

Temperature and water potential effects on *Carthamus tinctorius* L. seed germination: measurements and modeling using hydrothermal and multiplicative approaches

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Received: 14 April 2015 / Accepted: 12 December 2015 / Published online: 5 February 2016
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Abstract Seed germination is a biological process that is strongly affected by temperature and water potential. Our objective was to measure experimentally and model this combined effect and estimate robust parameter values that will assist researchers to estimate safflower germination rate under variable experimental conditions. A laboratory experiment was conducted to investigate the combined effect of seven temperatures regimes (10, 15, 20, 25, 30, 35 and 40 °C) and five water stress levels (0, -0.4, -0.8, -1.2 and -1.6 MPa) on safflower seed germination. The derived dataset was analyzed using two modeling approaches that combine temperature and water potential effects: the multiplicative and the hydrothermal time models. The associated parameter estimates for each model were determined through statistical optimization and model performance evaluated against an independent dataset. The hydrothermal time parameters were 493.3 MPa h, 8.2 °C, and -1.34 MPa for θ_{HT} (hydrothermal time constant) T_b (base temperature), and $\psi_{b(50)}$ (median base water potential) in sub-optimal temperatures, respectively. The parameter estimates for the multiplicative model were determined as 7.9 °C for T_b , 21.4 °C for T_{o1} (lower optimal temperature), 29 °C for T_{o2} (upper optimal temperature), and 40 °C for T_c (ceiling

temperature); 0 MPa for WP_c (critical water potential) and $1.18 \text{ h}^{-1}\text{MPa}^{-1}$ for water potential sensitivity coefficient (WPS); and 17.9 h for g_o (physiological hours for seed germination). Model evaluation showed that the multiplicative model predicted time to 50 % of seed germination more accurately (RMSE = 4.3 h and $R^2 = 0.98$) than the hydrothermal time model (RMSE = 9.5 h and $R^2 = 0.93$).

Keywords Modeling · Safflower · Temperature · Water potential

Introduction

Safflower (*Carthamus tinctorius* L.) is an annual oilseed crop that belongs to Asteraceae (Compositae) family. It is commercially cultivated for its dye, which is extracted from the flowers, and for high-quality vegetative oil that is extracted from the seeds (Dajue and Mündel 1996; Singh and Nimbkar 2006). Recently, its cultivation has received great interest in many countries across the world (Dajue and Mündel 1996; Ekin 2005; Dordas and Sioulas 2008); however, information available for safflower is little compared to other common crops. Further research on different aspects of safflower production is needed to support decision making and efficient cultivation of safflower in a variety of production areas. Among several research needs, knowledge of plant adaptability to different agro-ecological zones is fundamental, which is usually the starting point in accumulating information for an unexplored plant species. The most important parameters needed for this purpose are the cardinal temperatures (T_b , the temperature below which the germination rate is zero; T_o , the temperature at which the germination rate is maximal; and T_c , the temperature above which the germination rate is

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zero). These parameters are commonly assumed invariant over the crop cycle (Soltani and Sinclair 2012) although different cardinal temperatures for different crop phases have been found in some species (e.g., Jones et al. 2000).

Seed germination is the starting point in the crop's life cycle. Its duration is strongly influenced by temperature and water potential (Forcella et al. 2000; Qiu et al. 2006; Soltani et al. 2008). Commonly, the researchers perform lab experiments and manipulate temperature and moisture in the controlled conditions in order to accumulate a wide range of data to fit nonlinear models and estimate important parameters for seed germination and plant development (Jame and Cutforth 2004; Hardegee 2006a, b; Hardegee and Winstral 2006; Adam et al. 2007; Berti and Johnson 2008; Kamkar et al. 2012; Torabi et al. 2013).

Analysis of such experimental data and model selection depends on the research question asked (Archontoulis and Miguez 2013). When the objective is to predict cumulative seed germination over time, the researchers usually use hydrothermal time models (HTT; Gummerson 1986; Allen 2003; Rowse and Finch-Savage 2003; Bradford 2005; Soltani et al. 2013) or empirical sigmoid functions (Archontoulis and Miguez 2013). The estimates of hydrothermal time parameters (see Eq. 2–6) can be used in crop modeling (Soltani et al. 2013). The model predicts that under constant conditions of T and ψ , the given fraction of seeds (e.g., 50 %) in the population will germinate when the seed has accumulated hydrothermal time equal to the population's hydrothermal time constant (Bloomberg et al. 2009).

However, when the objective is to estimate time needed to achieve 50 % of seed germination, which is largely used in crop modeling (Soltani and Sinclair 2012), then the thermal time or the multiplicative modeling approaches are applied. The thermal time approach accumulates heat units above a certain threshold ($\sum DTT = \sum (T - T_b)$), and a phase is completed when a certain requirement has been satisfied. The multiplicative approach uses the rate of development (inverse of time needed, e.g., 1/days or 1/hours) which is multiplied by temperature and other (i.e., moisture) 0–1 modifiers. When the accumulation of the daily or hourly values reaches 1, the phase has been completed. Both approaches, thermal time method and multiplicative, are equivalent and use approximately the same input parameters and response functions (see Fig. 1; Archontoulis et al. 2014).

The response of germination to temperature is usually described by linear or bell-shaped functions or 2–3-segmented linear function (Shafii and Price 2001; Jame and Cutforth 2004; Adam et al. 2007; Berti and Johnson 2008; Ghaderi-Far et al. 2008; Kamkar et al. 2012; Torabi et al. 2013). For many plant species, the responses of germination rate to temperature have been simplified by a bilinear (segmented) response (Covell et al. 1986; Ellis et al. 1986;

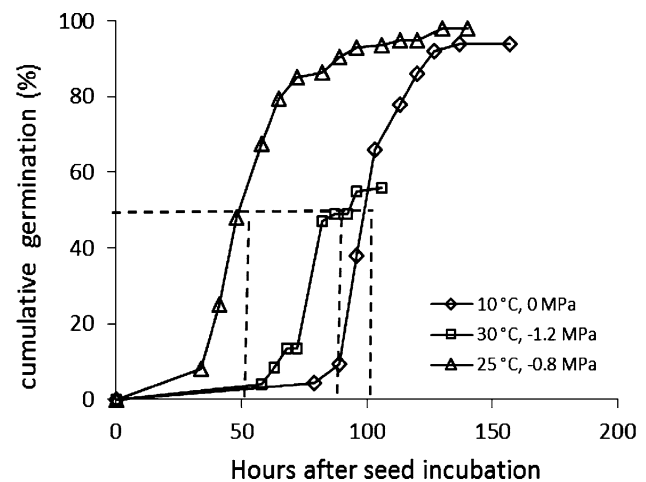


Fig. 1 Estimates of the T_{50} (time taken to 50 % of seed germination) for water potential under different temperatures and water potentials. The dashed line indicates time to 50 % of seed germination

Hardegee 2006a, b; Hardegee and Winstral 2006; Soltani et al. 2006b; Torabi et al. 2013).

In contrast, the response of germination rate to water potential has not been quantified yet, but the water uptake by the seeds is characterized by three phases: (a) an initial phase in which water is absorbed by seeds which is a physical process, viewed as satisfying the seed matric potential (Kebreab and Murdoch 1999; Allen 2003); (b) a middle phase in which major metabolic events take place in live seeds in preparation for radicle emergence (Bewley and Black 1978, 1994); and (c) a final phase in which water absorption increases sharply and radicle elongates. Therefore, reduction in water potentials progressively restricts progress toward germination.

The objective of this study is threefold: (a) to investigate safflower seed-germination rates under variable temperature and water potential conditions; (b) to estimate cardinal temperature parameters for safflower seed germination using two well-known modeling approaches—the hydrothermal time and the multiplicative models (Sinclair et al. 1991; Grimm et al. 1993; Rowse and Finch-Savage 2003; Hardegee 2006a, b; Hardegee and Winstral 2006; Soltani et al. 2006a, b; Soltani et al. 2013); and (c) to discuss differences in parameter estimations between the two models and evaluate their predictive abilities against independent dataset. The multiplicative modeling approach has been used to model temperature and photoperiod effects on plant development (e.g., Setiyono et al. 2010), and temperature and vernalization effects on plant development (e.g., Ritchie 1991; Jones et al. 2003), but to our knowledge, there is no application that combines temperature and moisture effects on seed germination. In this study, we introduce the multiplicative model as product of temperature and water potential functions for the first time.

Materials and methods

Germination experiments and dataset development

Safflower seeds (cv. Esfahan) were obtained from the Agricultural Research Center of Esfahan Province (32°38'N, 51°39'E) in 2011.

Two hundred seeds (in 50-seed replicates) were placed on a double layer of absorbent filter paper in a 10 cm Petri dish. The treatments comprised a complete factorial structure of seven temperatures (10, 15, 20, 25, 30, 35, and 40 °C) that combined with five water potential levels (0, -0.4, -0.8, -1.2, and -1.6 MPa) resulting in 35 different treatments. Each treatment was replicated four times. Solutions of water potential for each temperature treatment were obtained using the polyethylene glycol (PEG) of molecular weight 6000 Da (Michel and Kaufmann 1973). Seed-germination progress was monitored at every 8–12 h intervals over a period of 7–14 days. The longest period of inspections was related to temperature of 10 °C and water potential of -1.6 MPa. Inspection involved counting and removal of the germinated seeds, defined as seeds having 2 mm or more in length.

Estimates of the time required to 50 % of seed germination (T_{50}) in each replicate/treatment were interpolated from the progress of germination (%) versus time (hours) curve (Soltani et al. 2013; see Fig. 1). Germination rate (R , hour⁻¹) was then calculated as follows (Soltani et al. 2002, 2006a; Torabi et al. 2013):

$$R = 1/T_{50} \quad (1)$$

Hydrothermal time model description and parameter estimation method

The hydrotime model (Gummerson 1986; Bradford 1990; Soltani and Farzaneh 2014) is described by the following equivalent equations:

$$\theta_H = (\psi - \psi_b(g)) t_g \quad (2)$$

$$GR_g = 1/t_g = (\psi - \psi_b(g))/\theta_H \quad (3)$$

where θ_H is the hydrotime constant (MPa h), ψ is the actual seed water potential (MPa), $\psi_b(g)$ is the base water potential (MPa) defined for a specific germination fraction (g), t_g is the time (hours) to radicle emergence of fraction g (%) of the seed population, and GR_g is the germination rate for fraction g (%) of the seed population. Assuming that the variation in ψ_b within a seed population follows a normal distribution, hydrotime parameters were estimated by repeated probit analysis of Eq. (4) by varying the parameter θ_H until the best fit is achieved (Dahal et al. 1993; Windauer et al. 2011; Soltani and Farzaneh 2014).

$$\text{probit}(g) = [\psi - (\theta_H/t_g) - \psi_b(50)]/\sigma_{\psi_b} \quad (4)$$

where $\psi_b(50)$ is the median ψ_b , and σ_{ψ_b} is the standard deviation in ψ_b among the seeds within the population. All the three hydrotime parameters were estimated by this method for each temperature regime separately. When the sub-optimal temperature and ψ are both varied, then germination rates can be described based on a combined hydrothermal time scale model (Gummerson 1986; Bradford 1995, 2002; Soltani et al. 2013):

$$\theta_{HT} = (\psi - \psi_b(g)) (T - T_b) t_g \quad (5)$$

where θ_{HT} is the hydrothermal time constant (MPa h), i.e., a combination of accumulated thermal time at temperatures above T_b and accumulated hydrotime at ψ levels above $\psi_b(g)$. For the supra-optimal range of T , Eq. (5) is modified as follows (Alvarado and Bradford 2002; Bradford 2002; Rowse and Finch-Savage 2003; Soltani et al. 2013):

$$\theta_{HT} = \{ \psi - [\psi_b(g)_o + [k_T(T - T_o)]] \} (T_o - T_b) t_g \quad (6)$$

where k_T is a constant (the slope of $\psi_b(g)$ versus T line when $T > T_o$), and $\psi_b(g)_o$ represents the values of the $\psi_b(g)$ distribution at T_o .

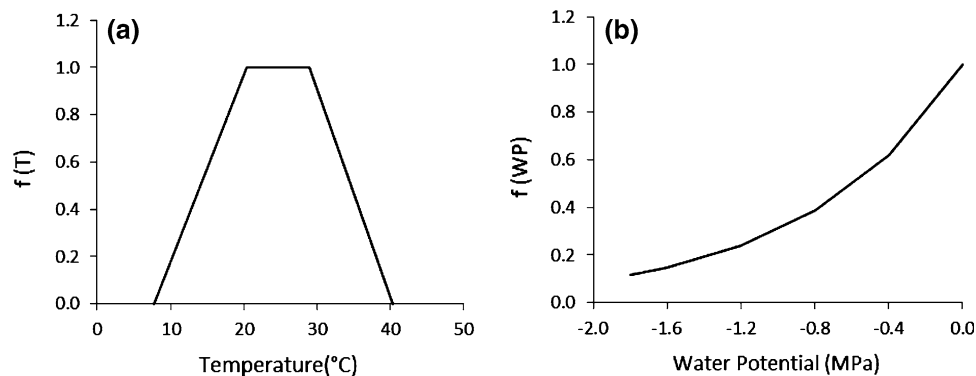
Multiplicative model description and parameter estimation method

The multiplicative relationship that combines temperature and water potential effects on germination rate is given by the following formula:

$$R_t = R_{\max} * f(T) * f(WP) \quad (7)$$

where R_t is the germination rate (1/hour), R_{\max} is the maximum rate of germination at optimal temperature and water potential conditions (1/hour), $f(T)$ is the temperature modifier function (0–1; see Eq. 8 and Fig. 2), and $f(WP)$ is the water potential modifier function (0–1, see Eq. 9 and Fig. 2). The inverse of R_{\max} indicates minimum hours required for seed germination under optimal temperature and water potential conditions ($f(T) = 1$ and $f(WP) = 1$). This minimum requirement is also termed optimal or physiological hours for 50 % of seed germination (g_o hereafter). The $f(T)$ and $f(WP)$ modifiers are calculated each hour, and their product is accumulated until a threshold of g_o is reached. At this point of time, germination is predicted to occur. We utilized a dent-like function (3-segmented) to describe temperature effects on germination and an exponential function to describe water potential effects on germination. Schematics of both temperature and water potential functions are presented in Fig. 2. The temperature function is described below:

Fig. 2 Functions used to describe the responses of germination rate to temperature (a) and water potential (b)



$$\begin{aligned}
 f(T) &= (T - T_b)/(T_{o1} - T_b) & \text{if } T_b < T < T_{o1} \\
 f(T) &= (T_c - T)/(T_c - T_{o2}) & \text{if } T_{o2} < T < T_c \\
 f(T) &= 1 & \text{if } T_{o1} \leq T \leq T_{o2} \\
 f(T) &= 0 & \text{if } T \leq T_b \text{ or } T \geq T_c
 \end{aligned} \quad (8)$$

where T is the temperature, T_b is the base temperature, T_{o1} is the lower optimal temperature, T_{o2} is the upper optimal temperature, and T_c is the ceiling temperature (all in °C).

The water potential function is described below:

$$\begin{aligned}
 f(WP) &= 1 & \text{if } WP \geq WP_c \\
 f(WP) &= \text{Exp}(WPS(WP_c - WP)) & \text{if } WP < WP_c
 \end{aligned} \quad (9)$$

where WP is the absolute value of water potential (MPa), WP_c the critical water potential below which germination rate decreases due to low water potential, and WPS is the absolute value of water potential sensitivity coefficient.

Model parameters were estimated by the least squares method using the nonlinear (NLIN) regression procedure in the Statistical Analysis System (SAS Institute 2011). The parameters WP_c , T_{o2} , and T_c were fixed at 0 MPa, 29 and 40 °C, respectively, because the best fit of model was obtained when they were fixed. Equation 7 was fitted to data of the germination rate and the root mean square of error (RMSE), and linear regressions of predicted versus observed values were computed to evaluate the goodness of fit.

Model evaluation dataset

We conducted an independent experiment to obtain independent data to evaluate the performances of these models: hydrothermal versus multiplicative. The experiment was conducted following the protocol described above. The temperature regimes were 16, 18, and 25 °C, and the water potential levels were -0.3, -0.6, and -0.9 MPa. In addition, we collected some independent datasets from other studies. The calibrated models were applied to fit the new data, and the models' performances were evaluated by

computing the RMSE and by using linear regression analysis.

Results

Germination duration

Safflower seeds required 18.7–250 h to germinate. This large variation was caused by the different temperatures and water potential levels used in this study (Table 1). The duration to germination varied as much as 3–4 folds within the range of temperature conditions used. In general, the duration of germination was the shortest at temperatures between 20 and 35 °C and was higher at temperature levels outside that range (Table 1). The duration of germination increased with the decreasing water potential. Seeds did not

Table 1 The ranges and means of observed duration (hours) for 50 % of seed germination for different temperatures (°C) and water potentials (MPa)

Temperature	Minimum	Maximum	Mean
10	100.0	250.0	172.2
15	40.0	125.0	76.0
20	19.6	66.7	41.9
25	18.9	76.9	44.5
30	20.4	76.9	49.6
35	23.8	55.6	38.4
40	–	–	–
Water potential			
0.0	18.7	100.0	37.1
-0.4	31.3	166.7	60.0
-0.8	50.0	250.0	91.9
-1.2	66.7	125.0	86.4
-1.6	–	–	–

germinate under treatment conditions of 40 °C and -1.6 MPa water potential treatment. (Table 1).

Hydrothermal time model

Data fits of the hydrotime model to germination are presented in Fig. 3. The predicted cumulative germination percentages over time at various water potential levels (ψ) and temperature regimes generally matched well with observations (R^2 values between 0.68 and 0.84; RMSE values ranged from 7.8 to 17.3 h, Table 2). The estimated values of $\psi_b(50)$, σ_{ψ_b} , and θ_H were specific for each temperature regime (Table 2). The lowest and the highest $\psi_b(50)$ were observed at 15 and 35 °C, respectively. The θ_H parameter decreased from 145.2 MPa h (at 10 °C) to 9.2 MPa h (at 35 °C). Average σ_{ψ_b} was 0.36 and it varied from 0.21 to 0.47. Hydrothermal time parameters were determined in sub- and supra-optimal temperatures, separately. These parameters

Table 2 Parameter estimates of the hydrotime model at six germination temperatures describing seed germination of safflower for different water potentials

Temperature (°C)	$\psi_b(50)$	σ_{ψ_b}	θ_H	R^2	RMSE
10	-1.371	0.206	145.24	0.68	14.40
15	-1.730	0.281	70.87	0.77	7.79
20	-1.157	0.388	21.13	0.68	10.13
25	-1.445	0.409	25.83	0.84	10.97
30	-1.013	0.377	20.70	0.69	17.28
35	-0.587	0.472	9.22	0.74	12.42

$\psi_b(50)$ is the median base water potential; σ_{ψ_b} is the standard deviation in base water potential; θ_H is the hydrotime constant; R^2 is the coefficient of determination of the regression hydrotime model at each temperature

were equal to 493.3 MPa h, 8.2 °C, and -1.34 MPa, respectively, for θ_{HT} , T_b , and $\psi_b(50)$ under sub-optimal temperatures (Table 3). The parameter θ_{HT} values under

Fig. 3 Germination time courses for *Carthamus tinctorius* seeds germinated in different temperatures and water potentials. The symbols indicate the interpolation of observed germination data, and the lines indicate the germination time courses predicted by the hydrotime model, based on parameter estimates shown in Table 2

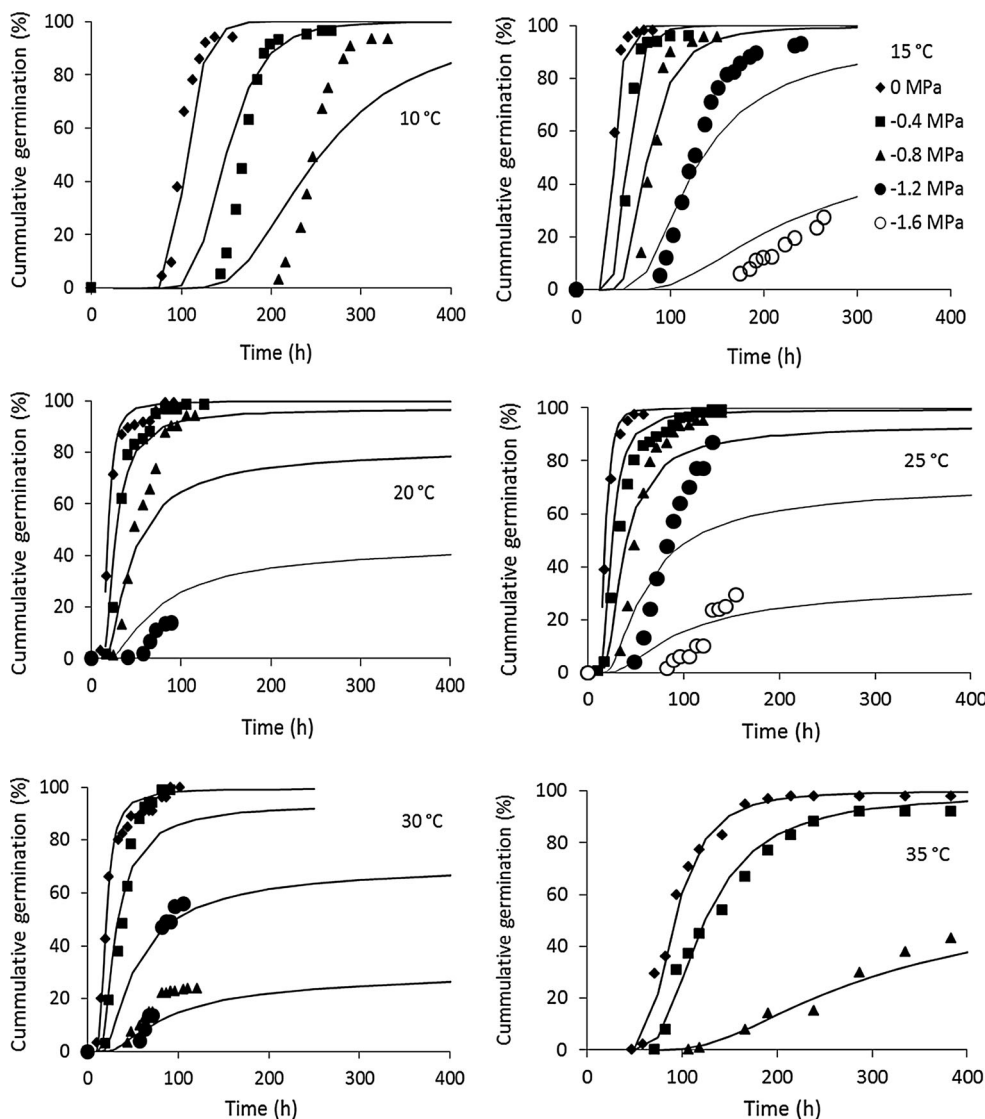


Table 3 Parameters estimate of the hydrothermal time model, describing seed germination of safflower in different temperatures and water potentials

Parameter	Sub-optimal	Supra-optimal
T_b	8.21 ± 0.074	8.21 ± 0.096
T_o	–	27.69 ± 0.201
$\psi_b(50)$	-1.34 ± 0.025	-0.53 ± 0.054
$\psi_b(50)_o$	–	-1.53 ± 0.092
k_T	–	0.101
θ_{HT}	493.3 ± 24.59	1234.6 ± 114.00
R^2	0.80	0.81
RMSE (h)	38.31	24.80

T_b and T_o are the base and optimal temperatures; $\psi_b(50)$ is the median base water potential; $\psi_b(50)_o$ is the value of the $\psi_b(g)$ at T_o ; k_T is a constant (the slope of the $\psi_b(g)$ versus T line when $T > T_o$); θ_{HT} is the hydrothermal time constant; R^2 is the coefficient of determination of the hydrothermal time model

sub-optimal temperatures were lower than those under supra-optimal temperatures (Table 3). On the other hand, the parameter $\psi_b(50)$ values were lower (more negative) under sub-optimal temperatures, showing that seeds could germinate at lower water potentials if their germinations take place under sub-optimal temperatures.

Modeling germination using the multiplicative approach

In contrast to the hydrothermal time model, the multiplicative model was designed to provide only the estimate of seed-germination rate and not the cumulative time course of germination. Figure 4 shows predicted versus observed hours to 50 % of seed germination as calculated by the multiplicative model. The root mean square of error (RMSE) was 11.1 h (i.e., 17.5 % of the mean), and the coefficient of determination (R^2) was 0.95. As indicated in Fig. 4, the model predictions have been well disposed around the 1:1 line, which indicates no bias. The multiplicative model accounted well for both temperature and water potential effects on rate of seed germination, without the need of discriminating between sub- and supra-optimal temperature ranges as was needed in the hydrothermal time model. Figure 5 presents parameter profile plots. These plots show the responses in SSE (sum of squares error) to changes in each parameter. The best estimate for each parameter is obtained when the lowest SSE occurs. On this basis, our estimates of cardinal temperatures and water potential parameters to describe safflower seed germination were obtained as 7.9 °C for T_b , 21.4 °C for T_{o1} , 29 °C for T_{o2} , 40 °C for T_c , 0 MPa for WPC, $1.18 \text{ h}^{-1} \text{ MPa}^{-1}$ for WPS, and 17.9 h for g_o (Table 4).

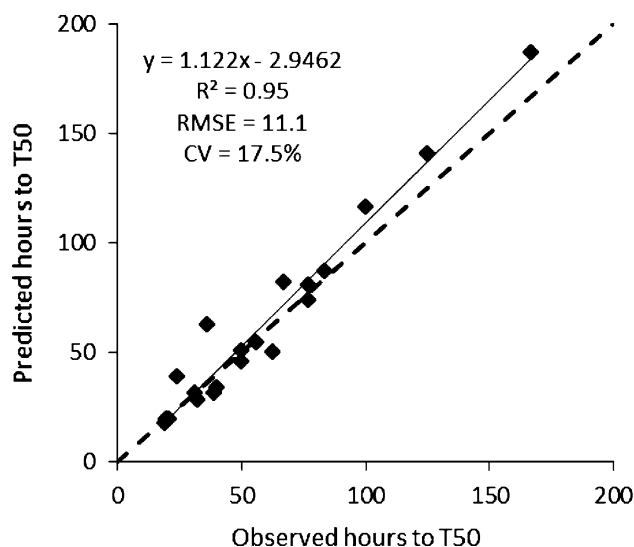


Fig. 4 Predicted versus observed hours to time to 50 % of seed germination (T_{50}) in a safflower cultivar ‘Esfahan’ using multiplicative model including dent-like temperature function and exponential water potential function. The *dashed line* is a 1:1 and the *solid line* is the *regression line*

Model evaluation

We fitted both models (hydrothermal and multiplicative) to an independent dataset using the parameter estimates derived from calibration (see Table 3 for the hydrothermal model and Table 4 for the multiplicative model). The results of this evaluation are presented in Fig. 6, which clearly showed that the multiplicative model (RMSE = 4.3 h) was better than the hydrothermal time model (RMSE = 9.5 h) in estimating time to 50 % of the safflower seed germination, which is the most important piece of information, especially for crop models. The multiplicative model accounted for 98 % of the variation in hours to germination without any detectable bias (Fig. 6). Simulated hours to germination varied from 18.1 to 116 for the multiplicative model and from 13.5 to 167.0 for the hydrothermal time model. Measured values of time to germination ranged from 17.1 to 104.6 h (Fig. 6).

Discussion

Germination response to temperature and water potential

A comprehensive dataset on safflower seed germination was developed to provide information needed for evaluating germination response to temperature and water potential. This dataset allowed us to parameterize and validate predictive models and to estimate important parameters for safflower seed germination.

Inappropriate temperatures decrease activity of enzymes and availability of oxygen during seed germination

Fig. 5 Profile plots of SSE (sum of squares error) for the six parameters of the multiplicative model fitted to, using PROC NLIN procedure. T_b is the base temperature, T_{o1} the lower optimal temperature, WPS is the water potential sensitivity coefficient, and g_o physiological hours requirement

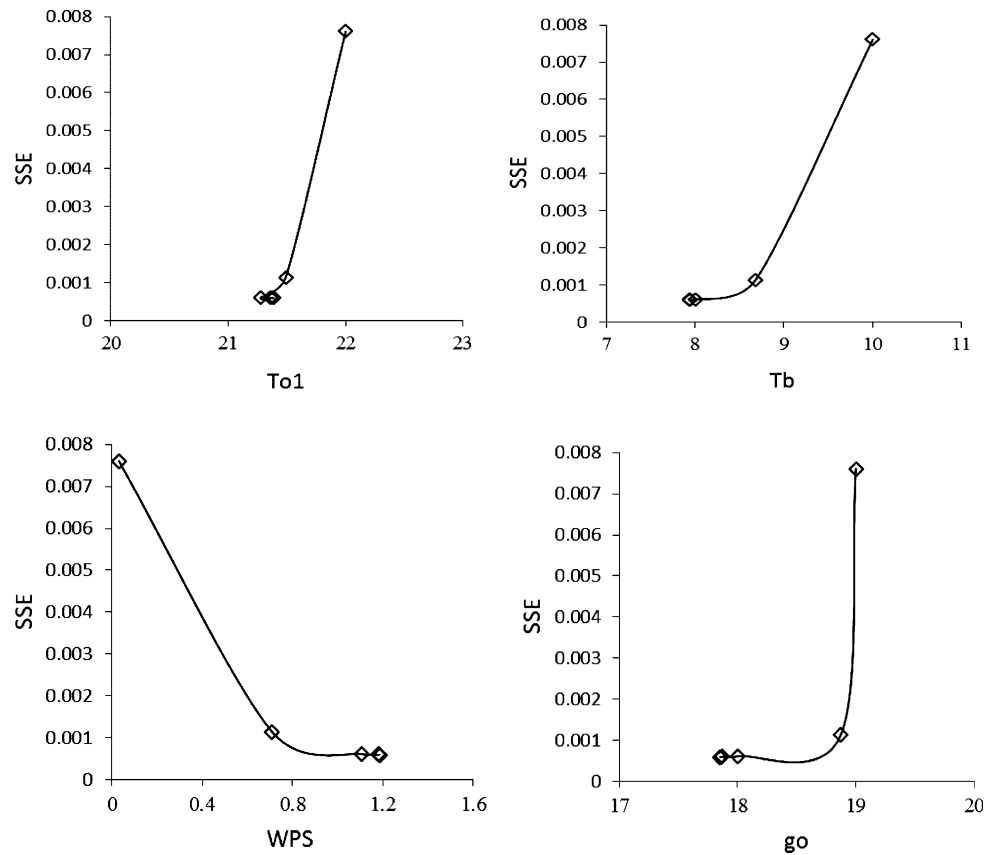


Table 4 Estimates of the base temperature (T_b), the lower optimal temperature (T_{o1}), the water potential sensitivity coefficient (WPS), and the physiological hours required (g_o)

Parameter	Estimate (SE)	Unit
T_b	7.9 (1.28)	°C
T_{o1}	21.4 (1.40)	°C
T_{o2}	29.0	°C
i_c	40.0	°C
WP_c	0.0	MPa
WPS	1.18 (0.14)	$h^{-1} MPa^{-1}$
g_o	17.9 (1.15)	H

The values for the upper optimal temperature (T_{o2}), the ceiling temperature (T_c) and critical water potential (WP_c) was fixed at 29.0 °C, 40.0 °C and 0 MPa

(Bewley and Black 1994). On this basis, germination time course is probably prolonged in the sub- and supra-optimal temperatures range. In the present work, however, for the seeds of safflower germinated over a wide range of temperatures ranging from 10 to 35 °C, the optimal temperature for germination was between 20 and 35 °C.

Seed germination can be also influenced by water potential levels. The seed germination requires minimum potential (ψ_b) to expand the radicle cells and the break

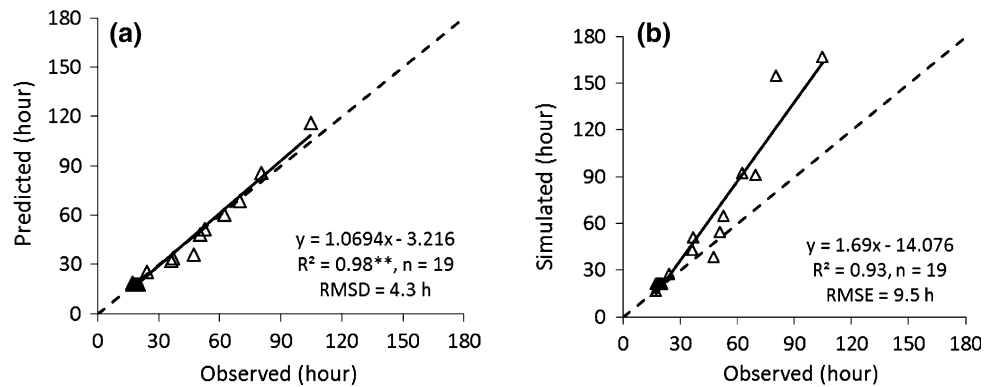
strength of the endosperm (Bradford 1990). Imbibition at water potential levels higher than ψ_b increases the rate of water uptake and enzyme’s activity and accelerates radicle emergence (Bradford 1986; Kebreab and Murdoch 1999). Therefore, in high water potentials, progress toward germination is improved.

Modeling germination

We quantified responses of germination to temperature and water potential by means of two models: the hydrothermal time (Alvarado and Bradford 2002; Bradford 2002) and multiplicative model. The first one provides estimates for cumulative germination percentage over time and it is temperature range specific. The latter provides estimates for the rate of germination, and this estimate is to capture variability under both temperature and water potential conditions.

The hydrothermal time model has been developed by Gummerson (1986) by combining thermal time and hydrotime models and has found a variety of applications (Bauer et al. 1998; Kebreab and Murdoch 1999; Windauer et al. 2007; Schutte et al. 2008). In this study, we estimated hydrothermal time model parameters separately for sub- and supra-optimal temperatures. The θ_{HT} parameter estimates (hydrothermal time constant, the most important)

Fig. 6 Simulated versus observed hours to T_{50} for safflower using the independent dataset for multiplicative model (a) and hydrothermal time model (b). The dashed line is a 1:1 line, and the solid line is the regression line



were 493.3 and 1234.6 MPa h for sub- and supra-optimal temperature ranges, respectively. Although there are no specific safflower data in the literature to compare our estimates, we found that our estimates for θ_{HT} are within the range reported for some plants such as *Lycopersicon esculentum* Mill. (271–408 MPa h; Cheng and Bradford 1999), *Bromus tectorum* L. (16–42 MPa days; Bair et al. 2006), *Festuca rubra* L. (84 and 86 MPa days; Larsen et al. 2004), *Lolium perenne* L. (59 and 74 MPa days; Larsen et al. 2004), *Poa pratensis* L. (160 and 377 MPa days; Larsen et al. 2004), *Elymus elymoides* Raf. (104 and 108 MPa days; Meyer et al. 2000), *Solanum tuberosum* L. (715–1800 MPa h; Alvarado and Bradford 2005), and *Brassica napus* L. (36 and 43 MPa days; Soltani et al. 2013).

Different versions of the multiplicative model have been used extensively in the literature to model temperature, photoperiod, and vernalization interaction on the organ/plant development rates. The multiplicative model comprises the standard way of estimating rate of development in many crop-production simulation models such as DSSAT (Jones et al. 2003), hybrid-Maize (Yang et al. 2004), Gecros (Yin and van Laar 2005), and many other models. This approach is well understood and flexible for adaptation in modeling developmental rates of plants (Soltani et al. 2006a, b). In the present study, we used the concept of the multiplicative model and developed the combined temperature/water potential response for seed germination (Eqs. 7–9). We used simple and well-known temperature and water potential response functions (Fig. 2). Of course, the selection of any equation from among many for use (e.g., Archontoulis and Miguez 2013) has an impact on model parameter estimates. In this study, we used the dent-like temperature function and the exponential one for the water potential in the multiplicative model and estimated parameters describing safflower seed germination fairly well ($T_b = 7.9$, $T_{o1-2} = 21.4$ – 29 and $T_c = 40$ °C; $WP_c = 0$ MPa and $WPS = 1.18$ h⁻¹ MPa⁻¹; Table 4).

Our estimates for T_b , T_o , and T_c are within the range of reported values in the literature for safflower and other species. Torabi et al. (2013) quantified responses of

germination rate to temperature in three safflower cultivars using different functions (2- and 3-segmented and beta functions) under optimal water potential condition (assuming that $f(WP) = 1$) for germination. Their estimates for cardinal temperatures using the dent-like function were determined as 4.3–6.4 °C for T_b , 30.0–31.5 °C for T_{o1} , 36.6–38.0 °C for T_{o2} , and 44.0 °C for T_c . In addition, our estimates for T_b , T_o , and T_c compare with the literature data as follows: *Zea mays* L. (7.6, 27.5 and 43.4 °C; Aflakpui 1996), *Plantago ovata* Forsk. (3.3, 21.2 and 35.0 °C; Ghaderi-Far et al. 2012), *Crupina vulgaris* Cass. (1.3, 10.6 and 20.0 °C; Shafii and Price 2001), *Papaver somniferum* L. (3.0, 27.4 and 36.3 °C; Kamkar et al. 2012), *Cuphea viscosissima* Jacq. (6–10, 18–24 and 33–38 °C; Berti and Johnson 2008), and *Kochia scoparia* L. (3.5, 24 and 50 °C; Jami Al-Ahmadi and Kafi 2007). However, we found no reports that quantify the response of germination rate to varying water potentials.

Model comparison

The hydrotime to germination is equal to inverse of the slope of the line (Kebreab and Murdoch 1999; Bradford 2002; Bradford and Still 2004). Therefore, it can be concluded that an essential assumption for use the hydrothermal time model is that there is a linear relationship between the germination rate with temperature and water potential, whereas these assumptions might not always be true. For example, Rowse and Finch-Savage (2003) indicated that there was a nonlinear relationship between germination rates and temperature. Also, Finch-Savage et al. (2005) indicated that there was not always a linear relationship between the germination rate and the water potential. Therefore, sometimes, a further lack of precision comes from the assumption of linearity within components of hydrothermal time model (Grundy et al. 2000).

In addition, Meyer et al. (2000) reported that the increased accumulation of hydrothermal time associated with the increasing temperature difference ($T - T_b$) was offset by the decreased accumulation of hydrothermal time associated with

a small difference ($\psi - \psi_{b(g)}$) due to the high base water potential. This relationship explains the independence of hydrothermal time from temperature and water potential. However, in the hydrothermal time model, prediction of germination time is based on some assumptions that may not always be true (Dahal et al. 1993). For example, it is assumed that base water potentials are the same at each temperature (Gummerson 1986); however, Kebreab and Morduch (1999) noted that there was substantial evidence to suggest that they are not independent. Bradford (1995) also noted that the assumptions that T_b is independent of water potential and that ψ_b is independent of temperature might be species specific and cannot be generalized. In addition, it has been assumed that in the hydrothermal time model ψ_b varies when T increases to greater than T_o ; however, Bakhshandeh et al. (2011) reported that ψ_b does not vary for supra-optimal temperatures.

The multiplicative model comprises two functions that can fit to dataset as linear and nonlinear. Therefore, in respect of the nature of multiplicative model, it is expected that the model estimates the occurrence of germination time in part of linear or nonlinear relationship between germination rate with the temperature and the water potential (Eqs. 8 and 9).

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