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Quantitative Description of the Germination of Littleseed Canarygrass (*Phalaris minor*) in Response to Temperature

Abolfazl Derakhshan, Javid Gherekhloo, Ribas A. Vidal, and Rafael De Prado*

Littleseed canarygrass is a troublesome grass weed in wheat fields in Iran. Predicting weed emergence dynamics can help farmers more effectively control weeds. In this work, four nonlinear regression models (beta, three-piece segmented, two-piece segmented, and modified Malo's exponential sine) were compared to describe the cardinal temperatures for the germination of littleseed canarygrass. Two replicated experiments were performed with the same temperatures. An iterative optimization method was used to calibrate the models and different statistical indices (mean absolute error [MAE], coefficient of determination [R^2], intercept and slope of the regression equation of predicted vs. observed hours to germination) were applied to compare their performance. The three-piece segmented model was the best model to predict the germination rate (R^2 = 0.99, MAE = 0.20 d, and coefficient of variation 1.01 to 4.06%). Based on the model outputs, the base, the lower optimum, the upper optimum, and the maximum temperatures for the germination of littleseed canarygrass were estimated to be 4.69, 22.60, 29.62, and 38.13 C, respectively. The thermal time required to reach 10, 50, and 90% germination was 31.98, 39.26 and 45.55 degree-days, respectively. The cardinal temperatures depended on the model used for their estimation. Overall, the three-piece segmented model was better suited than the other models to estimate the cardinal temperatures for the germination of littleseed canarygrass.

Nomenclature: Littleseed canarygrass, *Phalaris minor* Retz.
Key words: Cardinal temperatures, germination rate, modeling, temperature function, thermal time.

Weed seed germination is a key process because it determines both the number of weeds that could potentially emerge and the timing of their appearance in the field (Gardarin et al. 2011). Germination will be defined in the physiological sense as the initiation of embryo growth and is completed by penetration of the embryo through any covering tissues. Seed germination is responsive to many environmental signals, including temperature (T), water potential (ψ), light, nitrate, smoke, and other factors (Bewley and Black 1994). T is the single most important factor regulating the germination of nondormant seeds in irrigated annual agroecosystems at the beginning of the growing season, when light, nutrients, and moisture are typically not growth-limiting (Garcia-Huidobro et al. 1982). Roberts (1988) recognized three separate physiological processes in seeds affected by T: seed decay, dormancy status, and germination. First, T and moisture content determine the rate of deterioration in all seeds. Second, T affects the rate of dormancy loss in dry seeds and the pattern of dormancy change in moist seeds. Third, in nondormant seeds, T determines the rate of germination.

The effects of T on plant development are the basis for models used to predict the timing of germination. Minimum, optimum, and maximum T (cardinal temperatures) describe the range of this environmental variable over which seeds of a particular species can germinate (Bewley and Black 1994). The minimum (or base, T_b) and maximum (or ceiling, T_c) T are the temperatures below or above which the germination will not occur, whereas the optimum (To) T is that at which germination is most rapid. The seed germination rate is proportional to T: it increases in the suboptimal range and decreases above the optimum (Bradford 2002). The cardinal temperatures for germination are generally related to the environmental range of adaptation of a given species and serve to match the germination timing to favorable conditions for subsequent seedling growth and development (Alvarado and Bradford 2002). To accurately predict plant phenology, a nonlinear function is needed to describe the development rate over the full range of temperatures for plant

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* First and second authors: Graduate Student and Assistant Professor, Department of Plant Production, Gorgan University of Agricultural Sciences and Natural Resources, Gorgan, Iran; third author: Professor, Federal University at Rio Grande do Sul, Porto Alegre, Brazil; fourth author: Professor, University of Cordoba, Cordoba, Spain. Corresponding author's E-mail: derakhshan.abo@gmail.com

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development (Jame and Cutforth 2004). The thermal time model has been implemented successfully in predicting the phenology of crops and weeds, as well as seed germination under non–water-limiting conditions (Garcia-Huidobro et al. 1982).

Littleseed canarygrass is a serious grass weed of wheat in more than 60 countries (Singh et al. 1999). There is little information available with regard to the cardinal temperatures for littleseed canarygrass germination. This study was performed to evaluate and compare nonlinear regression models that can be used to quantify the cardinal temperatures for the germination of littleseed canarygrass.

Materials and Methods

Cardinal Temperatures Determination. Two replicated experiments were performed to determine the cardinal temperatures of littleseed canarygrass. The seeds of littleseed canarygrass were collected from several wheat fields located in Gorgan, northern Iran, at the time of their natural dispersal in June 2012. After harvest, the seeds were bulked, cleaned manually, placed in a paper bag, and stored at room T. Freshly harvested seeds exhibited dormancy that was relieved (97% germination) after 2 min seed scarification with undiluted sulfuric acid (98%). The experiments were conducted using germinators with controlled environments at the Seed Technology Laboratory, Gorgan University of Agricultural Sciences and Natural Resources, Iran. In each replication of the experiment, four replicates of 50 seeds were germinated in 9-cm-diam petri dishes on two layers of Whatman Cat. No. 1 (9-cm diam) filter paper containing 5 ml distilled water. The germination response was evaluated at eight constant temperatures of 5, 7, 10, 15, 20, 25, 30, and 35 C.

A seed was considered germinated when its radicle protruded through the seed coat by at least 2 mm. The germinated seeds were counted in different time intervals based on the observed germination rate under different temperatures, with shorter (4-h) and longer (8-h) periods for higher and lower temperatures, respectively. The counting concluded when no seed germinated over three consecutive days. The cumulative germination percentage was plotted against time (in hours). From this curve, the time to 50% germination (t_{50}) was determined by fitting a Weibull equation to cumulative germination percentage (G) against time (t, in hours) according to Guillemin et al. (2012):

$$\begin{aligned} &G = 0 \quad \text{if} \quad t < t_0, \\ &G = m\left[1 - e^{-\ln(2) \times (t - t_0/t_{50} - t_0)^b}\right], \quad \text{if} \quad t > t_0 \end{aligned} \qquad [1]$$

where m is the maximum germination percentage, t_0 is the time between the beginning of the incubation and the first germination and b is shape parameter. The times for 10, 30, 70, and 90% germination were also determined by interpolation and are designated t_{10}, t_{30}, t_{70}, and t_{90}, respectively.

The reciprocal of the time taken for a given fraction of the seed population to germinate was considered to be the germination rate (*GR*). To quantify the response of the germination rate to T and to determine the cardinal temperatures for germination, the following model was used:

$$GR = f(T)/f_o \qquad [2]$$

where $f(T)$ is a T function (reduction factor) that ranges between 0 at T_b and T_c and 1 at the optimal temperature (or temperatures), and $1/f_o$ is the inherent maximum rate of germination at the optimal T estimated via an iterative optimization method. Therefore, f_o indicates the minimum number of hours for germination at the optimal T (Soltani et al. 2006). The GR also shows germination rate of a given percentile.

SigmaPlot software (Sigma Plot 2002 for Windows, Version 8.0, SPSS Inc., 233 South Wacker Drive, 11th Floor, Chicago, IL 60606-6307) was used to calibrate the models (beta, three-piece segmented, two-piece segmented, and a modified Malo's exponential sine [ExpSine]) via an iterative optimization method (Table 1). To determine the best estimates of the parameters (lower biases of the intercept from 0 and the slope from 1 are criteria for increased reliability), the MAE (Equation 3), the coefficient of determination (R^2; Equation 4), and the intercept and slope of the regression equation of predicted vs. observed hours to germination were used. MAE was used because it avoids compensation between probable under- and overprediction as follows:

$$\text{MAE} = 1/n \sum_{i=1}^{n} |Di| \qquad [3]$$

and

$$R^2 = SSR/SST \qquad [4]$$

where *Di* is the difference between measured and calculated values, *SSR* is the sum of squares (*SS*) of

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Table 1. Beta, three-piece segmented, two-piece segmented and Malo's exponential sine (ExpSine) models that were fitted to germination rate vs. different constant temperatures.

Reference	Formula[a]	Function
Yin et al. 1995	$f(T)=[(\mathrm{T}-\mathrm{T_b})/(\mathrm{T_o}-\mathrm{T_b})][(\mathrm{T_c}-\mathrm{T})/\mathrm{T_c}-\mathrm{T_o}]^{[(\mathrm{T_c}-\mathrm{T_o})/\mathrm{T_o}-\mathrm{T_b}]c}$	Beta
Piper et al. 1996	$f(T) = (\mathrm{T} - \mathrm{T_b})/(\mathrm{T_{o1}} - \mathrm{T_b})$ if $\mathrm{T_b} < \mathrm{T} < \mathrm{T_{o1}}$ $f(T) = (\mathrm{T_c} - \mathrm{T})/(\mathrm{T_c} - \mathrm{T_{o2}})$ if $\mathrm{T_{o2}} < \mathrm{T} < \mathrm{T_c}$ $f(T) = 1$ if $\mathrm{T_{o1}} \leq \mathrm{T} \leq \mathrm{T_{o2}}$ $f(T) = 0$ if $\mathrm{T} \leq \mathrm{T_b}$ or $\mathrm{T} \geq \mathrm{T_c}$	Three-piece segmented
Soltani et al. 2006	$f(T) = (\mathrm{T} - \mathrm{T_b})/(\mathrm{T_o} - \mathrm{T_b})$ if $\mathrm{T_b} < \mathrm{T} < \mathrm{T_o}$ $f(T) = 1 - (\mathrm{T} - \mathrm{T_o}/\mathrm{T_c} - \mathrm{T_o})$ if $\mathrm{T_o} \leq \mathrm{T} < \mathrm{T_c}$ $f(T) = 0$ if $\mathrm{T} \leq \mathrm{T_b}$ or $\mathrm{T} \geq \mathrm{T_c}$	Two-piece segmented
Li et al. 2008	$f(T)=\left\{\sin\left[\pi(\mathrm{T}-\mathrm{T_o}/\mathrm{T_c}-\mathrm{T_b})^{\log^2 \mathrm{T_c}-\mathrm{T_b}/\mathrm{T_c}-\mathrm{T_b}}\right]\right\}^d$	ExpSine

[a] Abbreviations: T, temperature; $\mathrm{T_b}$, base temperature; $\mathrm{T_o}$, optimum temperature; $\mathrm{T_{o1}}$, lower optimum temperature (for three-piece segmented function); $\mathrm{T_{o2}}$, upper optimum temperature (for three-piece segmented function); $\mathrm{T_c}$, maximum temperature; c, shape parameter for the beta function that determines the curvature of the function; ExpSine, Malo's exponential sine; *d*, the parameter of the ExpSine function that indicates the sensitivity of the germination rate to temperature.

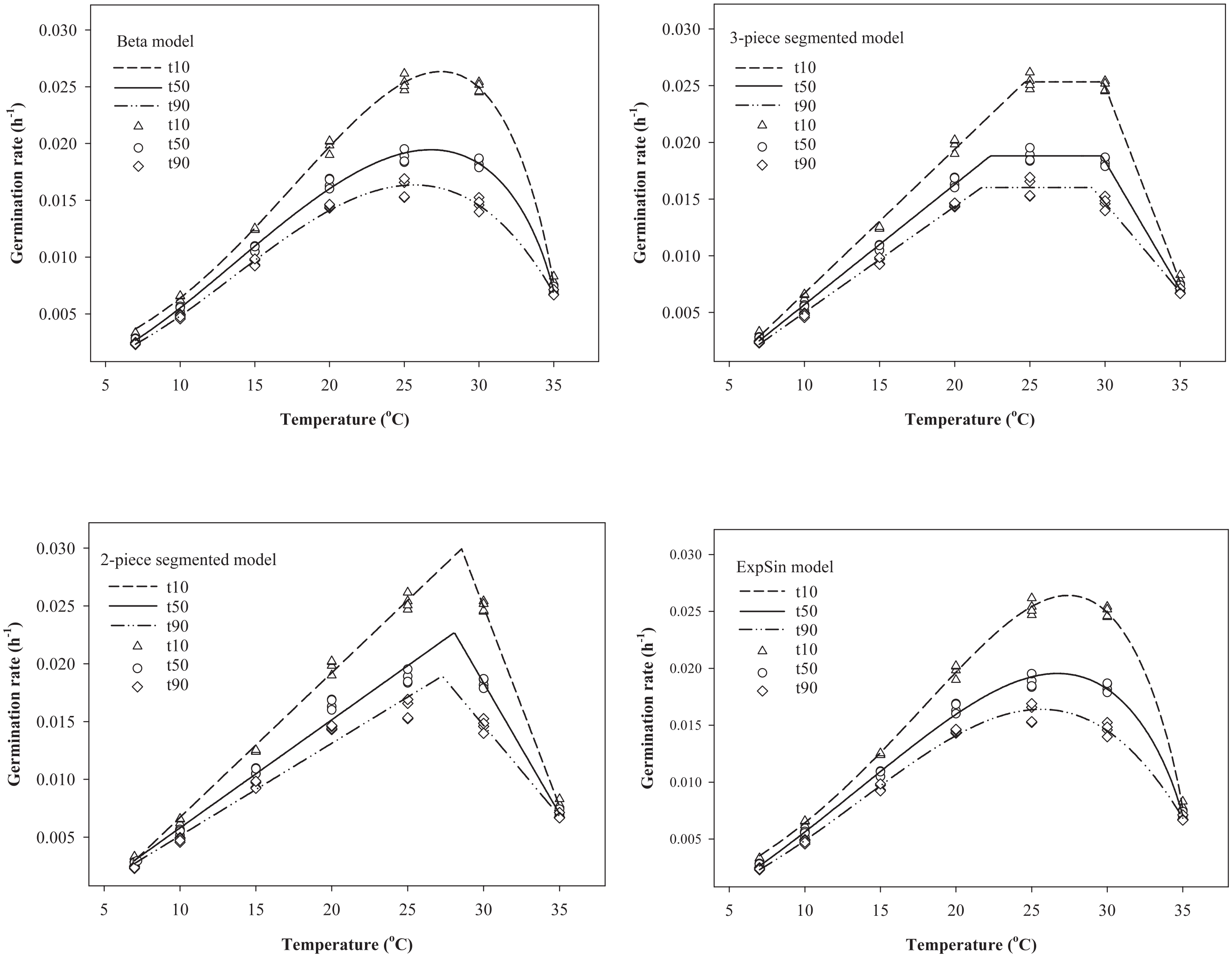

Figure 1. Predicted (lines) germination rate of littleseed canarygrass at different constant temperatures for different germination percentiles (t_{10}, t_{50}, and t_{90}) using four models: beta, three-piece segmented, two-piece segmented, and Malo's exponential sine.

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regression, $\sum_{i=1}^{n}\left(\hat{Y}-\overline{Y}\right)$, and SST is the total SS, $\sum_{i=1}^{n}\left(Y_i-\overline{Y}\right)$. Y_i is the observed value and Y is the correspondent estimated value. The parameters estimated by nonlinear models were exposed to descriptive statistical analysis for the pooled datasets, after which the best estimated values were used to calculate the thermal time needed for each germination percentile.

Thermal Time Determination. The daily thermal time (*DTT*) was calculated as $(T_{o1} - T_b) \times f(T)$, where *f(T)* is the T function, T_{o1} is the lower optimum T, and T_b is the base T. The first components of daily thermal time are the constant and nonoptimal temperatures that affect the daily thermal time through *f(T)*.

Results and Discussion

Cardinal Temperatures. The T_b and T_c values for all percentiles varied significantly in the four models (Figure 1; Table 2). For instance, T_b for different percentiles ranged from −3.39 to 2.07 C in the beta model, in contrast to the range of 4.61 to 4.79 C in the three-piece segmented model; the T_b ranges for the other models were situated between these two ranges. The least coefficient of variation (CV) for the estimated T_b was 1.56%. The maximum T for different percentiles varied between 35.57 and 39.33 C in the four models with the least CV being 1.56%. Based on the beta and the ExpSine models for different percentiles, the optimum T varied from 25.65 to 27.47 C and 25.63 to 27.45 C, respectively (Figure 1; Table 2).

The values of the mean absolute error suggest that the beta, the three-piece segmented, and the ExpSine models are more reliable than the two-piece segmented model (Table 2). The parameter contrasting the models on the predicted vs. observed hours to germination (Figure 2) was the number of days to germination, because small model errors in the germination rate produce large errors in the germination time at the lowest-temperature treatment. Thus, for the three-piece segmented model, the fitted linear equations for the predicted vs. observed hours to germination datasets were not significantly different from the 1 : 1 line (Figure 2). The CV values for all cardinal temperatures also indicate that the three-piece segmented model is more reliable than the beta and the ExpSine models (Table 2).

Table 2. Estimated parameters for four models (beta, three-piece segmented, 2-piece segmented and Malo's exponential sine) at five germination percentiles (t_{10} to t_{90}) for littleseed canarygrass seeds.

Beta							Three-piece segmented						Two-piece segmented						ExpSine					
Parameter[1]	t_{10}	t_{30}	t_{50}	t_{70}	t_{90}	CV	t_{10}	t_{30}	t_{50}	t_{70}	t_{90}	CV	t_{10}	t_{30}	t_{50}	t_{70}	t_{90}	CV	t_{10}	t_{30}	t_{50}	t_{70}	t_{90}	CV
T_b	−3.39	1.69	2.07	2.01	1.15	328.41	4.73	4.79	4.64	4.61	4.66	1.56	4.64	3.95	3.79	3.75	3.60	10.33	1.08	3.57	3.81	3.74	3.00	37.53
T_o	27.47	26.65	26.78	26.37	25.65	2.49	—	—	—	—	—	—	28.55	28.04	28.07	27.76	27.28	1.67	27.45	26.60	26.72	26.34	25.63	2.48
T_c	35.64	35.86	35.76	36.19	37.41	2.00	37.23	37.98	38.10	38.61	38.73	1.56	37.15	37.85	38.14	38.64	39.33	2.15	35.57	35.85	35.77	36.17	37.30	1.90
T_{o1}	—	—	—	—	—	—	24.18	22.31	22.36	22.36	21.78	4.06	—	—	—	—	—	—	—	—	—	—	—	—
T_{o2}	—	—	—	—	—	—	29.88	29.76	29.79	29.51	29.14	1.01	—	—	—	—	—	—	—	—	—	—	—	—
f_o	38.07	46.79	51.41	56.43	61.16	—	39.46	48.52	53.18	57.63	62.45	—	33.41	40.13	44.05	48.35	52.79	—	37.93	46.56	51.15	56.18	60.98	—
d	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.61	0.59	0.55	0.61	0.80	—
c	2.70	1.79	1.67	1.73	2.01	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
R^2	0.99	0.98	0.99	0.99	0.99	—	0.99	0.99	0.99	0.99	0.99	—	0.99	0.97	0.98	0.97	0.97	—	0.99	0.98	0.99	0.99	0.99	—
a	1.06*	0.98	0.97	0.89*	0.89*	—	0.95*	1.01	0.98	1.01	0.94*	—	0.88*	1.10*	1.19*	1.13*	1.15*	—	0.95*	0.94*	0.94*	0.89*	0.93*	—
y_0	−4.75	2.40	2.36	11.04	11.99	—	3.78	1.10	2.55	0.84	7.37	—	9.49	−7.34	−16.05	−12.12	−15.32	—	3.37	5.65	6.15	11.59	7.75	—
MAE	0.21	0.18	0.19	0.36	0.37	—	0.16	0.17	0.20	0.21	0.27	—	0.32	0.33	0.44	0.43	0.48	—	0.17	0.23	0.22	0.37	0.28	—

[a] Abbreviations: ExpSine, Malo's exponential sine; T_b, base temperature; T_o, optimum temperature; T_c, maximum temperature; T_{o1}, lower limit of optimum temperature; T_{o2}, upper limit of optimum temperature; f_o, minimum time to reach a given percentile; d, parameter of the ExpSine function; c, parameter of beta function; R^2, coefficient of regression; a, slope of linear regression between predicted vs. observed hours to germination; y_0, intercept of linear regression between predicted vs. observed hours to germination; MAE, mean absolute error.

* For a, significant difference with 1.

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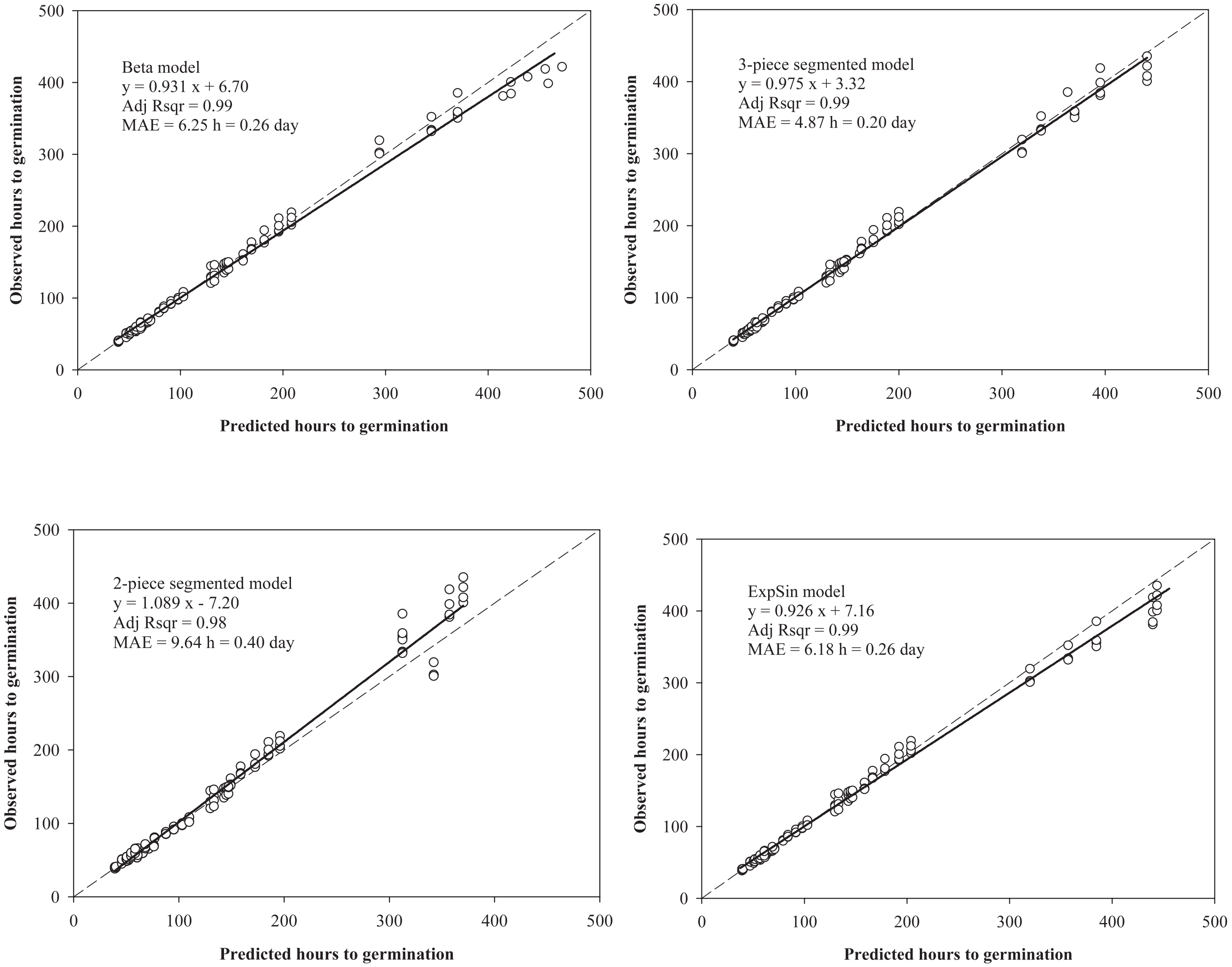

Figure 2. Predicted vs. observed hours to germination to describe response of germination rate to temperature for models (beta, three-piece segmented, two-piece segmented, and Malo's exponential sine function). The fitted linear equation is not statistically different from the 1 : 1 line for the three-piece segmented model ($P < 0.05$).

The descriptive statistics (Table 3) also confirmed that the three-piece segmented model had the smallest range and standard deviation. However, the other models also had acceptable descriptive statistics in many cases. Thus, the lower CV for cardinal temperatures and the lower simple linear regression coefficients, along with an acceptable MAE (lower MAE), confirmed the reliability of the

Table 3. Descriptive statistics results of estimated cardinal temperature by different models.

Cardinal temperature	Statistical indices	Model			
		Beta	Three-piece segmented	Two-piece segmented	ExpSine
T_b	Mean	0.71	4.69	3.94	3.04
	Range	5.46	0.18	1.04	2.73
	Standard deviation	2.32	0.07	0.41	1.14
T_o	Mean	26.58	22.60–29.62[a]	27.94	26.55
	Range	1.82	2.40–0.74[a]	1.27	1.82
	Standard deviation	0.66	0.92–0.30[a]	0.47	0.66
T_c	Mean	36.17	38.13	38.22	36.13
	Range	1.77	1.50	2.18	1.73
	Standard deviation	0.72	0.60	0.82	0.69

[a] Lower and upper limits of optimal temperature based on three-piece segmented model.

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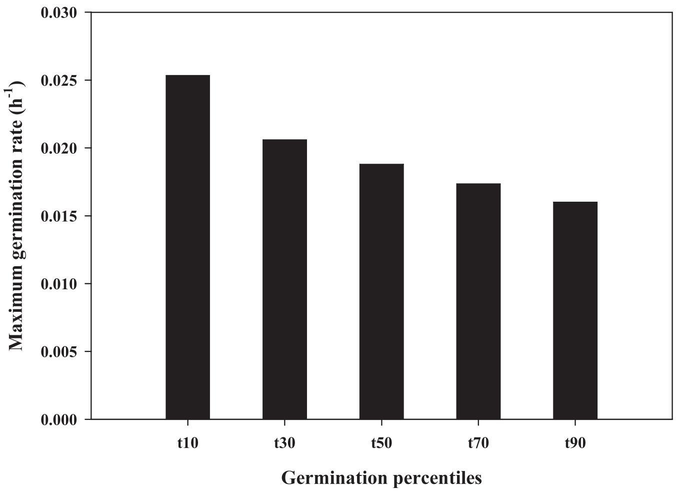

Figure 3. Estimated maximum germination rate (h^{-1}) for different germination percentiles of littleseed canarygrass using the three-piece segmented function.

three-piece segmented model and the estimated parameters. Based on the three-piece segmented model, the minimum times required to achieve t_{10}, t_{30}, t_{50}, t_{70}, and t_{90} percentiles were 39.46, 48.52, 53.18, 57.63, and 62.45 h after imbibition onset. The maximum germination rate ($1/f_o$) is illustrated in Figure 3.

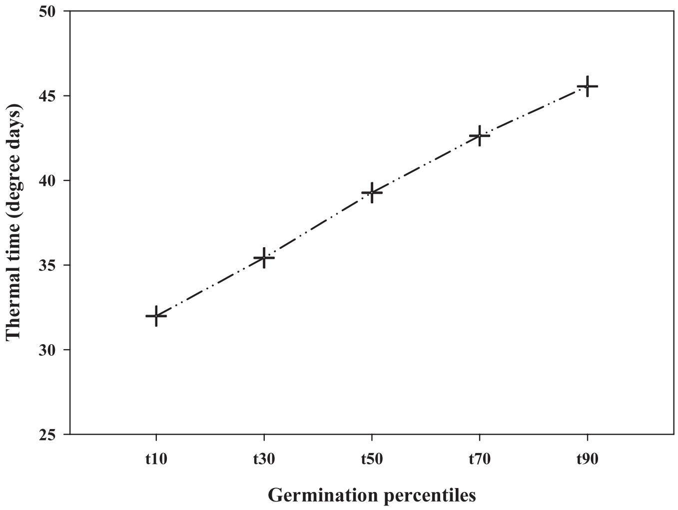

Figure 5. Thermal time (degree-days) required for different germination percentiles based on three-piece segmented model, when $T = T_{o1}$.

Thermal Time Requirements. Considering the calculated $f(T)$ for the constant temperatures used in this research based on the three-piece segmented model (Figure 4), the temperatures closer to the optimum have a small reducing effect on the germination rate. Using the estimated parameters of the three-piece segmented model, each germination percentile was achieved when $\sum DTT = TT$, $\sum f(T) = fo$, or $\sum f(T)/fo = 1$, as presented in Figure 5. The thermal time results also confirm the reliability of the three-piece segmented model. Thus, the mean values of the cardinal temperatures of the three-piece segmented model may be used with confidence in thermal time calculations. On the other hand, the regression between the degree-day sums and the mean temperatures for this work confirmed the independence between the degree-day sums and the temperatures of the trial (Figure 6).

The maximum germination percentage of littleseed canarygrass seeds in response to different constant temperatures varied little with temperatures ranging between 10 and 25 C (Figure 7).

The results of the present study confirm that, in the absence of other limiting factors (e.g., water, light), the germination of littleseed canarygrass seeds

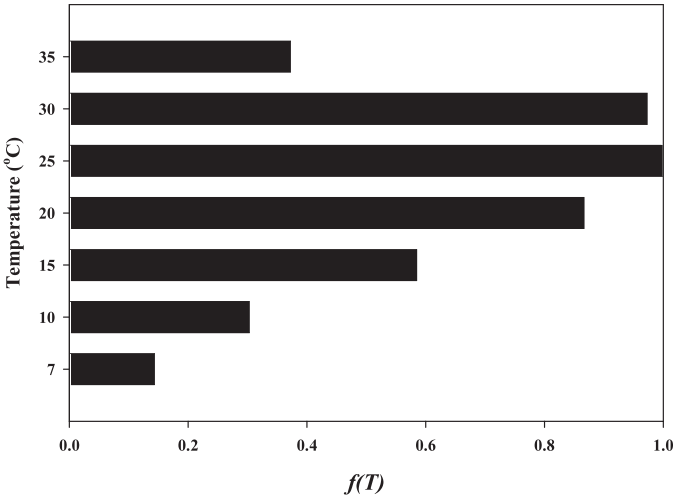

Figure 4. T function values for different constant temperatures base on the three-piece segmented model.

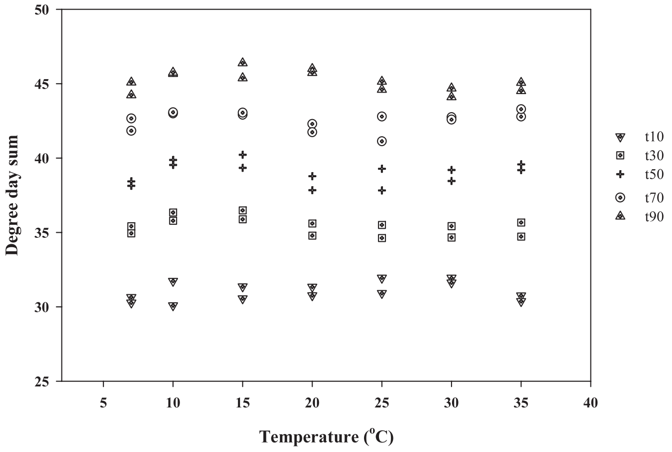

Figure 6. Regression between the degree-day sums and the mean temperatures to test independency between the degree-day sums and the temperatures for different germination percentiles.

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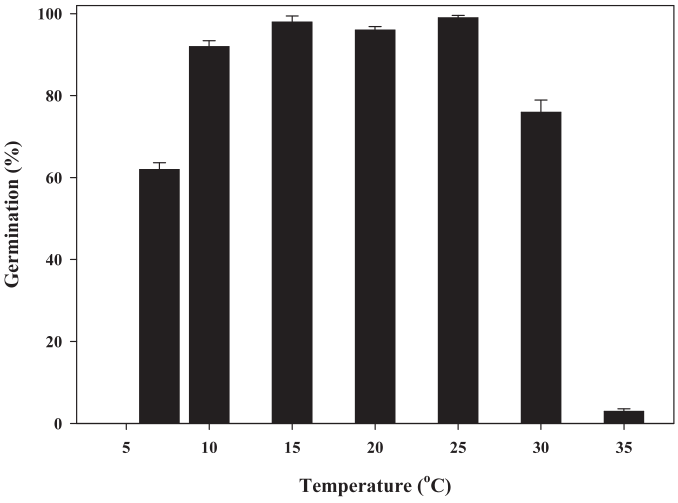

Figure 7. Maximum germination values of littleseed canarygrass seeds at different constant temperatures.

is largely influenced by T. According to the three-piece segmented model, the germination rate increased with temperatures ranging from 4.69 to 22.60 C, was constant from 22.60 to 29.62 C, and decreased from 29.62 to 38.13 C. These results are in contrast with some published results (Mehra and Gill 1988; Singh and Ghosh 1982). For instance, the ideal T for the germination of littleseed canarygrass ranged between 17 and 21 C (Singh and Ghosh 1982) or between 15 and 22 C (Mehra and Gill 1988).

The data suggest that the three-piece segmented model may be better suited than the beta, two-piece segmented, and ExpSine models to describe the germination rate response to T and to estimate the cardinal temperatures of littleseed canarygrass. According to the three-piece segmented model, the relative rate of development is zero at the T_b or lower temperatures. As the T increases, the relative development rate increases up to a particular T, i.e., the lower optimum temperature (T_{o1}). The relative rate of development is constant with further increases in T to reach the upper optimum temperature (T_{o2}), above which the relative rate of development again decreases and eventually ceases at T_c or higher temperatures. In this model, the thermal time requirement for the germination of each percentile is calculated from the reciprocal of the slope of the regression equation for the rate of germination vs. T below the lower optimum. Littleseed canarygrass seeds can germinate at different rates across a wide range of constant temperatures starting from 4.69 C and increasing to 38.13 C. Therefore, T_b and T_c are considered extreme temperatures in plant modeling. These mean values of cardinal temperatures may be used in thermal unit calculations to predict the occurrence of different percentiles of littleseed canarygrass seed germination. The model predictions of the time required for seed germination agree reasonably well with the observed times.

Seed germination is one of the most critical events for the establishment of any weed species because it represents the first stage at which the plant can compete for an ecological niche (Ghaderi-Far et al. 2010; Tanveer et al. 2013; Vidal et al. 2007). Germination is conditioned by both intrinsic and extrinsic factors. The efficacy of weed control practices, such as tillage and POST herbicide application, is affected by weed emergence timing. Therefore, understanding the T requirements for weed seed germination is important in the design and implementation of weed control strategies. In temperate regions, T is perhaps the most important factor in the germination of weed seeds (Derakhshan and Gherekhloo 2013; Vidal et al. 2007). Thus, the completion of databases for unknown ecological parameters could help modelers quantify the weed behavior in response to climatic variables, especially the most important variable: T. The error estimates are on a scale of several hours between the predicted and observed values and give an approximate idea of the improved precision afforded by these models. Several hours of improved precision are not likely to aid a farm manager but could be important for population dynamics models, where increased precision can significantly impact the model output or predicted competitive outcome between weed and crop. The cardinal temperatures for germination are important parameters of weed dynamics models. These models can be used to predict the long-term effects of cropping systems and management strategies on weed population dynamics. In fact, one of the simplest and most widely used approaches in plant modeling involves normalizing time with respect to T, which results in a quantity known as thermal time. The thermal time is expressed in units of growing degree-days and is highly correlated with many plant growth and developmental processes (Ritchie and NeSmith 1991). The T-related parameters quantified here provide the basic values needed to predict the time from seeding to germination of littleseed canarygrass. Additionally, these T-related parameters could be used to determine the best sowing dates for the crops to avoid the optimal weed germination period.

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The cardinal temperatures depended on the model used to estimate them. Overall, the three-piece segmented model is better suited to estimate the cardinal temperatures for the germination of littleseed canarygrass than are the beta, two-piece segmented, and ExpSine models.

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