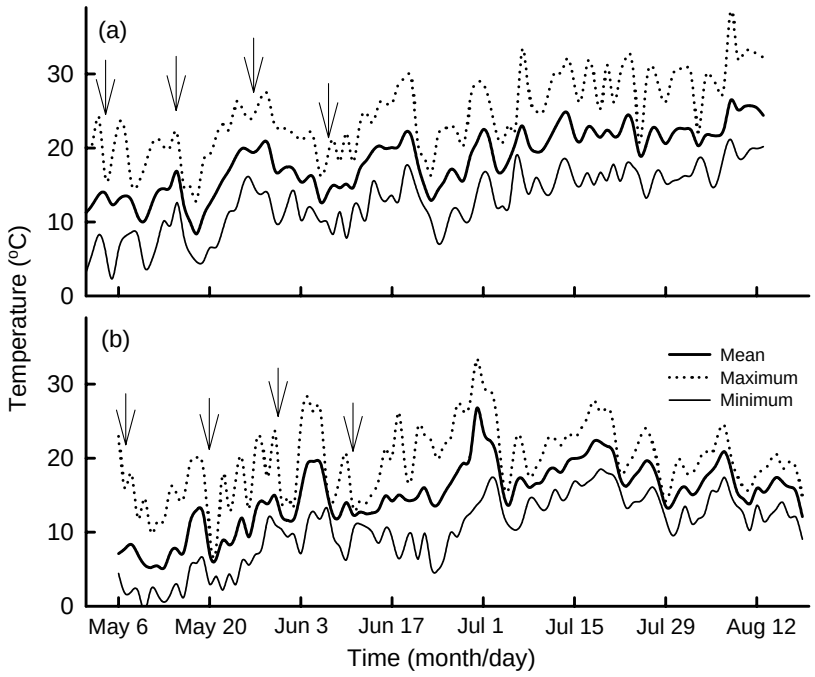


Figure 4. The daily mean, maximum and minimum temperatures at the 1-cm depth in the soil during the growing seasons of (a) 2003 and (b) 2004. Arrows indicate seeding dates (3 May, 15 May, 27 May and 8 June 2003; and 7 May, 19 May, 31 May and 10 June 2004).

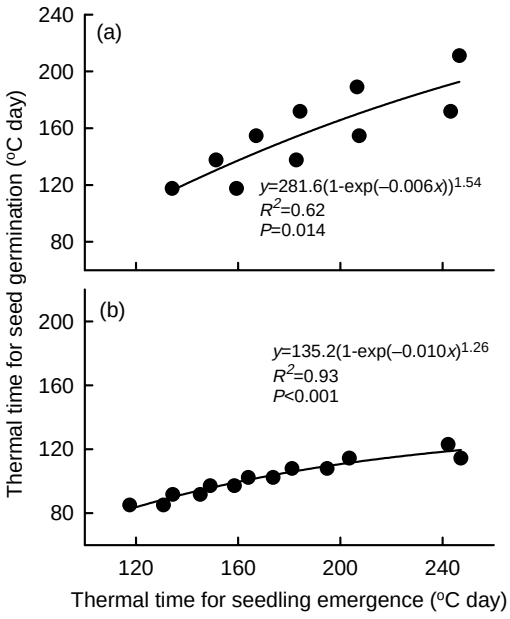


Figure 5. The relationship between the thermal times of seed germination, corresponding to the same subpopulation of seedling emergence, established using the Chapman–Richards function for (a) 'Arctic' and (b) 'Lineta' orchardgrass. Points were original data from seed germination and seedling emergence tests at 15/5 and 25/15°C.

The accuracy of modified thermal time models for predicting seedling emergence in the field

The modified thermal time models accurately predicted seedling emergence in the field as indicated by R^2 that ranged from 0.88 to 0.99 (data not shown). The RMSE was $<15\%$, indicating that the predicted and measured seedling emergence was similar (Figs 6 and 7). However, seedling emergence for 'Arctic' orchardgrass was overestimated on the fourth seeding date in 2003 (Fig. 6d), and underestimated for the first seeding date in 2004 (Fig. 6e). Seedling emergence was underestimated in 'Lineta' orchardgrass for the first two seeding dates in 2004 (Fig. 7e, f).

Discussion

Total germination and the rate that seeds germinated were higher under alternating temperatures than under constant temperatures for 'Arctic' and 'Lineta' orchardgrass, indicating that alternating temperatures break seed dormancy and accelerate the rate of germination in these cultivars of orchardgrass. After seed dormancy is broken, final germination is usually similar between alternating and constant temperatures, as demonstrated in *Orobanche* (Kebreab and Murdoch, 1999b), implying that the increment of the final germination in dormant seeds at a given mean

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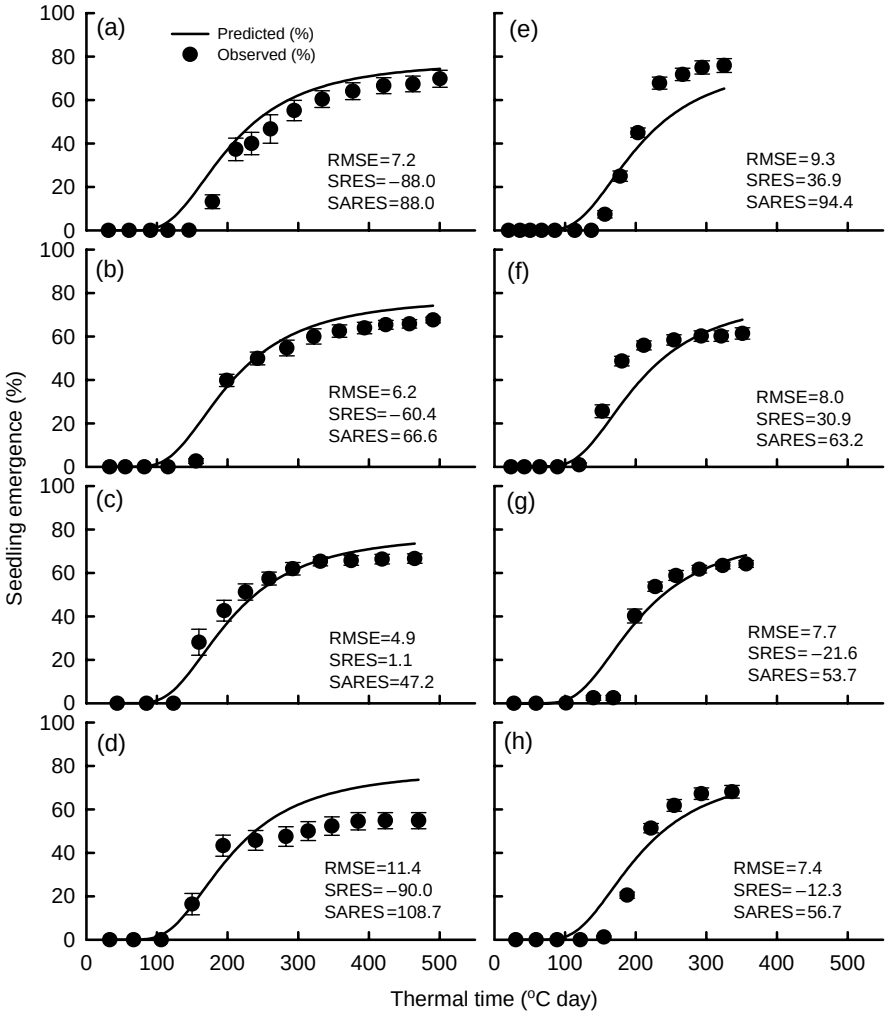


Figure 6. Predicted and observed seedling emergence for 'Arctic' orchardgrass in the field for seeding dates on (a) 3 May, (b) 15 May, (c) 27 May and (d) 8 June 2003; and on (e) 7 May, (f) 19 May, (g) 31 May and (h) 10 June 2004. Data are means ± SE ($n = 5$). Predicted seedling emergence was estimated using the modified thermal time model with a 10°C amplitude. RMSE is the root mean square error, SRES is the sum of the residuals and SARES is the sum of the absolute residuals.

temperature is probably due to more dormancy being alleviated by the alternating than constant temperatures.

The optimal mean temperature of 10–25°C for germination of orchardgrass seeds in this study agrees with previous reports (Pannangpetch and Bean, 1984). In the present study, total germination of both cultivars increased as the temperature amplitude increased from 0 to 10°C, but it did not increase further when the amplitude increased above 10–15°C. This germination response contrasts with European populations of orchardgrass, in which germination declined as the amplitude of temperature increased above 5–10°C, possibly due to the interaction between alternating temperature and light in that study (Probert *et al.*, 1985b). Wide temperature amplitudes also inhibit seed germination in *Orobanche* species (Kebreab and Murdoch, 1999a).

T_b values decreased from 3.6 to −1.9°C in 'Arctic' and from 0.9 to −0.1°C in 'Lineta' as temperature amplitudes increased from 0 to 10°C. T_b varies among species and genotypes, and seed treatment for dormancy release can modify the base temperature for seeds (Welbaum and Bradford, 1991; del Monte and Tarquis, 1997; Pritchard *et al.*, 1999; Hardegree *et al.*, 2002; Steadman and Pritchard, 2004). After-ripening of mature muskmelon (*Cucumis melo* L.) seeds reduced the estimated T_b by about 5°C, and it broadened the range of temperatures and water potentials under which seeds germinated (Welbaum and Bradford, 1991). Stratifying horse chestnut (*Aesculus hippocastanum* L.) seeds at 6°C increased the

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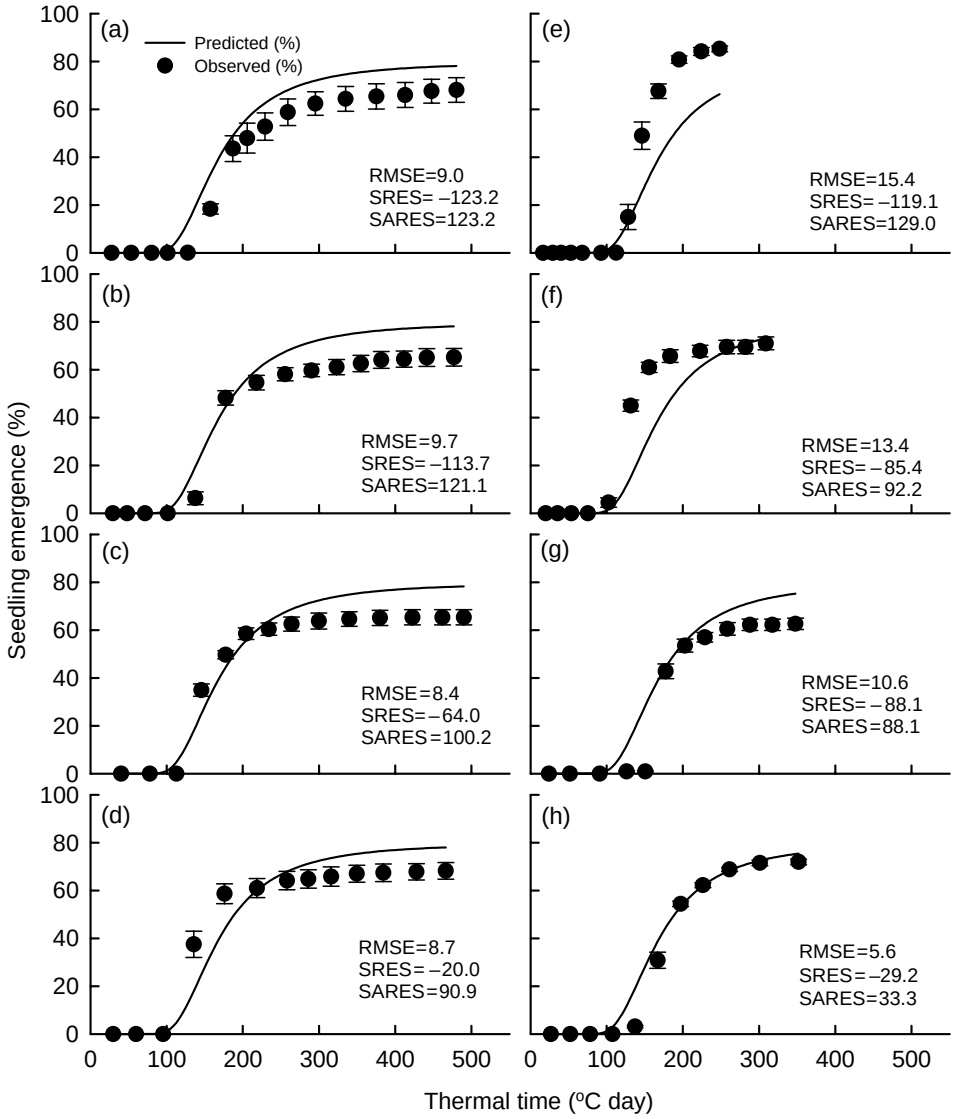


Figure 7. Predicted and observed seedling emergence for 'Lineta' orchardgrass in the field for seeding dates on (a) 3 May, (b) 15 May, (c) 27 May and (d) 8 June 2003; and on (e) 7 May, (f) 19 May, (g) 31 May and (h) 10 June 2004. Data are means ± SE ($n = 5$). Predicted seedling emergence was estimated using the modified thermal time model with a 10°C amplitude. RMSE is the root mean square error, SRES is the sum of the residuals and SARES is the sum of the absolute residuals.

germination rate, and T_b was decreased by 1°C for every 6 d of stratification (Pritchard *et al.*, 1999). Thus, T_b can be used to explain the physiological mechanisms of dormancy change or seed germination following treatments that release dormancy (Bradford, 2005). Base temperatures of both orchardgrass cultivars decreased as the temperature amplitude increased, indicating that alternating temperatures break seed dormancy, enhance germination and enable seeds to accumulate thermal time faster than at constant temperatures with the same mean temperature. A lower T_b widens the temperature range for germination.

The common T_b among subpopulations in orchardgrass was determined using the sum of squares reduction test. The method presented in the current study has several advantages for estimating T_b, compared to the use of T_b for the median (50%) subpopulation (Ellis and Butcher, 1988; Finch-Savage *et al.*, 1998), mean T_b of all subpopulations (Garcia-Huidobro *et al.*, 1982a, b; Wang *et al.*, 2004), or the best fit T_b using the screen method (Ellis *et al.*, 1986; Dahal *et al.*, 1990). In addition, the 95% confidential intervals for all parameters can be calculated, allowing comparison of parameters between treatments and seedlots.

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The thermal time model developed in this study used non-linear regression analysis with the Chapman–Richards growth function. Changes in daily germination and germination rate can be reflected in the first and second derivative Chapman–Richards function, respectively (Coble, 2004). Because of its sigmoidal flexibility in shape and its biological and statistical properties, the Chapman–Richards growth function is commonly used in other biological processes (Payandeh and Wang, 1994; Lee, 2002).

The modified thermal time model accurately predicted seedling emergence in the field for both orchardgrass cultivars when soil water was not limiting. The high correlation between germination tests and seedling emergence in the field is attributed to the use of alternating temperature regimes for constructing thermal time models and the modification of thermal time models. It should be noted that there are potential problems in using the cardinal temperatures concept when alternating temperatures go from sub- to supra-optimal. However, field temperatures in this study were low enough that the issue was only of marginal concern. Fluctuating temperatures in the field can break seed dormancy and promote non-dormant seeds to germinate (Bouwmeester and Karssen, 1992). The value of T_b was decreased by alternating temperature, resulting in greater germination percentages and rates in orchardgrass. Therefore, the use of alternating temperatures in the laboratory to mimic fluctuating temperatures in the field is appropriate for seedling emergence studies of species with seed dormancy.

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