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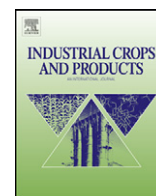139 PUBLICATIONS   3,608 CITATIONS

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ABSTRACT

The response of plant development rate (including germination rate) to temperature might be described as a non-linear function. We compared 3 non-linear regression models (Dent-like, segmented and beta) to describe the germination rate-temperature relationships of opium poppy (*Papaver somniferum* L.) over 6 constant temperatures to find cardinal temperatures and thermal time required to reach different germination percentiles. 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, coefficient of determination (R^2), intercept and slope of the regression equation of predicted vs. observed germination rate) were applied to compare their performance. The segmented was found to be the best model to predict germination rate ($R^2 = 0.92$, MAE = 0.0011 and CV of 1.4–3.6%). Estimated cardinal temperatures were similar for different germination percentiles ($P < 0.05$). Base on the model outputs, the base, the optimum and the maximum temperatures for germination were estimated as 3.02, 27.36 and 36.31 °C. The thermal time required to reach 50 and 95% germination was 57.27 and 87.55 degree-days, respectively. Model predictions of the time required for seed germination agreed reasonably well with the observed times (MAE = 0.56 day, $R^2 = 0.887$). All model parameters may be readily used in crop simulation models.

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1. Introduction

Seed germination is a complex biological process that is influenced by various environmental and genetic factors (Shafii and Price, 2001) and is considered as one of the most critical periods in the life cycle of plants (Ungar, 1978). Environmental conditions directly surrounding a seed determine germination success and subsequent seedling emergence and establishment (Harper, 1977). Temperature and water mainly drive the rate of seed germination when aeration is not restrictive (Gummerson, 1986a,b). When moisture is adequate, both the rate and final fractional germination of a sample of viable seeds are controlled by temperature

(Dubertz et al., 1962; Heydecker, 1977; Bierhuzen and Wagenvoort, 1974). Temperature is the most important driving force influencing crop development rate (Kamkar et al., 2008). The effects of temperature on plant development are the basis for models used to predict the timing of germination. Three cardinal temperatures (base, optimum and maximum) describe the range of temperature over which seeds of a particular species can germinate (Bewley and Black, 1994). Estimation of the cardinal temperatures is essential because rate of development increases between base and optimum, decreases between optimum and maximum, and ceases above the maximum and below the base temperatures (Mwale et al., 1994; Shafii and Price, 2001).

For most crop plants, the response of germination rate to temperature can be simplified to a bilinear response. There is usually a positive linear relationship between the rate of germination (defined as the reciprocal of the time taken for a given fraction of the seed population to germinate) and temperature (T), up to a well-defined optimum temperature (T_o) (Hegarty, 1973). Studies on seeds of different crops have shown that above T_o there is a negative

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and approximately linear relationship between the 2 parameters (Garcia-huidobro et al., 1982; Covell et al., 1986; Mohammed et al., 1988). The intersection of the 2 regression lines defines T_o, while extrapolation of the same lines to the temperature axis allows the estimation of temperature limits for germination: the base (T_b) and maximum temperature (T_m). The reciprocal of the slope between T_b and T_o is the thermal time required, i.e., the integral of time and temperature (degree-hours) for germination within the given temperature range (Monteith, 1977). Other non-linear models have been used also to quantify cardinal temperatures.

To accurately predict crop phenology, a non-linear function is needed to describe development rate over the full range of temperatures for plant development (Jame and Cutforth, 2004). Numerous non-linear functions of plant development rate vs. temperature have been proposed (Robertson, 1968; Shaykewich, 1995) including the case of germination (e.g., Garcia-huidobro et al., 1982). Non-linear curves may be used to model the time course of germination at various temperatures (Shafii and Price, 2001). This kind of regression models have been used to describe development rate in many crops. Angus et al. (1981) showed that development rate from sowing to radicle emergence responds to temperature following a non-linear function. Blackshow (1991) used a logistic model to study the emergence rate of wheat in terms of soil temperature and water potential. Kamkar et al. (2005, 2008) also used segmented and logistic models to determine cardinal temperatures of germination in 3 millet varieties and emergence in wheat cv. "Tajan". Many types of functions such as the beta (Yin et al., 1997), the power (Stapper and Lilley, 2001), the exponential (Angus et al., 1981), the sigmoid, and intersected functions (Kamkar et al., 2005, 2008) have been used to describe crop responses to temperature. Carberry and Campbell (1989) showed that cubic polynomials could describe the rates of development for germination and coleoptile elongation over the temperature range of 15–40 °C in pearl millet. Population-based modeling approaches to predict germination as a function of temperature and/or water potential have been well developed in the last 2 decades based on thermal time (Garcia-huidobro et al., 1982) or hydrothermal time (Gummerson, 1986a,b; Bradford, 1995; Finch-Savage et al., 1998; Allen et al., 2000). Several studies have illustrated the effectiveness of using thermal time models to predict germination in a variety of species including common lambsquarters (*Chenopodium album* L.), winterfat (*Eurotia lanata* (Pursh) Moq.), pearl millet (*Pennisetum glaucum* (L.) R. Br.), lentil (*Lens culinaris* Medik.), and many grasses (Ellis and Barrett, 1994; Hardegree and Van Vactor, 1999; Leblanc et al., 2003; Larsen and Bibby, 2005; Hardegree, 2006; Qiu et al., 2006; Qualtiere, 2008). The thermal time model has been implemented successfully in predicting phenology of crops and weeds as well as seed germination under non-water limiting conditions (Garcia-huidobro et al., 1982; Covell et al., 1986). Imbibed seeds are capable of germination in accordance with the accumulated thermal time, i.e., the temperature in excess of a base temperature (Garcia-huidobro et al., 1982). Once the base temperature for germination of a seed population is known, germination times may be normalized on a common thermal time scale (Dahal and Bradford, 1994).

A clear understanding of the germination responses of seeds is useful in screening for tolerance of crops and cultivars to either low or high temperatures and in identifying geographical areas where a species or genotype can germinate and establish successfully by using the cardinal temperatures. Information on cardinal temperatures is lacking for germination of opium poppy (*Papaver somniferum*), as one of the most important crops for the pharmaceutical industry for the production of natural opiate alkaloids, mainly morphine, codeine and the baine, that are extracted mainly from the crushed dried capsules emptied of seeds (Mahdavi-Damghani et al., 2010). This study was carried out to formulate and validate non-linear regression models that can be used to quantify cardinal temperatures and the effect of temperature on the time from sowing to germination of opium poppy.

2. Materials and methods

A 2 replicated experiment carried out to find cardinal temperatures of opium poppy (*P. somniferum* L.). The Cultivar "Madrigal" which is a commercial from Alcaliber SA (Spain) was used. The seeds had been harvested in June 2002. Seed viability was tested on 50 seeds in 4 replicates and was determined around 94.3%. Both replicates conducted in 2004 using germinators with controlled environments at the Instituto de Agricultura Sostenible of CSIC in Cordoba, Spain. In each replication of the experiment, 4 replicates of 80 seeds were germinated in 9 cm diameter Petri dishes on 2 layers of Whatman Cat. No. 1001 150 (9 cm diameter) filter paper containing 10 ml of distilled water. The seeds were incubated in the dark at 6 temperatures (from 10 °C to 35 °C with 5 °C intervals). Temperature in the germinators was measured using thermocouples.

A seed was considered as germinated when its radicle protruded through the seed coat at least 2 mm. At this stage, no differentiation between normal and abnormal seedlings was made. Germinated seeds were counted in different time intervals based on observed germination rate under different temperatures, with shorter and longer periods for higher and lower temperatures, respectively. Counting finished when no seed germinated during 2 consecutive days. The time from the beginning of incubation to the last germination was considered as the total time to maximum germination. Cumulative germination percentage was plotted against time (h). From this curve, time to 50% of germination was determined by fitting a logistic model to cumulative germination percentage (*G*) against time (*t*, h) as below:

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

G_x is the maximum germination percentage, b is the time for 50% germination and a is a parameter. The time for 5%, 10%, 90% and 95% germination were also determined by interpolation and are designated as D5, D10, D90 and D95.

The reciprocal of time to reach cumulative germination percentage to 50% of total germinated seeds was considered as the germination rate (G_R). To quantify the response of germination rate to temperature and to determine cardinal temperatures for germination, the following model was used:

$$\frac{1}{e} = \frac{f(T)}{f_o} \tag{2}$$

where $f(T)$ is a temperature function (reduction factor) that ranges between 0 at the base and ceiling temperature and 1 at optimal temperature(s) and $1/f_o$ is the inherent maximum rate of germination at optimal temperature estimated via iterative optimization method using the NLIN procedure. Thus, f_o indicates the minimum number of hours for germination at optimal temperature (Soltani et al., 2006). $1/e$ also shows germination rate of a given percentile.

An iterative optimization method was applied to calibrate the models (dent-like, segmented and beta; Table 1) based on the NLIN procedure in Microsoft Excel ver. 2003. For this purpose, mean absolute error (MAE; Eq. (3)), coefficient of determination (R^2; Eq. (4)), intercept and slope of the regression equation of predicted vs. observed germination rate, were used as criteria to detect the best estimates of parameters (lower biases of the intercept from 0 and the slope from 1 are criteria for more reliability). MAE was used because it avoids compensation between probable under- and over-prediction.

$$\text{MAE} = \frac{1}{n}\sum_{i=1}^{n} |D_i| \tag{3}$$

Table 1
Dent-like, segmented and beta models were fitted to germination rate vs. different constant temperatures, where T is the temperature, T_b the base temperature, T_o the optimum temperature, T_{o1} the lower optimum temperature (for dent-like function), T_{o2} the upper optimum temperature (for dent-like function), T_m the ceiling temperature and a^* is the shape parameter for the beta function which determines the curvature of the function.

Function	Formula
Dent-like (Abr. D)	$f(T) = \frac{(T-T_b)}{(T_{o1}-T_b)}$ if $T_b < T < T_{o1}$ $f(T) = \frac{T_m - T}{T_m - T_{o2}}$ if $T_{o2} < T < T_m$ $f(T) = 1$ if $T_{o1} \le T \le T_{o2}$ $f(T) = 0$ if $T \le T_b$ or $T \ge T_m$
Segmented (Abr. S)	$f(T) = \frac{T-T_b}{T_o - T_b}$ if $T_b < T < T_o$ $f(T) = 1 - \left(\frac{T-T_o}{T_m-T_o}\right)$ if $T_o \le T < T_m$ $f(T) = 0$ if $T \le T_b$ or $T \ge T_m$
Beta (Abr. B)	$f(T) = \left(\left(\frac{(T-T_b)}{(T_o-T_b)}\right) \times \left(\frac{(T_m-T)}{(T_m-T_o)}\right)\right)^{((T_m-T_o)/(T_o-T_b))^{a^*}}$

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

where D_i is difference between measured and calculated values. SSR is sum of squares (SS) of regression ($\sum_{i=1}^{n}(\hat{Y} - \bar{Y})$) and SST is total SS ($\sum_{i=1}^{n}(Y_i - \bar{Y})$). Y_i is observed value and $\hat{Y}$ is correspondent estimated value.

Estimated parameters by non-linear models were exposed to descriptive statistics analysis for the pooled datasets. Then the best estimated values were used to calculate thermal-time needed for each germination percentile.

2.1. Thermal time determination

Daily thermal time (DTT) also was calculated as $(T_o - T_b) \cdot f(T)$, where $f(T)$ is the temperature function, T_o is the optimum temperature, and T_b is the base temperature. The first component of daily thermal time is constant and non-optimal temperatures will affect daily thermal time through $f(T)$.

3. Results

Models fitted to relative germination rate vs. mean temperature for pooled datasets and 3 percentiles (D10, D50 and D90) are presented in Fig. 1, while the estimated parameters are shown in Table 2. The base and the maximum temperatures for different percentiles did not vary significantly for the 3 models. The base temperature for all percentiles for pooled data varied from 3 °C to 3.42 °C. The least coefficient of variation (CV%) for the estimated base temperature was 1.4%. Maximum temperature varied between 32 °C and 38.2 °C with the least CV of 3.6%.

According to the dent-like model for percentiles of D5, D10 and D50, the optimum temperature varied between 23.78 and 27.7 °C. This model was not reliable for D90 and D95, because of the low determination coefficient between observed and predicted values ($R^2 = 0.44$ and 0.26 for pooled data). The beta and segmented models, also, were not reliable for D90 and D95 (Tables 1 and 2), because R^2 was low for both models. The beta model overestimated germination rate in D90 ($b = 1.48$, Table 2), while R^2 was significantly low for D95 (0.62). The segmented model, also, underestimated germination rate in D90 and the dent-like was a poor model to describe germination rate against temperature (R^2 low, Tables 1 and 2). The values of mean absolute error, which avoids compensation between probable under- and over-prediction showed that the segmented and beta models are more reliable than the dent-like (Table 2), but the coefficient of variation for all cardinal temperatures indicates that the segmented model is more reliable than the beta model (Tables 1 and 2). Based on the segmented model, the

Table 2
Estimated parameters for the Dent-like, Beta and segmented models for different germination percentiles of opium poppy seeds. T_b, T_o, T_m, T_{o1}, T_{o2}, f_o, a^*, a and b are 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, coefficient of regression, intercept and slope of linear regression between predicted and observed germination rate, respectively.

Dataset I

	Dent-like						Beta						Segmented					
	D5	D10	D50	D90	D95	CV	D5	D10	D50	D90	D95	CV	D5	D10	D50	D90	D95	CV
T_b	3	3.35	3.12	3.13	3.1	4.08	3.25	3.25	3.26	3.42	3.25	2.2	3	3	3.1	3.0	3	1.4
T_o	–	–	–	–	–	–	25.88	25.26	23.82	24.59	25.91	3.5	28	27.04	26.29	27.35	28.13	2.7
T_m	35.53	37.3	34.88	35.1	32	5.46	35	38.2	34.75	34.99	35	4.1	34.79	35	36.94	37.46	37.38	3.6
T_{o1}	24.4	24	25.33	23.78	25.1	2.75	–	–	–	–	–	–	–	–	–	–	–	–
T_{o2}	25.56	27	27.75	27.1	27	2.98	–	–	–	–	–	–	–	–	–	–	–	–
f_o	44.1	55.34	59.48	91.44	81.35	–	47	50.72	67.04	119.14	120.03	–	36.96	39.94	56.47	82.00	86.32	–
a^*	–	–	–	–	–	–	1.26	1.32	1.33	0.62	0.945	–	–	–	–	–	–	–
R^2	0.75	0.911	0.93	0.44	0.26		0.895	0.91	0.97	0.58	0.626		0.92	0.91	0.93	0.55	0.575	
a	0.0011	−0.0033	−0.002	0.0015	0.0016		0.0002	0.00003	0.0004	−0.0003	0.0009		−0.0003	−0.001	−0.0027	0.0009	−0.00001	
b	0.846	1.13	1.21*	0.76	0.91*		0.98	1.009	0.97	1.48	0.62*		1.01	1.05	1.07	0.86	1.12	
MAE	0.0016	0.0018	0.0009	0.0016	0.0021		0.0013	0.0018	0.0003	0.001	0.0008		0.0013	0.0012	0.0009	0.0012	0.0014	

* For b: means significant difference with 1.
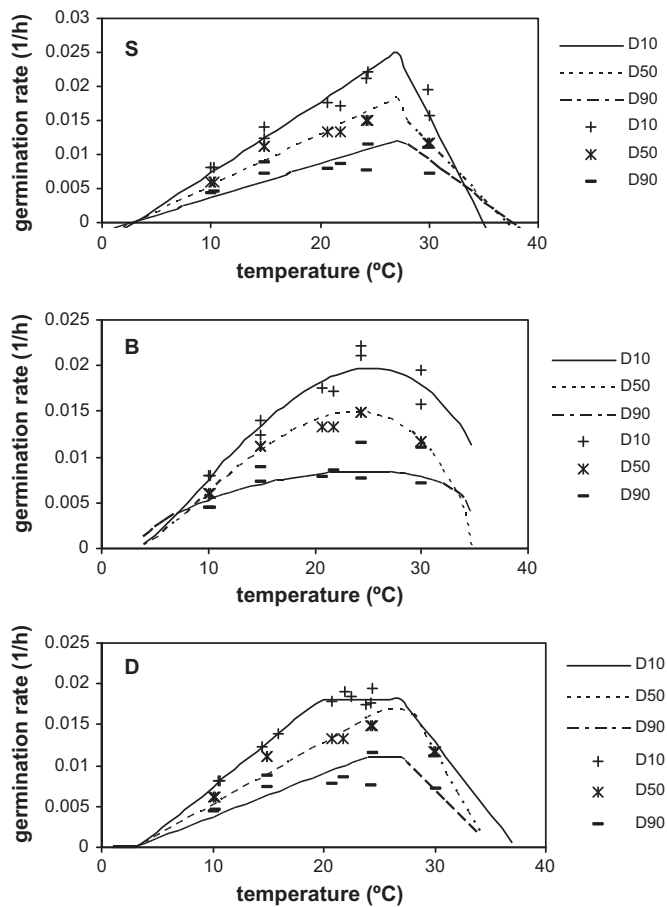
Fig. 1. Predicted (lines) vs. observed (symbols) germination rate of *Papaver somniferum* L. at different constant temperatures for different germination percentiles (D10, D50 and D90) using segmented (S), beta (B) and dent-like (D) models.
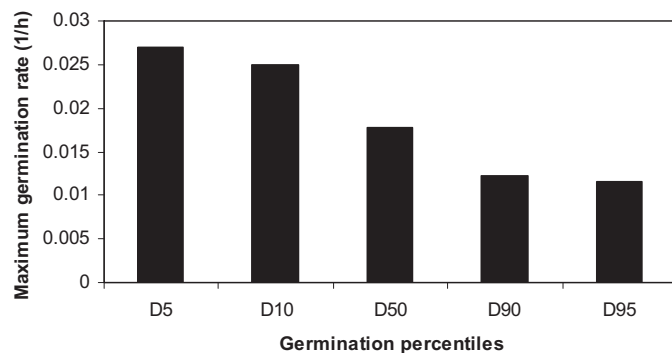

Fig. 2. Estimated maximum germination rate (1/*h*) for different germination percentiles of poppy using the segmented function.

minimum time required to D5, D10, D50, D90 and D95 percentiles were 36.96, 39.94, 56.47, 82 and 86.32 h after imbibition started. The maximum germination rate (1/f_o) is illustrated in Fig. 2.

The optimum temperatures estimated by the segmented and the beta models were within the estimated optimum temperature range of the dent-like model.

Descriptive statistics on estimated cardinal temperatures including the mean, the range (maximum–minimum), and the standard deviation also confirmed that the segmented is the best model, showing the smallest range and standard deviation (Table 3). Although the other models also had acceptable descriptive statistics in many cases, they are more uncertain because of
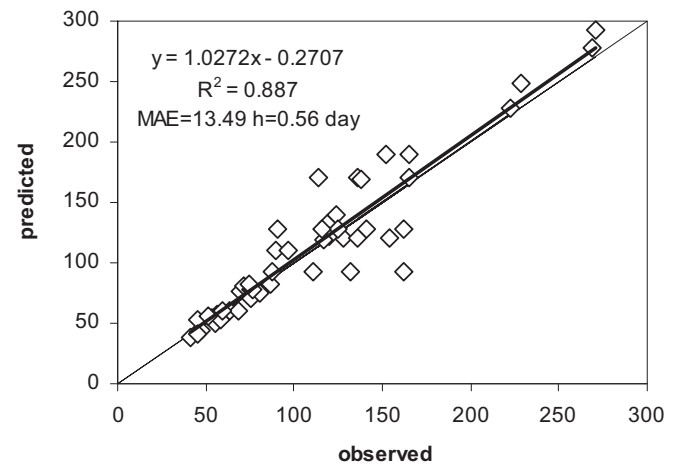
Fig. 3. Predicted (base on segmented function) vs. observed hours to germination in pooled datasets to describe response of germination rate to temperature. The fitted linear equation is not statistically different from the 1:1 line.
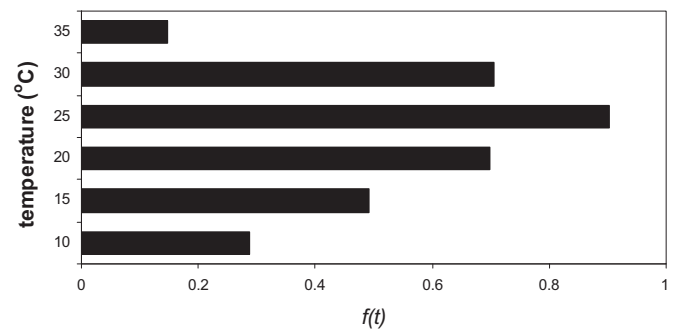

Fig. 4. $f(T)$ values for different constant temperatures base on the segmented model.

more inappropriate statistical indices (Table 3). Fig. 3 shows predicted (based on Eq. (2)) vs. observed hours to germination in the pooled datasets by the segmented model. High R^2 and regression lines not different from the 1:1 line, along with acceptable MAE confirmed the reliability of the segmented model and the estimated parameters.

3.1. Thermal time requirements

Calculated $f(T)$ for constant temperatures used in this research based on the segmented model is illustrated in Fig. 4. It is clear
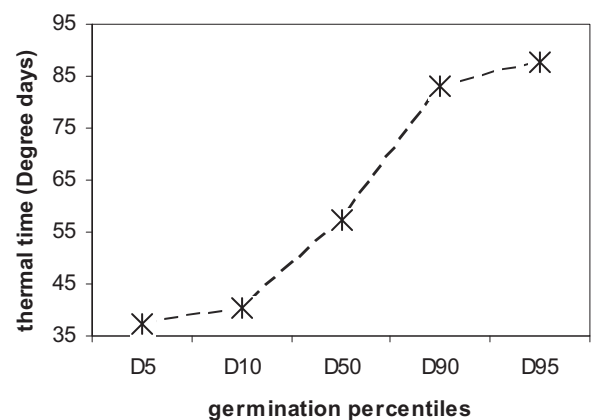

Fig. 5. Thermal time (degree-days) required for different germination percentiles in based on pooled data, when $T = T_o$.

Table 3
Descriptive statistics results on estimated cardinal temperature by different models (pooled on percentiles).

Cardinal temperature	Statistical indices	Model		
		Dent-like	Beta	Segmented
T_b	Mean	3.14	3.28	3.02
	Range	0.35	0.17	0.1
	Standard deviation	0.128	0.075	0.044
T_o	Mean	–	25.09	27.36
	Range	–	2.09	1.84
	Standard deviation	–	0.892	0.74
T_m	Mean	34.96	35.58	36.31
	Range	5.3	3.45	2.67
	Standard deviation	1.9	1.46	1.3
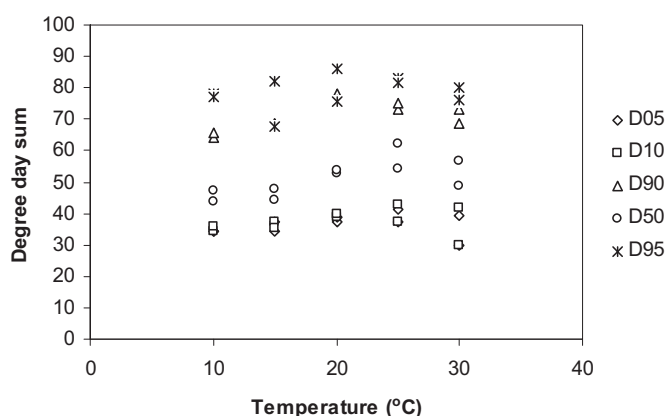
Fig. 6. Regression between the degree day sums and the mean temperatures to test independency between the degree day sums and the temperatures for pooled data and different germination percentiles.

that temperatures closer to T_o have a small reducing effect on germination rate (see Eq. (2)). Using the estimated parameters of the segmented model, each germination percentile will be achieved when $\sum DTT = TT$, or $\sum f(T) = f_0$, or $\sum f(T)/f_0 = 1$.

The calculated thermal times for each germination percentile based on pooled data are presented in Fig. 5. Our results confirm the certainty of the estimated parameters and the reliability of the segmented model. Thus mean values of cardinal temperatures of the 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 our experiment confirmed independency between the degree day sums and the temperatures of trials (Fig. 6). This independency has emphasized by Bonhomme (2000) in using degree days unit in such experiments.

4. Discussion

Bare et al. (1978) stated that temperature plays an important role in the regulation processes, even at the germination phase. This may be manifested in the blockage (Bare et al., 1978) or induction of germination, or in influencing the whole course of germination. Practical research is usually concerned with the determination of the minimum temperature required for germination or its maximum range (Földesi, 1994). Bare et al. (1978) using a modern thermogradient germinator to determine the temperature dependence of seed germination of *P. somniferum* variety of Afghan origin found that this variety germinated between a minimum of 8 °C and a maximum of 35 °C. Other results (e.g., Dobos and Bernáth, 1985) have indicated that the germination of *P. somniferum* varieties and their requirements reflect their earlier adaptation processes. Pop-

ulations from Spain taken from the UN collection had the same characteristics as wild types, i.e., seed showed a very low germination percentage and the inhibition of germination at low (no germination at 5 °C) and relatively high temperature regimes (25–30 °C) was also noted. Comparison of the germination characteristics of spring (*P. somniferum* cv 'Kék Duna' from Hungary) and autumn types (*P. somniferum* cv 'Ankara' from Turkey) shows another aspect of adaptation. The optimum range for the spring variety is between 10 °C and 25 °C, but this shifts to 15–30 °C for the variety with an autumn–spring cycle. The higher heat sensitivity of the spring variety is also apparent as a temperature of 30 °C causes partial inhibition of germination; while 35 °C results in total inhibition. These confirmed by our study and a previous work by Bare et al. (1978). This may be interpreted as a form of adaptation of spring varieties, which have a protective mechanism to prevent themselves from germinating at higher temperatures and are capable of rapidly initiating their physiological processes in early spring. Dobos and Bernáth (1985) reported that germination of the spring varieties occurs at temperatures above 2–3 °C, but the optimum is 7–10 °C. They also reported that the optimum germination temperature of the winter poppy, however, is around 15–20 °C. They defined germination as rupture of the testa until the appearance of the cotyledones.

All the above studies show that contradictions in reported values on the cardinal temperatures of opium poppy are origin-specific and maybe even taxa-specific. For example, Popov et al. (1975) reported that varieties of Eurasian origin could not tolerate temperatures lower than 7 or 8 °C. However, materials classified as being part of the Anatolian group are able to survive at much lower temperatures. This may be correct for germination responses. Different reported values suggest that the response of opium poppy germination to temperature may depend on the variety.

On the other hand, optimum temperature for the genus Papaver has been reported in a wide temperature range (e.g., 15–30 °C or 10–25 °C; as cited by Bernáth, 2006). Germination of *papaver* seeds in darkness over 30 isotherms from 6 °C to 35 °C was studied by Bare et al. (1978). They showed that *P. somniferum* germinated in darkness from 8 °C to 35 °C which is coincident with our findings on the ceiling temperature, but not for the base temperature. In this study, they reported that maximum germination and germination rate (as summing of the quotients produced by dividing the number of seeds germinated by the number of days on which the count was made) was from 13 °C to 33 °C. According to Bare et al. (1978) the maximum germination rate ranged between 22 °C and 30 °C. The dent-like model results for optimum temperature also showed that optimum temperature for poppy might vary from 24 °C to 27.75 °C (Table 2). In addition, the optimum temperature base on segmented model also is located in this range. These findings reveal that with assuming a stochastic seed germination response for *P. somniferum*, the values upper than 22 °C are more probable. To determine pre-

cise range of optimum temperature, more temperatures with small increments between 20 °C and 30 °C are advised to test.

It seems that different reports on cardinal temperatures of poppy stem from 2 reasons: In some cases, the germination phase is defined from the rupture of the testa until the appearance of the first leaves. Under optimum conditions the duration of this period for opium poppy is 15–20 days (Bernáth, 2006), thus it includes processes beyond seed germination. While in routine germination experiments is defined as the period from seed imbibition until the radicle protrudes through the seed coat at least 2 mm.

Another reason for variability in cardinal temperatures of *P. somniferum* ssp. *somniferum* which has been cultivated from ancient times, is the loss of its dormancy, because of artificial selection (Karlssson and Milberg, 2007). This is another important factor to interpret different reports on cardinal temperature and other temperature-related parameters in the poppy family.

5. Conclusions

Our data suggest that the bilinear-shape response model of germination rate to temperature may be used to estimate the cardinal temperatures of opium poppy. In this model, germination rate is regressed separately against temperature, both for those below and above optimum temperature. Then T_b and T_m are the intercepts of each regression line and T_o is calculated from the intersection of the 2 linear regression lines (Covell et al., 1986; Phartyal et al., 2003). In this model, the thermal time requirement for germination for each percentile is calculated from the reciprocal of the slope of the regression equation of rate of germination vs. temperature below the optimum (Thornley, 1987).

The results of the present study confirm that, in the absence of other limiting factors (e.g., water, light and media), the germination of cultivated poppy (*P. somniferum* L.) seed is largely influenced by temperature. In addition, our results indicate that the germination rate of poppy based on the segmented model often has sharply defined cardinal temperatures. The germination rate increased linearly with temperature in the range of 3.02–27.36 °C and decreased linearly in the range of 27.36–36.31 °C. Then T_b and T_m are considered as extreme temperatures in crop modeling. Ong and Monteith (1985) stated that in general, temperate crops germinate between 0 °C and 35 °C, which is basically coincident with the range found for poppy during the germination stage. Base on the model outputs, the base, the optimum and the maximum temperatures for germination were estimated as 3.02, 27.36 and 36.31 °C. These mean values of cardinal temperatures may be used in thermal unit calculations to predict occurrence of different percentiles of poppy seed germination.

The thermal time required to reach 50 and 95% germination based on the segmented model was 57.27 and 87.55 degree-days, respectively. Model predictions of the time required for seed germination agreed reasonably well with the observed times.

The functions developed herein are valid only under no additional limiting factors (lack of water, salinity, etc.). Additional reduction factors should be included in Eq. (2) to tackle with those situations. Also, these cardinal temperatures are just relevant for the cultivated type of poppy, but not for wild populations where seed dormancy would be the main factor regulating seed germination response to temperature. The temperature-related parameters, which were quantified here, provide the basic values are needed to predict time from seeding to germination of opium poppy, as the first development phase. The modelers can add thermal time requirement of this phase to equivalent value from germination to emergence to precise prediction of seedling emergence. These kinds of information may be used by producers, researchers, and extension personnel to make informed sowing date decisions with respect to long time climatic and edaphic infor-

mation. Also crop modelers may use our results as a starting point for developing temperature response functions of opium poppy development.

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