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Quantifying cardinal temperatures and thermal time required for germination of *Silybum marianum* seed



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ABSTRACT

The response of seed germination to environmental factors can be estimated by nonlinear regression. The present study was performed to compare four nonlinear regression models (segmented, beta, modified, and dent-like) to describe the germination rate–temperature relationships of milk thistle (*Silybum marianum* L.) at six constant temperatures, with the aim of identifying the cardinal temperatures and thermal times required to reach different germination percentiles. Models and statistical indices were calibrated using an iterative optimization method and their performance was compared by root mean square error (RMSE), coefficient of determination (R^2) and Akaike information criterion correction (AICc). The beta model was found to be the best model for predicting the required time to reach 50% germination (D50), ($R^2 = 0.99$; RMSE = 0.004; AICc = -276.97). Based on the model outputs, the base, optimum, and maximum temperatures of seed germination were 5.19 ± 0.79 , 24.01 ± 0.11 , and 34.32 ± 0.36 °C, respectively. The thermal times required for 50% and 90% germination were 4.99 and 7.38 degree-days, respectively.

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1. Introduction

Herbal medicine is an alternative approach to conventional medical therapies. Medicinal plants may incur smaller side effects than chemical drugs. *Silybum marianum* is a broadleaf plant with highly valued medicinal properties. Its seeds contain flavonolignans, silybin, silychristin, and silydianin, together called silymarin [1]. Silymarin is used in liver disease therapy [2].

Successful production of medicinal plants requires a strong knowledge of plant ecophysiology. Most medical plants have

unknown ecophysiology, owing to their existence in harsh and wild habitats. Vigorous seed germination and seedling establishment are highly desirable, especially in arid and semiarid climates. Studying basic seed germination requirements will increase the chance of successful plant establishment under different climatic conditions [3]. Upon receiving special cues from the environment, seeds initiate germination. In some circumstances, plants spread the risk of early germination for their seeds or apply alternative mechanisms to maximize fitness for germination [4,5]. The seed environment consists of soil temperature, moisture, gases, light, and

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chemical substances, also considered to be abiotic germination regulators [6,7]. Among all effective factors of seed germination, temperature and moisture are considered the most important.

Usually, a linear increase in germination rate is associated with an increase in temperature from base temperature (T_b) to an optimum. An increase of temperature from the optimum will reduce the germination rate to zero [8-12]. To determine the best planting date for plants, it is necessary to find the base (T_b), optimum (T_o) and maximum temperatures (T_c) for seed germination. These are known as cardinal temperatures [6]. Although there is a rich body of data describing the cardinal temperatures for many agronomic crops and plant species, information about the thermal requirements of many weedy and medicinal plants is lacking. Modeling of seed germination is considered an effective approach to determining cardinal temperatures for most plant species, although these methods have some limitations due to unpredictable biological changes. Two main concepts widely used by researchers to model seed germination include empirical and mechanical models [13]. Empirical models perform well for fitting individual germination data over time, but may need empirical variables [14]. It is difficult to ascribe biological significance to model parameters estimated by empirical methods [9,13]. Mechanical models are developed based on the experimental quantification of environmental effects on seed germination and seedling emergence. In the long term, this approach is likely to be most successful [9,15]. The application of mechanical threshold models of seed germination and seedling emergence has shown some success [11,12,15-18]. The results of fitting mechanical models are useful for evaluating seed quality, germination rate, germination percentage, germination uniformity [13,19] and seed performance under different environmental stresses such as salinity, drought, and freezing [11]. Regression models incorporating more parameters can produce more precise estimates. Nonlinear curves are used to model the time course of germination at different temperatures [20]. Such regression models have been used to explain development rate in many crops [21]. Seedling emergence of wheat as a function of soil temperature and water potential has been studied using logistic models [22-24]. Cardinal temperature was determined using segmented and logistic models in millet varieties and seedling emergence of wheat [25-27]. In the dent-like model at lower-than-optimum temperature, a linear relationship holds between temperature and germination rate. This relationship remains linear at higher-than-optimum temperatures, but with a reducing trend. With increasing temperature, germination rate increases linearly up to an optimum temperature. Beta and beta modified models fit curvilinear relationships between germination rate and temperature. These models are thus more flexible than other models.

This study was performed to determine the effectiveness of nonlinear regression models including dent-like, segmented, beta, and beta modified for cardinal temperatures estimation of *Silybum marianum* seeds. The results of this study will be useful for characterizing the ecophysiology of seed germination of milk thistle seeds. Such knowledge may be useful for identifying the best planting dates for this medicinal plant in a range of climates and regions.

2. Material and methods

An experiment was performed to determine the cardinal temperatures of *S. marianum*. Seeds of *S. marianum* were purchased from the Pakanbazar Co., Iran. The experiment was conducted using germinators with controlled environments in the Seed Technology Laboratory, Faculty of Agriculture, Mohaghegh Ardabili University, Ardabil, Iran. Four replicates of 50 seeds were germinated in 9-cm-diameter Petri dishes on two layers of Whatman No. 1 (9 cm diameter) filter paper containing 5 mL distilled water. The germination responses were evaluated at six constant temperatures: 10, 15, 20, 25, 30, and 35 °C.

Seeds with radicles elongated at least 2 mm were considered as germinated. Germinated seeds were counted every 24 h and cumulative germination percentage was plotted against time. From this curve, the time required to reach 50% germination (D50) was determined by fitting a logistic model of cumulative germination percentage (G) against time (t) as described by Eq. (1):

$$G = \frac{G_x}{1 + \exp[a(t-b)]} \quad (1)$$

where G_x is the maximum germination percentage, t is the time required for 50% germination, and a and b are constants. The times for 10%, 50%, and 90% germination were also determined by interpolation and are designated as D10, D50, and D90, respectively [20,28,29].

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 temperature and cardinal temperatures for germination, the following equation was used:

$$GR = f(T)/f_o, \quad (2)$$

where $f(T)$ is a T function (reduction factor) that ranges between 0 at the base and maximum temperatures and 1 at the optimal temperature(s), and $1/f_o$ is the inherent maximum rate of germination at the optimal temperature, estimated by an iterative optimization method. Thus, f_o represents the minimum number of hours for germination at the optimal temperature [30]. The GR also shows the germination rate of a given percentile. Sigma Plot, Ver 12 software was used to calibrate the models (beta, beta modified, segmented, and dent-like) using an iterative optimization method (Table 1). To determine the best estimates of the parameters (lower deviations of the intercept from 0 and of the slope from 1 correspond to increased reliability (RMSE; Eq. (3)), the coefficient of determination (R^2 ; Eq. (4)), and the intercept and slope of the regression of predicted vs. observed germination rate were used.

$$RMSE = \sqrt{\left(\frac{1}{n}\right) \sum (Y_{obs} - Y_{pred})^2} \quad (3)$$

Table 1 – Beta, segmented, and dent-like models that were fitted to model germination rate at different constant temperatures.

| Function | Formula | Reference |
|----------------------|---|-----------|
| Beta, five-parameter | $f(T) = \left(\frac{T-T_b}{T_o-T_b}\right) \left(\frac{T_c-T}{T_c-T_o}\right) \left(\frac{T_c-T_o}{T_o-T_b}\right)^c$ | [34] |
| Beta, four-parameter | $f(T) = \left(\frac{T-T_b}{T_c-T_o}\right) \left(\frac{T-T_b}{T_o-T_b}\right) \left(\frac{T_o-T_b}{T_c-T_o}\right)$ | [35] |
| Dent-like | $f(T) = (T - T_b) / (T_{o1} - T_b) \dots \dots$ if $T_b < T < T_{o1}$ $f(T) = (T_c - T) / (T_c - T_{o2}) \dots \dots$ if $T_{o2} < T < T_c$ $f(T) = 1 \dots \dots$ if $T_{o1} \leq T \leq T_{o2}$ $f(T) = 0 \dots \dots$ if $T \leq T_b$ or $T_c \leq T$ | [36] |
| Segmented | $f(T) = (T - T_b) / (T_o - T_b)$ if $T_b < T < T_o$ $f(T) = 1 - \left(\frac{T-T_b}{T_c-T_o}\right)$ if $T_o \leq T < T_c$ $f(T) = 0$ if $T \leq T_b$ or $T_c \leq T$ | [37] |

T, the temperature; T_b, the base temperature; T_o, the optimum temperature; T_{o1}, the lower optimum temperature for a 3-piece segmented function; T_{o2}, the upper optimum temperature for a 3-piece segmented function; T_c, the maximum temperature, c, a shape parameter for the beta function that determines the curvature of the function; d, the parameter of the beta modified function that indicates the sensitivity of the germination rate to temperature.

where Y_{obs} denotes observed value, Y_{pred} predicted value, and n the number of samples [31], and

$$R^2 = SSR/SST \tag{4}$$

where SSR denotes the sum of squares (SS) for regression $\left(\sum_{i=1}^n (\hat{L}_i - \bar{L})\right)$ and SST the total SS $\left(\sum_{i=1}^n (L_i - \bar{L})\right)$. L_i is the observed value and \hat{L}_i is the corresponding estimated value. The parameters estimated by nonlinear models were subjected to descriptive statistical analysis of the pooled datasets, after which the best estimated values were used to calculate the thermal time needed for each germination percentile.

Low RMSE and R² near 1 correspond to better model estimation.

To identify the best model for estimating cardinal temperature, the Akaike Information Criterion (AIC) was used. This statistic incorporates the amount of reduction of RSS and the model complexity [32].

$$AIC = n \ln \left(\frac{RSS}{n}\right) + 2k \tag{5}$$

where RSS denotes the residual sum of squares, n the number of observations, and k is the number of model parameters.

It is possible to use a corrected AIC (AICc) instead of AIC. This statistic is used to identify the most accurate model [33,34].

$$AICc = n \ln \left(\frac{RSS}{n}\right) + 2k + \left(\frac{2k(k+1)}{n-k-1}\right). \tag{6}$$

The model that yields the most accurate estimate is the one with the lowest AICc value. Although the best model is the one that yields the lowest AICc, there is a method that permits description, ranking, and fitting different models. This method requires the calculation of Δ_i:

$$\Delta_i = AICc - AICc_{\min}, \tag{7}$$

where min AICc is the minimum calculated AICc among all models, and corresponds to the best-fitting model. If Δ_i < 10, there is no significant difference between models, and a model with higher AICc also could be well-fitting. If Δ_i > 10, a model with higher AICc is not suitable and not well-fitting.

The daily thermal time (DTT) was calculated as DTT = (T_o - T_b) 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 non-optimal temperatures that affect the daily thermal time through f(T).

3. Results

In this study, AICc was our main criterion for choosing the best experimental models by which to evaluate cardinal temperatures. The calculated AICc values for the segmented model were -198.78, -248.53, and -237.07 for D10, D50, and D90, respectively. The AICc indices for the beta model output were -247.11, 276.97, and -258.98 for D10, D50, and D90, respectively, and those for the output of beta modified were -217.17, 262.02, and -252.28 for D10, D50, and D90, respectively (Table 2). The calculated AICc for the dent-like model in D10, D50, and D90 were -205.63, -264.94, and -257.72, respectively. Models of relative germination rate vs. mean temperature were fitted (Fig. 1), and their parameter estimates are presented in Table 1. T_b was estimated for D10, D50, and D90 using segmented (8.32 ± 0.47, 7.49 ± 0.32, 6.98 ± 0.66), beta (4.47 ± 0.39, 5.19 ± 0.79, 6.05 ± 0.11), beta modified (7.49 ± 1.27, 5.79 ± 0.79, 3.94 ± 1.79), and dent-like (8.32 ± 0.44, 7.49 ± 0.23, 6.98 ± 0.43). The base and maximum temperatures for different percentiles showed no significant difference for any of the tested models. According to the beta model for D10 and D50, the optimum temperature varied between 24.12 ± 0.14 and 24.01 ± 0.11. This model was most reliable for D10, D50, and D90, because of the higher determination coefficient between observed and predicted values (R² values of 0.99, 0.99, and 0.96 for the pooled data). The beta-modified and segmented models also appeared reliable for D10 and D550 (Table 2), with high calculated R² values for both models.

Table 2 – Estimated parameters for segmented, beta, beta modified, and dent-like models for different germination percentiles of *Silybum marianum* seeds.

| Parameter | Segmented | | | Beta | | | Beta modified | | | Dent-like | | |
|------------|--------------|--------------|--------------|--------------|--------------|--------------|---------------|--------------|--------------|--------------|--------------|--------------|
| | D10 | D50 | D90 | D10 | D50 | D90 | D10 | D50 | D90 | D10 | D50 | D90 |
| T_b | 8.32 ± 0.47 | 7.49 ± 0.32 | 6.98 ± 0.66 | 4.47 ± 0.39 | 5.19 ± 0.79 | 6.05 ± 0.11 | 7.49 ± 1.27 | 5.79 ± 0.79 | 3.94 ± 1.79 | 8.32 ± 0.44 | 7.49 ± 0.23 | 6.98 ± 0.43 |
| T_o | 24.49 ± 0.43 | 24.28 ± 0.26 | 24.53 ± 0.52 | 24.12 ± 0.14 | 24.01 ± 0.11 | 24.64 ± 0.33 | 24.66 ± 0.25 | 24.16 ± 0.18 | 24.45 ± 0.32 | - | - | - |
| T_c | 34.70 ± 0.50 | 34.64 ± 0.30 | 35.72 ± 0.69 | 35.28 ± 0.77 | 34.32 ± 0.36 | 32.94 ± 0.23 | 33.07 ± 0.13 | 33.20 ± 0.10 | 33.57 ± 0.21 | 33.75 ± 0.43 | 33.75 ± 0.21 | 33.72 ± 0.29 |
| T_{o1} | - | - | - | - | - | - | - | - | - | 23.35 ± 0.95 | 22.80 ± 0.46 | 23.10 ± 0.82 |
| T_{o2} | - | - | - | - | - | - | - | - | - | 27.08 ± 0.72 | 26.99 ± 0.36 | 28.26 ± 0.38 |
| f_o | 2.34 ± 0.86 | 4.57 ± 0.10 | 6.50 ± 0.26 | 2.46 ± 0.03 | 4.99 ± 0.05 | 7.38 ± 0.20 | 2.56 ± 0.06 | 5.16 ± 0.08 | 7.19 ± 0.19 | 2.52 ± 0.10 | 5.01 ± 0.10 | 7.07 ± 0.23 |
| c | - | - | - | 4.05 ± 0.95 | 3.64 ± 0.57 | 1.47 ± 0.28 | - | - | - | - | - | - |
| R^2 | 0.95 | 0.98 | 0.94 | 0.99 | 0.99 | 0.97 | 0.98 | 0.99 | 0.97 | 0.96 | 0.99 | 0.97 |
| RMSE | 0.028 | 0.008 | 0.011 | 0.009 | 0.004 | 0.007 | 0.018 | 0.006 | 0.008 | 0.025 | 0.006 | 0.007 |
| AIC | -206.78 | -256.53 | -245.07 | -251.11 | -290.97 | -262.95 | -225.17 | -270.02 | -260.28 | -209.63 | -268.94 | -261.72 |
| AICc | -198.78 | -248.53 | -237.07 | -247.11 | -276.97 | -258.95 | -217.17 | -262.02 | -252.28 | -205.63 | -264.94 | -257.72 |
| Δ_i | 48.33 | 28.44 | 21.88 | 0 | 0 | 0 | 29.94 | 14.95 | 6.67 | 41.48 | 12.03 | 1.23 |

T_b , T_o , T_c , T_{o1} , T_{o2} , f_o , and c denote base temperature, optimum temperature, maximum temperature, lower limit of optimum temperature, upper limit of optimum temperature, minimum time to reach a given percentile, parameter of beta function, and coefficient of regression, respectively.

According to the output of the segmented model, the optimum temperature varied between 24.28 °C and 24.50 °C in D10 to D90. The output of the dent-like model was not reliable for predicting D10, D50, and D90, as evident from the low determination coefficients (R^2 values of 0.96, 0.99, and 0.97, respectively). The segmented model estimated the base, optimum, and maximum temperatures for D50 as 7.49 ± 0.32, 24.28 ± 0.26, and 34.64 ± 0.30, respectively. The beta modified model estimated the base, optimum, and maximum temperatures for D50 as 5.79 ± 0.79, 24.16 ± 0.18, and 33.20 ± 0.10, respectively. The optimum temperature for all models was very close to 24 °C. The beta model yielded the best-fitting output for cardinal temperatures, as shown by its higher R^2 for D10, D50, and D90: 0.99, 0.99, and 0.97, respectively (Table 2). In addition, the beta model yielded the lowest RMSE values for D10, D50, and D90 (0.009, 0.004, and 0.007) among all models (Table 2).

The optimum temperature of D50 was estimated by the segmented, beta, and beta modified models as 24.28 ± 0.26; 24.01 ± 0.11, and 24.16 ± 0.18, respectively, whereas for the dent-like model the optimum temperature for D50 ranged from 22.80 ± 0.46 (T_{o1}) to 26.99 ± 0.36 (T_{o2}). The calculated cardinal temperatures using the beta and beta modified models both exhibited a sigmoidal shape (Fig. 1a and b). The graphical output of the segmented model is illustrated in part C of Fig. 1. The dent-like model could not estimate an exact optimum temperature and instead yielded a temperature range (Fig. 1d). The calculated $f(T)$ for the constant temperatures used in this study, based on the beta model, is illustrated in Fig. 2. It shows an increasing trend up to 25 °C, after which it starts to decrease. This observation suggests that the optimum temperature is around 25 °C. The calculated thermal times for each germination percentile based on the pooled data are shown in Fig. 3.

Our results confirmed the accuracy of estimated parameters and the reliability of the beta model.

4. Discussion

Thermal time (degree days or hours) is the basic and most important temperature factor in plant growth and development processes [35] such as seed germination and seedling emergence [36]. Thermal time is widely used to quantify and model seed germination. Temperature plays a critical role in the regulation of plant vital processes, including seed germination [37]. Practical research in plant science usually attempts to establish the minimum temperature required for germination or its maximum range [38]. Seed germination of spring poppy varieties occurs at temperatures above 2–3 °C, but the optimum temperature is 7–10 °C. In contrast, the optimum germination temperature of winter poppy is 15–20 °C [39].

Our study suggested that a bilinear-shaped response model of germination rate to temperature is applicable for determination of the cardinal temperatures of *S. marianum*. In this model, germination rate is regressed separately on temperature for two extremes of temperature (below and above the optimum temperature). Base (T_b) and maximum

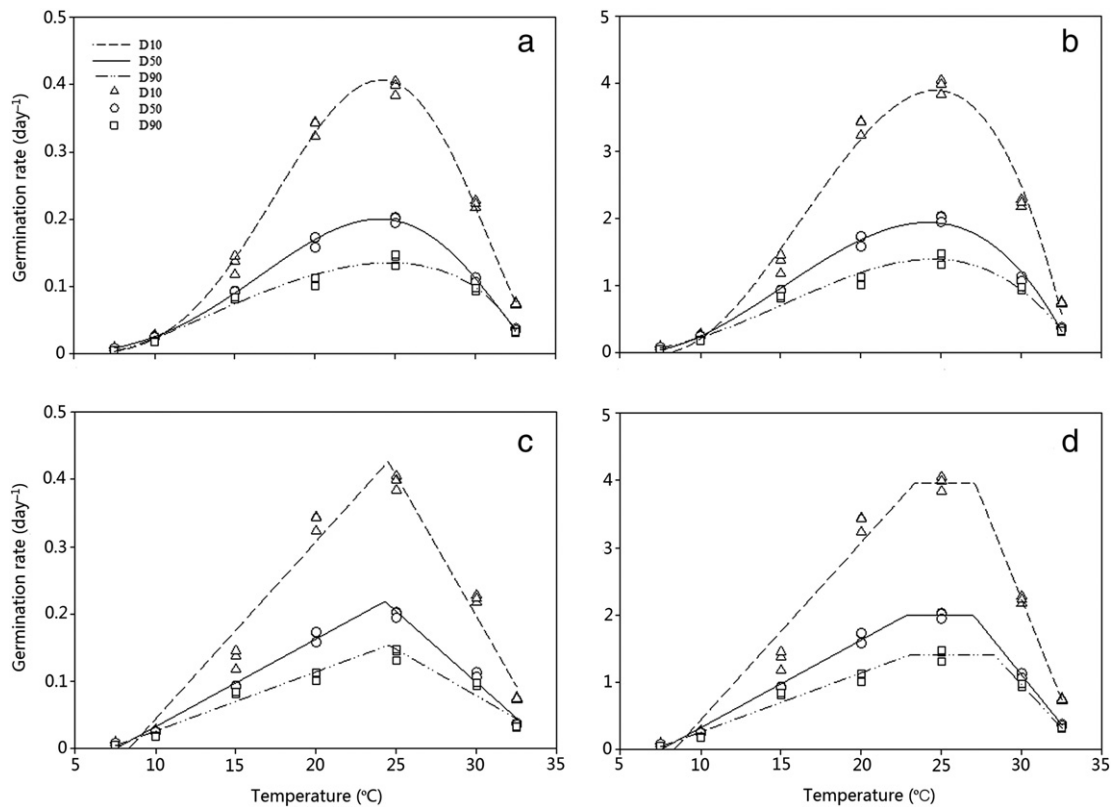


Fig. 1 – Predicted (lines) vs. observed (symbols) germination rate of *Silybum marianum* seeds at different constant temperatures for different germination percentiles (D10, D50, and D90) using beta (a), beta modified (b), segmented (c), and dent-like (d) models.

temperatures (T_c) are the intercepts of each regression line [40,41]. The thermal times required to reach specified germination percentiles (D10, D50, and D90) were calculated from the reciprocal of the slope of the regression equation of rate of germination vs. temperature below the optimum [42].

The results of the present study confirmed that, in the absence of other limiting factors (such as light and water), the germination of *S. marianum* seed was highly influenced by temperature. In addition, our results indicated that the beta model of germination rate sharply defines the cardinal temperatures of *S. marianum*.

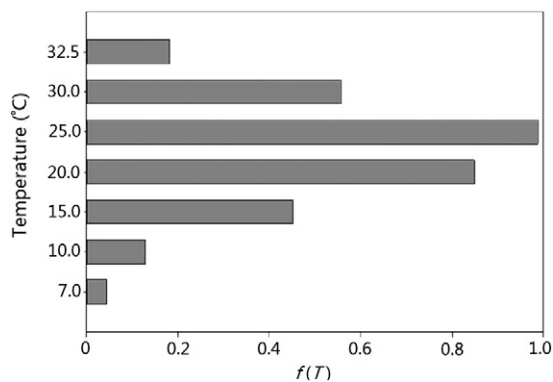


Fig. 2 – $f(T)$ values for different constant temperatures based on the beta model.

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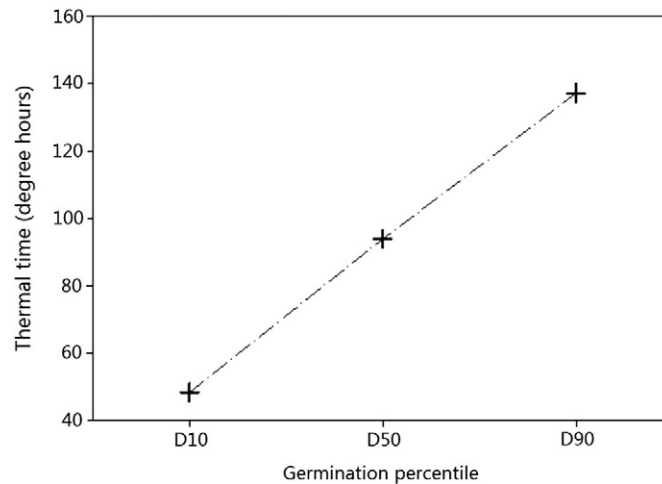


Fig. 3 – Thermal time (degree hours) required for different germination percentiles, based on pooled data, when $T = T_0$.

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