Modeling Seed Aging Effects on the Response of Germination to Temperature in Wheat

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ABSTRACT

Seed germination is strongly dependent on temperature. Reduced germination rate as a consequence of seed aging might be due to changing the type of response function to temperature or changing the parameters that govern the function. The objectives of this research were: (1) to determine the effect of seed aging on the type of response function describing the relationship of germination rate to temperature, and (2) to evaluate how the parameter(s) of the response function are changed when the germination rate is reduced as a result of seed aging. Seeds (cv. 'Zagros') were kept at a high temperature (43°C) and high relative humidity (90-95%) to create different classes of seed aging. Seed aging had no effect on the type of response function or cardinal temperatures. A dent-like function adequately described the response of germination rate to temperature in all the aging treatments. Cardinal temperatures of 2.2°C for the base, 28.6°C for the lower optimum, 38.0°C for upper optimum and 45°C for ceiling temperatures were obtained. Inherent maximum rate of germination (R_{max}) was the sole parameter that was affected by seed aging periods and characterized differences between seed aging periods with respect to germination rate at various temperatures.

INTRODUCTION

Seed germination is strongly dependent, when moisture is adequate, on temperature (Kamaha and Maguire 1992; Mwale *et al*. 1994; Phartyal *et al*. 2003). A variety of mathematical functions have been used to describe the relationship between germination rate and temperature (Shafii and Price 2001; Soltani *et al*. 2006). Soltani *et al*. (2006) used several linear and non-linear functions to describe the relationship between emergence rate and temperature in chickpea. The advantage of these functions is that they have parameters that are meaningful from a biological point of view, such as cardinal temperatures and maximum inherent rate of germination or emergence.

Some researchers have used these functions to obtain cardinal temperatures, i.e., base, optimum and ceiling temperatures (Jame and Cutforth 2004; Hardegree 2006; Hardegree and Winstral 2006; Jami Al-Ahmadi and Kafi 2007). Germination rate is maximal at optimum temperature(s), and then reaches zero at base and ceiling temperatures (Mwale *et al*. 1994; Seefelt *et al*. 2002; Hardegree 2006). Cardinal temperatures may vary significantly between species, biotypes or cultivars (Mwale *et al*. 1994; Phartyal *et al*. 2003).

It is well-known that seed deterioration results in reduced germination rate (Basra *et al*. 2003; Khajeh-Hosseini *et al*. 2003). This might lead to reduced yield potential by lengthening the days from sowing to complete ground cover and a delay in the establishment of an optimum canopy (Soltani *et al*. 2001). Optimum canopy establishment is required to minimize interplant competition and to maximize crop yield. Reduced germination rate as a consequence of seed aging might be due to a change in the type of response function or a change in the parameters that govern a function. So far, this aspect of seed aging has not been evaluated. Therefore, our objectives were: (1) to determine the effect of seed aging on the type of response function describing the relationship of germination rate to temperature, and (2) to evaluate how the parameter(s) of the response function are changed when germination rate is reduced as a result of seed aging.

MATERIALS AND METHODS

Accelerated aging treatments

Seeds of wheat (*Triticum aestivum* L.) cv. 'Zagros' were obtained from Gorgan Agricultural Research Center, Gorgan, Iran. Accelerated aging treatments were created by aging the seeds (with initial moisture content of 11.8%) at 43°C and relative humidity of 90-95% for 0, 48, 72, 96 and 144 h periods (Modarresi *et al*. 2002; Basra *et al*. 2003). For each aging treatment, about 100 g of seeds were scattered within a vacuum container on wire screens; the floor of the container was covered by distilled water (10% of total container volume). The containers were placed in an incubator at a fixed temperature of 43°C. After aging, seed moisture content was determined, and ranged between 29.1 and 33.2%.

Germination

Four replicates were conducted, each consisting of 30 seeds for each seed aging treatment in which seeds were germinated at constant temperatures ranging from 10 to 40°C with 5°C increments. Seeds were placed on two moistened paper towels. After covering the seeds with a third sheet of paper, the three towels were loosely rolled to form a tube and placed in plastic bags (23 × 33 cm) to prevent evaporation. Seeds were observed twice daily and considered germinated when the radicle was approximately ≥2 mm long. Estimates of time taken for cumulative germination to reach 50% of its maximum at each replicate (D50) were interpolated from the germination progress curve versus time. Germination rate (R50 1/h) was then calculated according to Soltani *et al*. (2001, 2002):

$$R50 = \frac{1}{D50} \tag{1}$$

Data analysis

Data were subjected to analysis of variance (ANOVA) to examine the effect of temperature and aging period and their interaction on germination rate. ANOVA was performed using the GLM procedure of the Statistical Analysis System (Soltani 2007).

To quantify the response of germination rate to temperature and to determine cardinal temperatures for germination, the following model was used:

$$R50 = f(T) \, R_{max} \qquad (2)$$

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 R_{max} is the inherent maximum rate of germination at optimal temperature. Thus, $1/R_{max}$ indicates the minimum number of hours for germination at optimal temperature. Three temperature functions ($f(T)$) were tested (Soltani *et al.* 2006):

1. segmented function (Ritchie and NeSmith 1991):

$$
\begin{aligned}
f(T) &= (T - T_b) / (T_o - T_b) & if \quad T_b < T \le T_o \\
f(T) &= (T_c - T) / (T_c - T_o) & if \quad T_o < T < T_c \\
f(T) &= 0 & if \quad T \le T_b \text{ or } T \ge T_c
\end{aligned} \qquad (3)
$$

2. beta function (Yin *et al.* 1995):

$$
f(T) = \left\{ \left[\left(\frac{T-T_b}{T_o-T_b} \right) \left(\frac{T_c-T}{T_c-T_o} \right) \right]^{(T_c-T_o)/(T_o-T_b)} \right\}^{\alpha}
$$

$$
\begin{aligned}
& if \quad T > T_b \text{ and } T < T_c \\
f(T) = 0 \quad & if \quad T \le T_b \text{ or } T \le T_c
\end{aligned} \qquad (4)
$$

and 3. dent–like function (Piper *et al.* 1996):

$$
\begin{aligned}
f(T) &= (T - T_b) / (T_{o1} - T_b) & if \quad T_b < T < T_{o1} \\
f(T) &= (T_c - T) / (T_c - T_{o2}) & if \quad T_{o2} < T < T_c \\
f(T) &= 1 & if \quad T_{o1} < T < T_{o2} \\
f(T) &= 0 & if \quad T \le T_b \text{ or } T \ge T_c
\end{aligned} \qquad (5)
$$

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_c the ceiling temperature and α is the shape parameter for the beta function which determines the curvature of the function. The parameters were estimated by the least squares method using the non-linear (NLIN) regression (R_{50} as y and T as x) procedure in the Statistical Analysis System (Soltani 2007). The effect of seed aging period on these parameters was evaluated using simple, linear regression analysis.

RESULTS

Examples of the time course of germination as influenced by seed aging and temperature are shown in **Fig. 1**. There were clear differences between aging treatments with respect to cumulative germination. Germination rate and the maximum percentage germination increased as the seeds experienced shorter durations of accelerated aging. The highest and the lowest maximum germination were observed in control seeds (98.3% at 20°C) and in seeds that were aged for 144 h (25.8% at 40°C), respectively. The cumulative germination percentage in all of the aging treatments was most quickly attained at 30°C than at other temperatures (**Fig. 1**).

Temperature, aging, and the temperature × aging interaction significantly affected germination rate, indicating that the response of seeds to temperature was dependent upon the duration of the aging process (**Table 1**). Statistics from model fitting to the germination rate-temperature relationships for different aging treatments are shown in **Table 2**. Predicted versus observed time (hours) to germination are shown in **Fig. 2**. The root mean squares of deviations (RMSD) and R^2 values were similar for all the temperature functions (**Table 2**). However, the segmented and beta func-
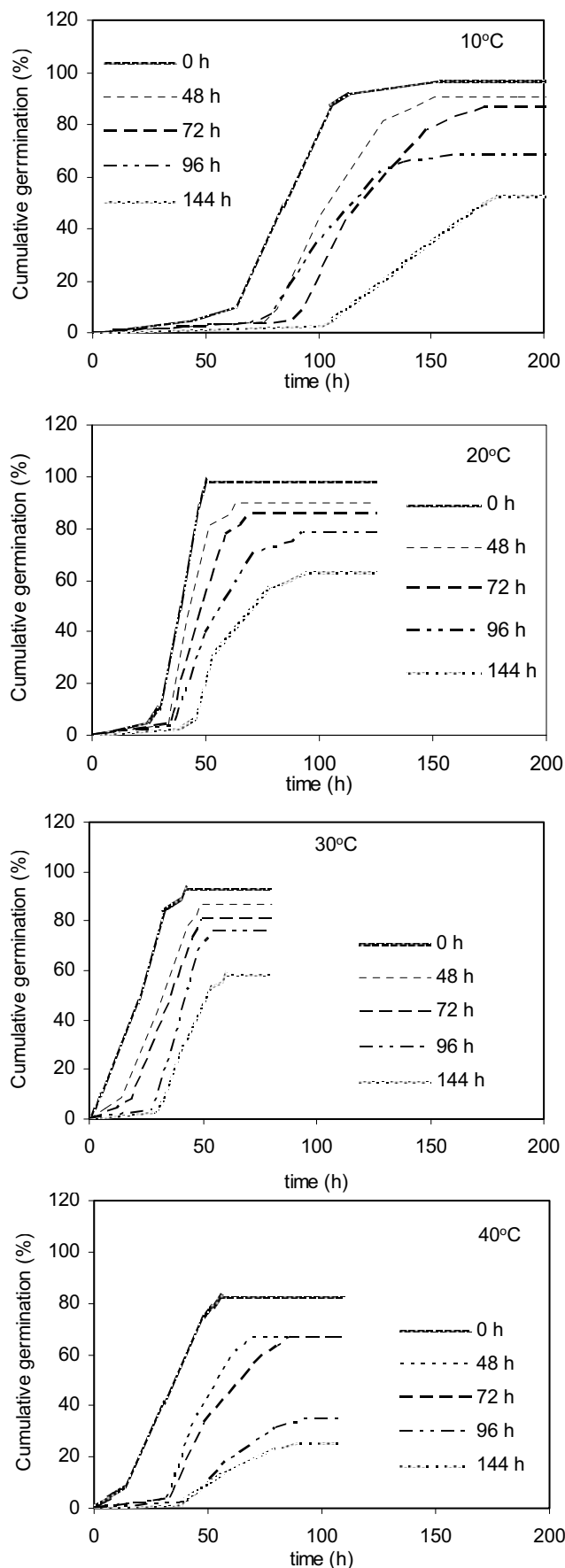

Fig. 1 Cumulative germination percentage versus time for the different aging treatments.

tions had more coefficients with significant bias as indicated by the significant *a* and *b* coefficients in the linear regression between predicted and observed time to germination. With the dent-like function only one significant bias was
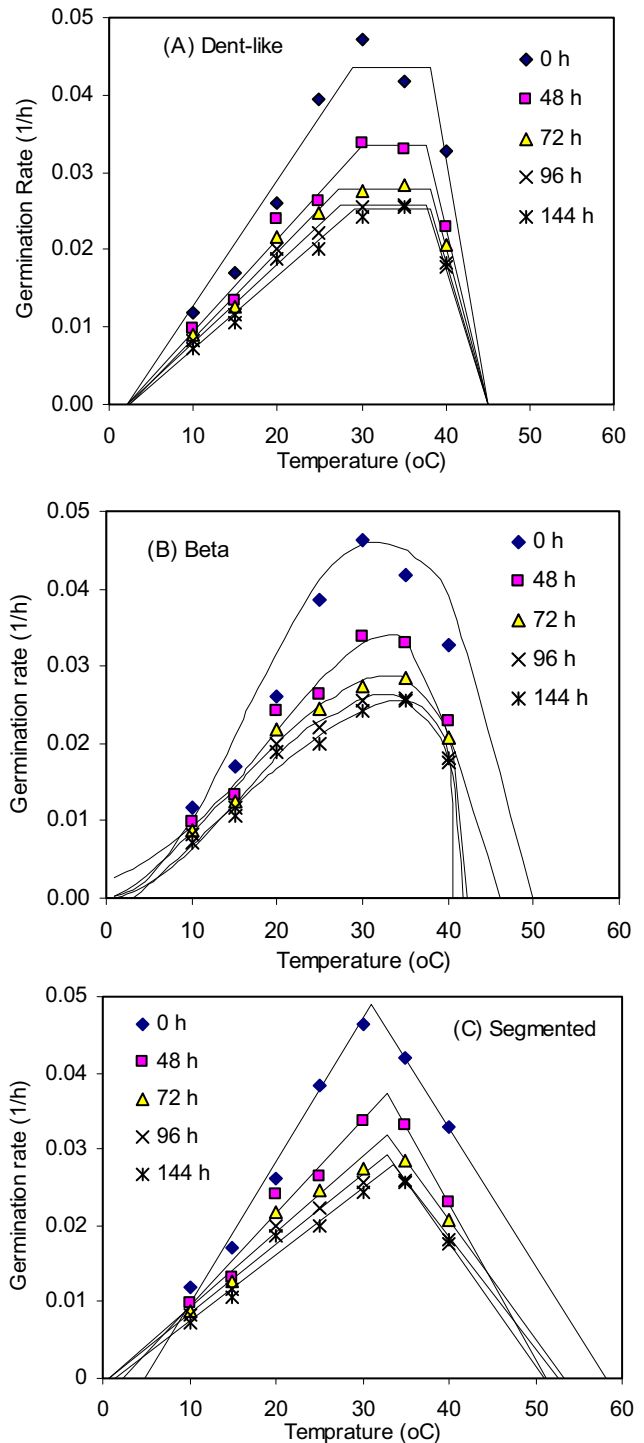
Table 1 Results of analysis of variance (mean squares) for germination rate.

Source of variation	Df	Germination rate
Temperature (T)	6	0.0015***
E1	21	0.00001
Aging period (A)	4	0.0008***
T × A	24	0.00004***
E2	84	0.000004

*** Significant at 0.1% level of probability.
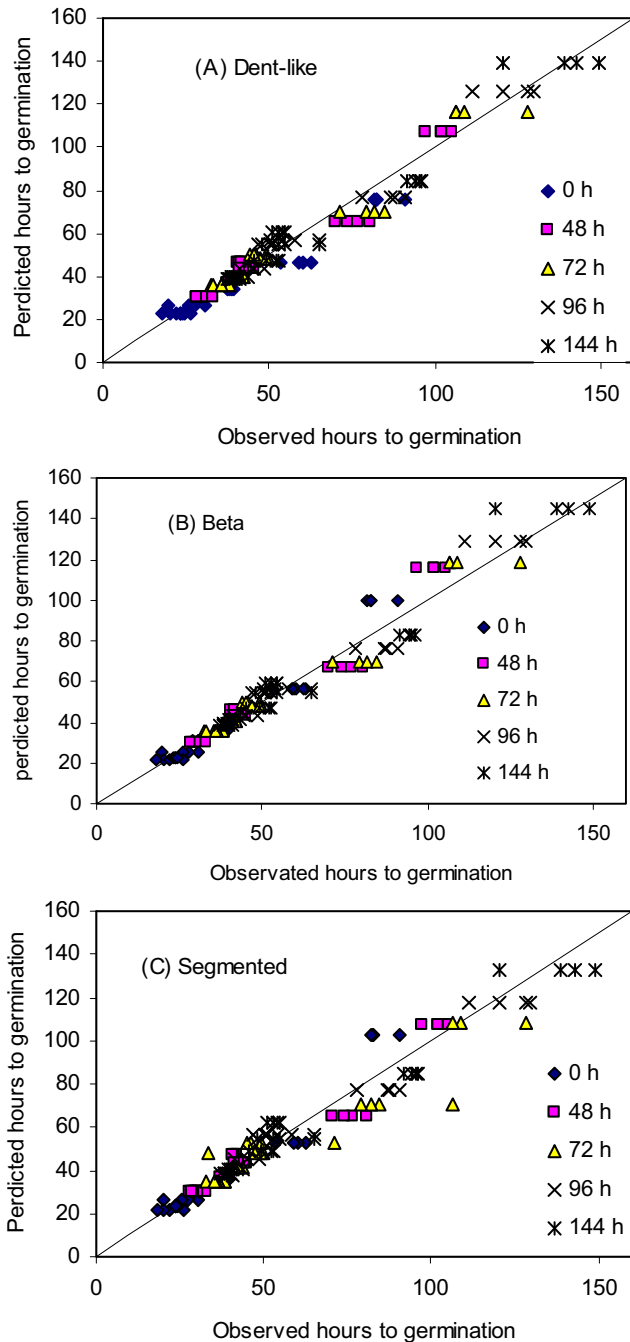
Fig. 2 Predicted vs. observed hours to germination in five aging treatments using (**A**) dent-like, (**B**) beta, and (**C**) segmented functions to describe response of germination rate to temperature. The solid line is a 1:1 line.

Fig. 3 (**A**) Dent-like, (**B**) beta and (**C**) segmented functions used to describe the response of germination rate to temperature in the aging treatments.

detected, i.e., *a* and *b* values for the 0 h aging period (**Table 2**). Therefore, it was concluded that dent-like function was an adequate function for all the aging treatments. The function resulted in a RMSD of less that 7 h and R^2 values of more than 0.84. Thus, aging had no effect on the type of response function to germination. The curve fitting of the dent-like, beta and segmented functions, as described germination response to temperature for 0, 48, 72, 96 and 144

h aging periods are shown in **Fig. 3**.

Estimates of cardinal temperatures and R_{max} are given in **Table 3**. There was no significant difference between aging treatments for cardinal temperatures based on their confidence limits (**Table 3**) and regression analysis (**Fig. 4A-E**). Using a dent-like function, a base temperature of 2.2°C, optimal temperatures of 28.6 to 38.0°C and a ceiling temperature of 45°C were obtained. However, seed aging had a significant effect on R_{max}, the inherent maximum rate of germination. R_{max} decreased from 0.044 h^{-1} in the control treatment to 0.025 h^{-1} for 144 h aging period (**Table 3**). Regression analysis indicated that the inherent maximum rate of germination decreased by 0.0001 h^{-1} per day during the aging period (**Fig. 4E**). Therefore, seed aging in this wheat cultivar affected the germination response to temperature by changing the inherent maximum rate of germination with-

Table 2 Root mean square of deviations (RMSD, h), coefficient of determination (R^2) for the relationship between germination rate (R50; Eqs. (1) and (2)) and temperature as affected by seed aging periods described by various functions. Regression coefficients (*a* and *b*) and correlation coefficient (r) for the relationship between observed and predicated time to germination are also included.

Function-aging period (h)	RMSD	R^2	a ± s.e.	b ± s.e.	r
Segmented					
0	6.75	0.91	-6.69 ± 2.71*	1.20 ± 0.06*	0.97
48	5.61	0.96	-0.15 ± 2.42	1.00 ± 0.04	0.98
72	5.27	0.95	5.72 ± 2.33*	0.88 ± 0.04*	0.98
96	5.43	0.94	5.76 ± 2.45*	0.89 ± 0.04*	0.98
144	6.40	0.95	5.68 ± 2.69*	0.90 ± 0.04*	0.98
Beta					
0	5.14	0.92	-5.71 ± 2.06*	1.18 ± 0.05*	0.98
48	5.10	0.96	-0.28 ± 2.20	1.04 ± 0.01*	0.98
72	6.39	0.90	0.01 ± 2.83	1.00 ± 0.04	0.97
96	6.55	0.95	-0.31 ± 2.95	1.00 ± 0.04	0.97
144	7.67	0.95	0.14 ± 3.23	0.99 ± 0.04	0.97
Dent-like					
0	6.53	0.90	-6.16 ± 2.62*	1.18 ± 0.06*	0.97
48	5.50	0.96	0.23 ± 2.37	0.99 ± 0.04	0.98
72	6.04	0.85	1.01 ± 2.67	0.98 ± 0.04	0.97
96	6.07	0.95	1.44 ± 2.73	0.97 ± 0.04	0.98
144	6.86	0.84	2.79 ± 2.89	0.95 ± 0.04	0.98

* Significant difference (P<0.05) from 0 for *a* and significant difference from 1 for *b*.

Table 3 Estimates of base temperature (T_b), lower optimum temperature (T_{o1}), upper optimum temperature (T_{o2}), ceiling temperature (T_c) and inherent maximum rate of germination (R_{max}), by dent-like function.

A.A. Periods (h)	T_b	T_{o1}	T_{o2}	T_c	R_{max}
0	(2.1)*	28.9 ± 1.91	38.2 ± 0.55	45.0 ± 0.00	0.0444 ± 0.0017
48	2.3 ± 1.07	30.0 ± 1.04	37.7 ± 0.31	45.0 ± 0.00	0.0334 ± 0.0006
72	2.3 ± 0.99	27.4 ± 0.85	38.2 ± 0.29	45.0 ± 0.00	0.0280 ± 0.0005
96	2.1 ± 1.07	27.5 ± 0.92	37.8 ± 0.34	45.0 ± 0.00	0.0257 ± 0.0005
144	2.3 ± 1.25	29.1 ± 1.16	38.2 ± 0.34	45.0 ± 0.00	0.0250 ± 0.0006

*Standard error was not obtainable.

out changing the cardinal temperatures.

DISCUSSION

There are many reports that seed deterioration caused a decline in germination rate, for example, Dell'Aquila and Di Turi (1996) in wheat, Rehman *et al.* (1999) in *Acacia tortilis*, de Figueiredo *et al.* (2003) in sunflower, soybean and maize, Khajeh-Hosseini *et al.* (2003) in soybean and Basra *et al.* (2003) in cotton. This decline might be the consequence of a change in the type of response function of germination rate to temperature or a change in the parameters of the response function, i.e., cardinal temperatures and inherent maximum rate of germination, as influenced by seed deterioration.

Jame and Cutforth (2004) used a beta function to quantity the relationship between germination rate and temperature in spring wheat, i.e. 'Neepawa'. They found cardinal temperatures of 0°C for base, 30°C for optimum and 42°C for ceiling temperatures. Seefeldt *et al.* (2002) reported that the base temperature ranged from 1.2 to 1.6°C among six spring wheat varieties, i.e. 'Edwall', 'Vanna', 'Wawawai', 'Wampum', 'Experss', and 'Spillman'. Addae and Pearson (1992) indicated the base temperature for germination and coleoptile elongation was 1°C in two wheat cultivars, i.e. 'Hartog' (a spring type) and 'Rosella' (winter), but it was 0.4°C for emergence. They reported that the rate of seedling elongation and emergence increase linearly with temperatures between 5 and 25°C. The cardinal temperatures for germination we obtained in our study were similar to those reported by other researchers and did not change with seed deterioration.

Therefore, for seeds aged by environmental stress, the reduced germination rate in response to increased temperature resulted from a reduction in the maximum rate of germination and not from changes to either the type of response function or the cardinal temperatures.

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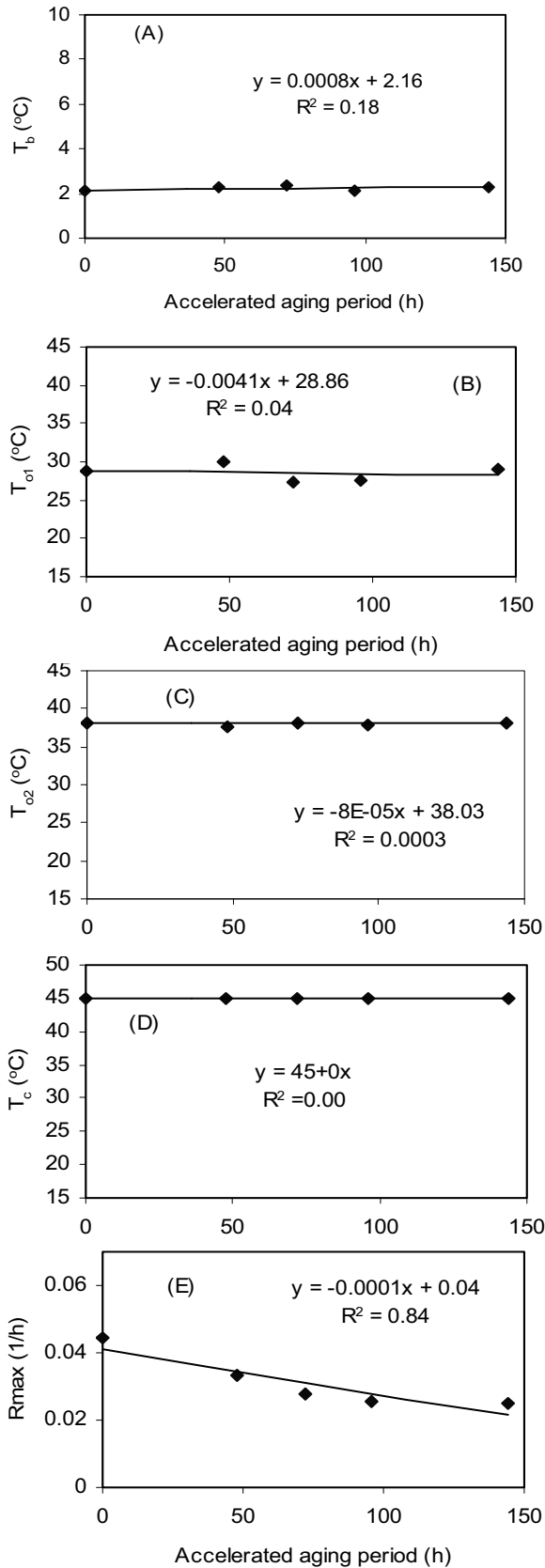
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Fig. 4 Regression analysis to examine the effect of aging period on (**A**) base temperature (T_b), (**B**) lower optimum temperature (T_{o1}), (**C**) upper optimum temperature (T_{o2}), (**D**) ceiling temperature (T_c) and (**E**) inherent maximum rate of germination (R_{max}). All regressions are not significant except for R_{max} (**E**).