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Determination of cardinal temperatures for seed germination in *Thymus kotschyanus, T. daenensis,* and *T. lancifolius*

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ABSTRACT

To evaluate the germination characteristics and determine the cardinal germination temperatures of *Thymus kotschyanus* Boiss. & Hohen*, T. daenensis* Celak., and *T. lancifolius* Celak., a factorial experiment was conducted in 2023, at the Seed Technology Research Laboratory of the Natural Resources Gene Bank of Iran. This experiment, designed in a completely randomized format with three replications, aimed to evaluate the germination characteristics and determine the cardinal temperatures of germination of three thyme species: *Thymus kotschyanus*, *Thymus daenensis*, and *T. lancifolius*. The seeds were exposed to a range of temperatures from 5 to 40 °C, a crucial step in understanding their germination behavior. Three non-linear regression models, including dent-like, segmented, and beta, were employed to characterize the germination rate response of three thyme species across eight temperature levels. Statistical indices such as root mean squared error (RMSE) and coefficient of determination (R^2) were utilized to compare the models. Results from this experiment demonstrated that the studied thyme species exhibited similar germination peaks due to similar initial growth rates. Based on the results, the dent-like model provided the best fit for *T. lancifolius* with a basic temperature of 7.58 °C, a lower optimum temperature of 15.10 °C, an upper optimum temperature of 15.65 °C, and a ceiling temperature of 36.19 °C, with R^2 and RMSE values of 0.97 and 0.15, respectively. For *T. kotschyanus*, the dent-like model with a basic temperature of 5 °C, lower optimum temperature of 17.47 °C, upper optimum temperature of 19.73 °C, and a ceiling temperature of 34.24 °C, and R^2 and RMSE values of 0.92 and 0.08, respectively, also showed a good fit. However, for *T. daenensis*, the segmented model with an essential temperature of 6 °C, optimum temperature of 20 °C, and ceiling temperature of 36 °C, and R^2 and RMSE values of 0.99 and 0.06, respectively, provided the most reliable fit. Conclusively, the germination temperature range for all three thyme species was 10 to 35 °C, with an optimal germination temperature of 15 to 20 °C. These results emphasized the high adaptability and promising cultivation potential of the three thyme species in temperate natural resource areas, offering a significant implication for future agricultural practices.

Keywords: Basic temperature, Ceiling temperature, Optimal temperature, Thyme

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INTRODUCTION

Thyme (*Thymus*) is a perennial herb belonging to the Labiatae family, comprising over 250 species and subspecies. Its food and medicinal applications and the growing demand for diverse thyme products emphasize the importance of further research on this herb [1]. The thyme plant (*Thymus*) is one of the most economically significant medicinal and aromatic herbs, highly valued for its medicinal properties, culinary uses, industrial applications, and export potential [2]. Seed germination is one of the most critical stages in a plant's life cycle. Environmental factors determine seed germination, subsequent seedling emergence, and establishment [3]. Temperature is a critical environmental factor influencing seed germination, affecting both the percentage and rate of germination [4]. The germination rate generally increases with rising temperature to an optimal point, beyond which it declines sharply [5]. The differential response of germination to varying temperatures is attributed to the enhanced enzymatic activity at optimal temperatures. As temperature increases to an optimum level, enzymatic reactions become more efficient, improving germination percentage and rate. Conversely, extremely high or low temperatures can inactivate certain enzymes, reducing the rate of these reactions and consequently decreasing the germination percentage [6]. Protein degradation and impaired membrane function are among the factors that decrease seed germination rate at temperatures higher than the optimum [7]. Reduced seed metabolic efficiency is another factor observed to decrease germination rate at temperatures above the optimum [3]. To determine the optimal planting date for crops, the basic (Tb), optimum (To), and ceiling (Tc) temperatures for seed germination must be identified. These are cardinal temperatures, which are highly influenced by the conditions governing on germination, particularly temperature. The basic and ceiling temperatures are the lowest and highest temperatures below and above which germination does not occur in these situations, while the optimum temperature is the temperature at and germination occurs fastest [8]. Alternate application of cardinal temperature is in the parameter called growing degree days (GDD) that is designed using cardinal temperatures to estimate plant growth and normalize plant responses to varying temperatures [9].

Cardinal germination temperatures are linked to a species' environmental tolerance range, ensuring that germination timing aligns with optimal conditions for subsequent seedling growth and development [8]. The temperature range at which maximum germination occurs varies depending on species and seed quality (Ellis et al., 1986). Species' minimum, optimum, and maximum germination temperatures differ [4]. Numerous reports have been published on the germination characteristics of various plant species, including crop, forage, and medicinal plants [10, 11, 12, 4, 14, 15, 16, 17, 18]. The cardinal temperatures for germination of *Kochia scoparia*, a species with a wide temperature distribution, are 3.5, 24, and 50 °C for the basic, optimum, and ceiling temperatures, respectively [4]. The findings of the study conducted by Banayan et al. (2006), investigating the germination characteristics of several medicinal plants in Iran, revealed that the highest germination percentage was obtained in the temperature range of 20-30 °C for *Nepeta binaludensis* and *Nepeta crassifolia*, 15-20 °C for *Zataria multiflora*, 15-30 °C for *Thymus kotschyanus*, *Rubia tinctorum*, and *Achillea millefolium* [12]. In a linear regression analysis between germination rate and temperature, cardinal temperatures (basic, optimum, and maximum) were estimated to be 4.4, 19, and 25.5 °C for *Plantago ovate* and 9.4, 28.8, and 35 °C for *Plantago psyllium*, respectively [15]. The basic germination temperature for *Anethum graveolens*, *Foeniculum vulgare*, and *Trachyspermum ammi* has been reported as 5, 0.86, and 2.88 °C, respectively [19]. Optimal temperatures are required to develop predictive models for seed germination in desired plant species [20]. Various mathematical models have described the relationship between seed germination and temperature. These include beta, segmented, dent-like, and modified Beta functions. These are advantageous because they incorporate biological concepts such as cardinal temperatures, germination rate, and the number of biological hours required to attain a specific germination percentage [21]. The dent-like model was employed to determine the optimal temperatures for the germination of two thyme ecotypes in response to various temperature levels [22]. [23] employed beta, segmented, and dent-like models to simulate chickpea germination at various temperatures and depths. They concluded that the dent-like model was the most superior model for predicting germination in this plant. This study evaluated the effectiveness of beta, segmented, and dent-like nonlinear regression models in estimating cardinal temperatures for three thyme species: *Thymus kotschyanus, T. daenensis*, and *T. lancifolius*. The goal was to determine the optimal temperature and time conditions for cultivating these medicinal plants.

MATERIALS AND METHODS

To investigate the germination response of seeds from *T. kotschyanus, T. daenensis,* and *T. lancifolius* under temperature stress (cold and heat) and to determine the cardinal temperatures for germination, a factorial experiment was conducted in a completely randomized design with three replications in the seed technology laboratory of the Iran Natural Resources Gene Bank. The temperature was manipulated across eight levels (5, 10, 15, 20, 25, 30, 35, and 40 °C) in separate incubators. Each experimental unit maintained a constant temperature within ±0.5 °C. Germination percentage, defined as the emergence of a 2 mm radicle, was assessed daily for 21 days [24]. The germination percentage was calculated using the formula "ng/nt×100," where ng is the number of germinated seeds and the total number of seeds sown [25]. The germination rate was calculated as '∑ ni/di,' where ni is the daily germination count, and di is the corresponding day [26]. An analysis of variance (ANOVA) was conducted using Duncan's multiple range test in SAS software to compare the means of mean germination rate and mean germination time [27]. Dent-like, segmented and beta models were employed to describe the occurrence of germination rate variations at different temperatures (Table 1) [17].

Table 1 Dent-like, segmented and beta models

Dent-like	$f(T) = (T - T_b)/(T_{o1} - T_b)$ if $T_b < T < T_{o1}$ $f(T) = (T_c - T)/(T_c - T_{o2})$ if $T_{o2} < T < T_c$ $f(T) = 1$ if $T_{o1} \le T < T_{o2}$ $f(T) = 0$ if $T \le T_b$ *or* $T_c \le T$
Segmented	$f(T) = (T - T_b)/(T_o - T_b)$ if $T_b < T < T_o$ $f(T) = 1 - (\frac{T - T_o}{T_c - T_o})$ if $T_o \le T < T_c$ $f(T) = 0$ if $T \le T_b$ or $T_c \le T$
Beta	$f(T) = \left(\frac{(T - T_b)}{(T_o - T_b)}\right)\left(\frac{(T_c - T)}{(T_c - T_o)}\right)^{\left(\frac{(T_c - T_o)}{(T_o - T_b)}\right)^c}$ if $T > T_b$ and $T < T_c$ $f(T) = 0$ *if* $T \le T_b$ *or* $T \ge T_c$

T: Mean daily temperature (experimental temperature), T_b: basic temperature, T_{O1}: lower optimal temperature, T_{O2}: upper optimal temperature, and T_c: ceiling temperature; all in degrees Celsius.

RESULTS

Temperature Response of *T. daenensis* and its Quantification

Analysis of variance revealed a significant effect of temperature (5, 10, 15, 20, 25, 30, 35, and 40 °C) on the germination characteristics of *T. daenensis* seeds at the 5% level (Table 2). Based on the comparison of mean traits (Fig. 1), it can be stated that at 5 °C, the germination percentage of *T. daenensis* seeds was zero, and germination improved with increasing temperature from 5 °C to 10 °C, reaching 20% at 10 °C, along with an increased germination rate. As the temperature increased to 15 and 20 degrees Celsius, both germination percentage and rate increased. Increasing the temperature to 25 °C did not significantly affect the germination percentage or rate compared to 20 °C. At 20 °C, the germination percentage reached its maximum (86.66%), and the germination rate also increased to 6.52 Compared to 25 °C, germination characteristics significantly decreased when the temperature was increased to 30 °C. Germination characteristics of *T. daenensis* seeds were reduced considerably when the temperature was increased to 35°C. At 35°C, the germination percentage decreased to 10.66%, and the germination rate dropped to 0.71. The germination percentage declined to zero as the temperature increased to 40 °C. Therefore, *T. daenensis* seeds exhibit a broad germination range from 10 to 35 °C, indicating their potential as a cold- and heat-tolerant medicinal plant for cultivation in natural resources areas. The germination response of *T. daenensis* seeds to varying temperatures was quantified using segmented, dent-like, and beta models (Table 3). The segmented model predicted a basic temperature of 6 °C, an optimum temperature of 20 °C, and a ceiling temperature of 36 °C, with R^2 and RMSE values of 0.99 and 0.06, respectively, indicating a high degree of fit and accurate prediction of cardinal temperatures for seed germination in *T. daenensis* (Fig. 2). In the dent-like model, the basic temperature was predicted to be 6 °C, the lower optimal temperature 19 °C, the upper optimal temperature 21°C, and the ceiling temperature 37 °C, with R^2 and RMSE values of 0.98 and 1.10, respectively. Considering the slight decrease in R^2 and the slight increase in RMSE, it can be concluded that this model has a fitting accuracy for estimating the cardinal temperatures of *T. daenensis* seeds compared to the segmented model (Fig. 2). The beta model predicted a basic temperature of 6 °C, an optimum temperature of 18 °C, and a ceiling temperature of 35 °C. The R^2 and RMSE values were 0.92 and 0.35, respectively. These results indicate that this model is not as suitable as previous models for predicting cardinal temperatures of *T. daenensis* seeds (Fig. 2).

Temperature Response of *T. kotschyanus* and its Quantification

Analysis of variance revealed a significant effect of temperature (1, 5, 10, 15, 20, 25, 30, 35, and 40 °C) on the germination characteristics of *T. kotschyanus* seeds at the 5% level (Table 2). Based on the comparison of mean traits (Fig. 1), it can be stated that at 5 °C, the germination percentage of *T. kotschyanus* seeds was zero. As the temperature increased from 5 °C to 10 °C, germination improved slightly, reaching 25.33% at 10 °C, and the germination rate also improved. With a further increase in temperature to 15 °C, both germination percentage and rate increased. At 20 °C, the germination percentage reached its maximum (37.33%), and the germination rate also increased to 2.39. When the temperature was increased to 30 °C, germination characteristics decreased significantly compared to 25 °C. At 35 °C, germination characteristics of *T. kotschyanus* seeds decreased significantly, with the germination percentage dropping to 6.66% and the germination rate decreasing to 0.43. When the temperature was increased from 35 °C to 40 °C, the germination percentage decreased to zero. Therefore, *T. kotschyanus* seeds can germinate within a temperature range from 10 to 35 degrees Celsius. This indicates that *T. kotschyanus*, as a forage plant, exhibits a high tolerance to cold and hot temperatures and thus has a strong potential for cultivation and adaptation in natural habitats. The germination response of *T. kotschyanus* seeds to different temperatures was quantified by using segmented, dent-like, and beta models (Table 3). In the segmented model, the basic temperature was predicted to be 5 °C, the optimum temperature 22.2 °C, and the ceiling temperature 24.35 °C, with R^2 and RMSE values of 0.87 and 0.10, respectively. Considering the slight increase in RMSE, it can be concluded that this model has a lower fitting accuracy for estimating the cardinal temperatures of *T. kotschyanus* seeds compared to the dent-like model (Fig. 2). In the dent-like model, the basic temperature was predicted to be 5 °C, the lower optimal temperature 17.47 °C, and the upper optimal temperature 19.73 °C, with a ceiling temperature of 34.24 °C. The R^2 and RMSE values were predicted to be 0.92 and 0.08, respectively, indicating this model's high degree of accuracy in fitting the data and predicting the cardinal temperatures of seed germination in *T. kotschyanus* (Fig. 2). The beta model predicted a basic temperature of 5 °C, an optimum temperature of 18 °C, and a ceiling temperature of 36.12 °C. The R^2 and RMSE values were 0.85 and 14.0, respectively, indicating that this model is not as suitable as previous models for predicting cardinal temperatures of *T. kotschyanus* seeds (Fig. 2).

The results of this study indicate that the segmented model is the most accurate regression function for determining cardinal temperatures. The segmented regression function outperforms the other two functions, as evidenced by the lowest RMSE (Root Mean Square Error) and the highest correlation coefficient. The results of the fitted models between germination rate and temperature are presented in Table 2.

Temperature Response of *T. lancifolius* and its Quantification

Analysis of variance revealed a significant effect of temperature (1, 5, 10, 15, 20, 25, 30, 35, and 40 °C) on germination characteristics of *T. lancifolius* seeds at the 5% level (Table 1). Based on the comparison of mean trait values (Fig. 1), it can be stated that at 5 °C, seed germination of *T. lancifolius* was zero. As the temperature increased from 5 °C to 10 °C, germination significantly increased, reaching 48% at 10 °C. With further increases in temperature to 15 °C and 20 °C, both germination percentage and rate continued to rise. However, there was no significant difference in germination percentage or rate between 20 °C and 25 °C. The highest germination percentage (92%) and germination rate (6.98) were observed at 20 °C. At 30 °C, germination characteristics significantly decreased compared to 20 °C. When the temperature was increased to 35°C, germination characteristics of *T. lancifolius* seeds decreased significantly, with the germination percentage dropping to 8% and the germination rate to 0.5. At 40 °C, germination was completely inhibited. Our findings indicate that *T. lancifolius* seeds show optimal germination between 10 °C and 35 °C, implying their adaptability to a broad spectrum of climatic conditions. This adaptability suggests the potential for successfully cultivating *T. lancifolius* in various natural habitats, providing valuable insights for agricultural professionals and botanists. The germination response of *T. lancifolius* seeds to varying temperatures was modeled using segmented, dent-like, and beta functions (Table 3). The segmented model yielded basic, optimum, and ceiling temperatures of 7.58, 15.25, and 36.19 °C, respectively, with an R^2 of 0.97 and RMSE of 0.16. While providing a good fit, the slightly higher RMSE value indicates that the segmented model may be marginally less accurate in estimating *T. lancifolius* seeds' cardinal temperatures than the dent-like model (Fig. 2). In the dent-like model, the basic temperature was predicted to be 7.58 °C, the lower optimal temperature 15.10 °C, the upper optimal temperature 15.65 °C, and the ceiling temperature 36.19 °C. The R^2 and RMSE values were 0.97 and 0.15, respectively, indicating this model's high degree of accuracy in fitting the data and predicting the cardinal temperatures of germination for *T. lancifolius* seeds (Fig. 2). The beta model estimated the basic temperature at 6.03 °C, the optimum temperature at 17.01 °C, and the ceiling temperature at 36.70 °C. The R^2 and RMSE values were 0.87 and 0.48, respectively, indicating that despite a slight increase in RMSE, the model exhibited a lower goodness-of-fit in estimating the cardinal temperatures of *T. lancifolius* seeds compared to the segmented and dent-like models (Fig. 2).

Table 2 Summary of analysis of variance showing the mean square values of germination percentage and rate of germination in three thyme species seeds under eight temperatures

S.O.V	df	*T. daenensis*		*T. kotschyanus*		*T. lancifolius*	
		Germination %	Germination rate	Germination %	Germination rate	Germination %	Germination rate
Treatment	7	3294.09 **	17.13 **	718.85 **	8.19 **	4464.66 **	29.01 **
Error	16	43.52	0.200	36.28	0.13	28.09	0.14
CV %		6.6	7.9	7.3	7.2	9.6	8.3

**: Significant at 1% probability level.

Table 3 Estimated parameters of cardinal temperatures of thyme species using the segmented, Dent-like and beta models

Species	Cardinal temperature	Segmented model	Dent-like model	Beta model
T. daenensis	Base temp.	6 °C	6 °C	6 °C
	Optimum temp.	20 °C	19-21 °C	18 °C
	Maximum temp.	36 °C	37 °C	35 °C
	RMSE	0.06	0.11	0.35
	R^2	0.99	0.98	0.92
T. kotschyanus	Base temp.	5 °C	55 °C	5°C
	Optimum temp.	20.22 °C	17.47-19.73 °C	18 °C
	Maximum temp.	35.24 °C	34.24 °C	36.12 °C
	RMSE	0.10	0.08	0.14
	R^2	0.87	0.92	0.85
T. lancifolius	Base temp.	7.58 °C	7.58 °C	6.03 °C
	Optimum temp.	15.25 °C	15.10-15.65 °C	17.01 °C
	Maximum temp.	36.19 °C	36.19 °C	36.70 °C
	RMSE	0.16	0.15	0.48
	R^2	0.97	0.97	0.87

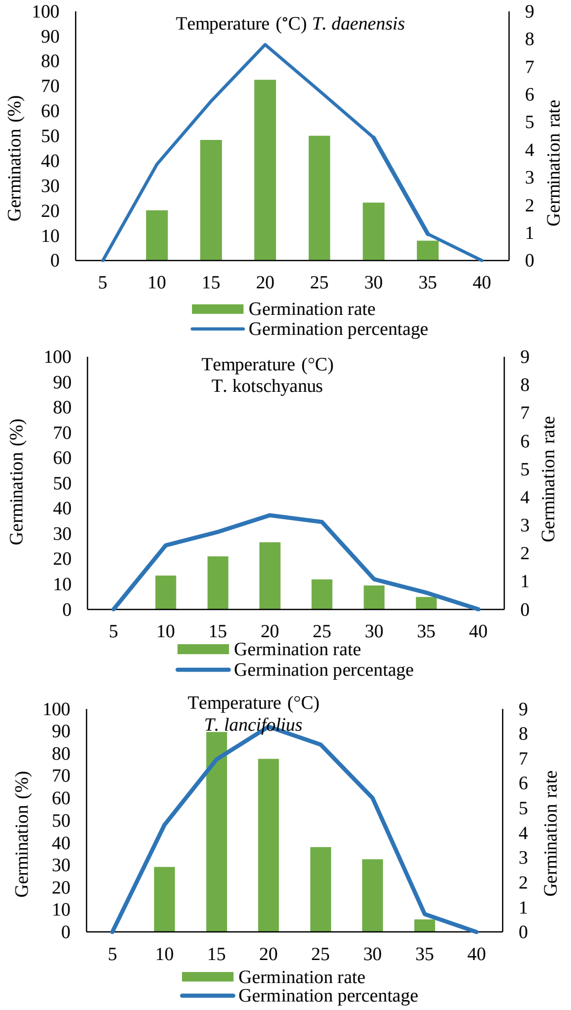
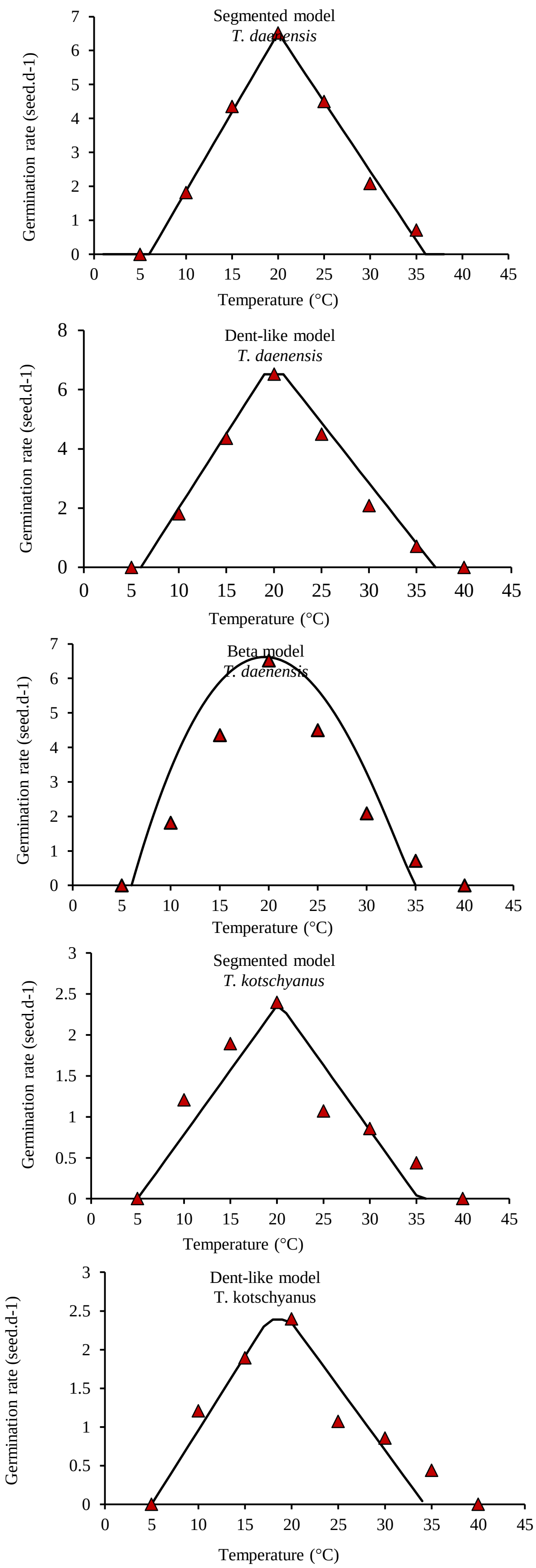


Fig. 1 Trends of variations for germination percentage and rate of thyme species seeds under different temperatures



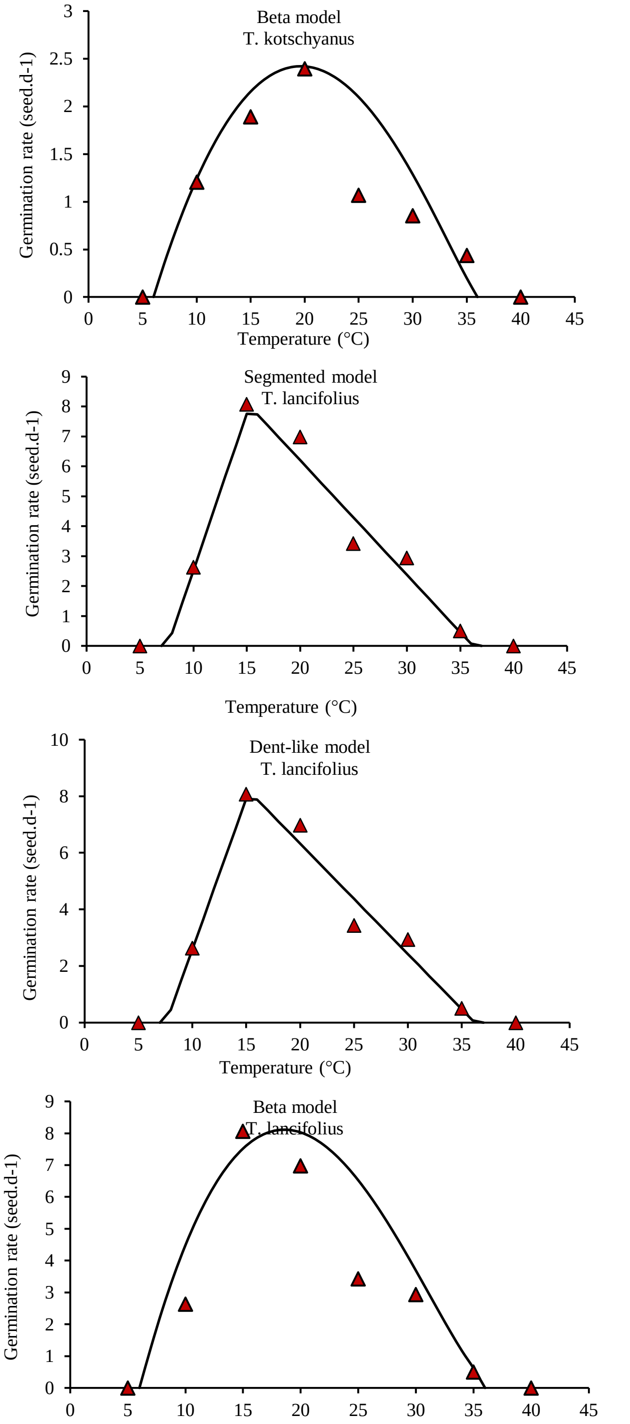


Fig. 2 The relationship between temperature and germination rate of *three thyme species* based on segmented, Dent-like and beta models

DISCUSSION

The response of seed germination and seedling emergence to temperature and the identification of cardinal temperatures (basic, optimum, and ceiling) are examined for developing predictive models of germination and emergence, selecting appropriate planting dates, screening species and genotypes for tolerance to low or high temperatures, and determining geographic regions where species or genotypes can successfully germinate and establish, [5]. Quantitative analysis of seed germination responses to varying temperatures suggests that the segmented model provides the most accurate germination predictions for *T. daenensis*. In contrast, a dent-like model is optimal for *T. kotschyanus* and *T. lancifolius*. These results indicate that a fixed model cannot be proposed for all species within a genus. Therefore, it can be stated that germination response to temperature depends on various factors, including plant species, variety, geographic origin, seed quality, and time after harvest [28]. Temperature significantly influences seed germination in three thyme species (*T. kotschyanus, T. daenensis, and T. lancifolius*). The optimal temperature ranges for germination were determined to be 19-21 °C for *T. daenensis*, 17.47-19.73 °C for *T. kotschyanus*, and 15.10-15.65 °C for *T. lancifolius*. This experiment showed that the different thyme species studied had similar germination peaks due to similar initial growth rates. [12] investigated the germination characteristics of several medicinal plants. They found that *Nepeta binaludensis* and *Nepeta crassifolia* exhibited the highest germination percentages at 20-30 °C, *Nepeta glomerulosa* at 20-25 °C, *Zataria multiflora* at 15-25 °C, and *Thymus kotschyanus* at varying optimal temperatures. The study suggested that the optimal germination temperature of seeds is influenced by the plant's genetics and the climatic conditions of its growth environment. For most plant species, the optimal germination temperature has been reported to be between 15 and 30 degrees Celsius [29]. By determining cardinal temperatures, it is possible to assess the geographical limitations of species and choose the most suitable planting time [30]; [31, 32, 33]. Temperatures above the optimal imbibition temperature can prevent seeds from entering the third germination phase [7]. This elevated temperature may stimulate the biosynthesis of the inhibitory hormone abscisic acid and, conversely, inhibit the synthesis of the growth hormone gibberellin [7]. Furthermore, the decreased germination observed at temperatures exceeding 30 °C in the studied species is likely due to alterations in essential proteins. It has been reported that increased temperature limits the germination capacity of several perennial grasses, such as *Lolium* and *Festuca*, by inducing secondary dormancy until germination occurs under suitable environmental conditions [34]. In addition to the effects above, increased temperature can lead to seed deterioration [35]. Although the germination percentage decreased with the increasing temperature of all three species studied, *T. lancifolius* exhibited a higher germination percentage than the other two species at temperatures above the optimum (30 °C). The higher germination percentage of *T. lancifolius* at high temperatures indicates its greater adaptability for cultivation in warmer regions or during warmer months. The decrease in germination percentage at high temperatures has been reported in many other plants, including *Plantago* [36], *Papaver* 37], *Scabiosa*, and *Cannabis* [16]. Decreased germination at low temperatures is attributed to reduced cellular respiration of the seed embryo during imbibition. Numerous studies have reported that low temperatures diminish gas exchange and oxygen availability, inhibiting cellular respiration and hindering embryo growth [38]. Alternatively, some researchers have postulated that the reduced growth rate at low temperatures might be due to decreased auxin production in the embryonic radicle. Thus, the auxin produced at low temperatures may not support thyme embryo growth. Furthermore, reduced cellular metabolism at low temperatures also contributes to decreased germination. Among the studied species, *T. lancifolius and T. daenensis* exhibited higher germination percentages at lower temperatures (15°C), indicating a higher adaptability for cultivation in temperate regions or months. Studies on poppy seeds [37] and sunflower seeds [5] have shown that germination rate and percentage increase with increasing temperature up to a certain point and then decrease more sharply at higher temperatures, which is in agreement with the present study.

CONCLUSION

Based on the results, the dent-like model provided the best fit for *T. lancifolius* with a basic temperature of 7.58 °C, a lower optimum temperature of 15.10 °C, an upper optimum temperature of 15.65 °C, and a ceiling temperature of 36.19 °C, with R^2 and RMSE values of 0.97 and 0.15, respectively. For *T. kotschyanus*, the dent-like model with a basic temperature of 5 °C, lower optimum temperature of 17.47 °C, upper optimum temperature of 19.73 °C, and a ceiling temperature of 34.24 °C, and R^2 and RMSE values of 0.92 and 0.08, respectively, also showed a good fit. However, for *T. daenensis*, the piecewise model with an essential temperature of 6 °C, optimum temperature of 20 °C, and ceiling temperature of 36 °C, and R^2 and RMSE values of 0.99 and 0.06, respectively. The results of this study, which was conducted with great care and attention to detail, confirmed that in the absence of other limiting factors (such as light and water), seed germination of thyme species is highly influenced by temperature. Due to their similar initial growth rates, the different thyme species studied have similar germination peaks. Additionally, the results showed that the dent-like is the best model for predicting cardinal temperatures in *T. lancifolius* and *T. kotschyanus*, while the segmented model is the best for *T. daenensis*. This leads to the conclusion that a fixed model cannot be proposed for all species within a genus. The importance of this research cannot be overstated, as it provides valuable insights into the germination characteristics and plant domestication potential of thyme species, thereby contributing to the body of knowledge in this field. *T. lancifolius* shows high adaptability for cultivation in warmer regions or during warmer months, while *T. daenensis* and *T. lancifolius* exhibit high adaptability for cultivation in temperate regions or during cooler months. Thus, the impact of cardinal temperatures on seed germination helps evaluate germination characteristics or establishment potential of plant species and is particularly important in plant domestication.

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