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Original article

Modeling the effect of moisture stress on the shift in optimal and maximum temperatures for germination of *Malva parviflora* L. seeds: Introducing a new hydrothermal time model

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Introduction

Seed germination is largely controlled by the temperature and moisture content of the seedbed. Therefore, hydrothermal time models have been widely used to describe seed germination patterns in response to temperature and water potential (Ψ) of the seedbed. The majority of these models assume a Normal distribution for base water potential ($\Psi_{b(g)}$) to describe the variation in time to germination. In some of these models, it is assumed that the thermoinhibition of germination induced by the shift in $\Psi_{b(g)}$ to more positive values occur only at temperatures above the optimum (T_o) and that the T_o is independent of drought stress levels. In this study, the Weibull hydrothermal time was used to quantify the $\Psi_{b(g)}$ changes in response to temperature and to model the effect of drought stress on the shift in the optimal ($T_{o(g)}$) and maximum ($T_{m(g)}$) temperatures for different germination fractions of *malva parviflora* seeds.

Materials and methods

The experiment was conducted at the Seed Technology Laboratory of Agricultural Sciences and Natural Resources University of Khuzestan in 2016. Germination test was performed at eight constant temperatures of 8, 12, 16, 20, 24, 28, 32 and 36 (± 0.2) °C in light/dark conditions (12 h/12 h). In each of the above temperature regimes, seed germination response to different levels of drought stress, i.e. osmotic solutions with concentrations of 0, -0.2, -0.4, -0.6, -0.8 and -0.1 MPa was evaluated. Germination test was performed with four replications (each Petri dish as one replicate). In each replicate, 50 seeds were placed on a layer of Whatman No 1 filter paper in a 9 cm glass Petri dish, and then moistened with 7 ml distilled water or other osmotic solutions. The number of germinated seeds was counted twice every day until germination stopped at each temperature regime (when no germination occurred for 5 consecutive days). The following equation was used to describe the germination behavior of *M. parviflora* seeds in response to the interaction of temperature and Ψ of seedbed:

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$$g = 1 - \exp\left[-\left(\frac{\left(\Psi - \left(\frac{\theta_{HT}}{(T - T_b)t_{(g)}}\right)\right) - \Psi_{base} - K_T(T - T_b) + \left(\beta \times \left((\ln(2))^{\frac{1}{\alpha}}\right)\right)}{\beta} \right)^{\alpha} \right] \quad (1)$$

The optimum and maximum temperatures for germination were also determined using the following equations:

$$T_o = \frac{\Psi - \Psi_{base} + \left(\beta \times \left((\ln(2))^{\frac{1}{\alpha}}\right)\right) - \beta \times (-\ln(1-g))^{\frac{1}{\alpha}}}{2K_T} + T_b \quad (2)$$

$$T_m = \frac{\Psi - \Psi_{base} + \left(\beta \times \left((\ln(2))^{\frac{1}{\alpha}}\right)\right) - \beta \times (-\ln(1-g))^{\frac{1}{\alpha}}}{K_T} + T_b \quad (3)$$

All models, having been formulated into the hydrotime and then hydrothermal models, were fitted to data using PROC NLMIXED procedure of SAS software version 9.4.

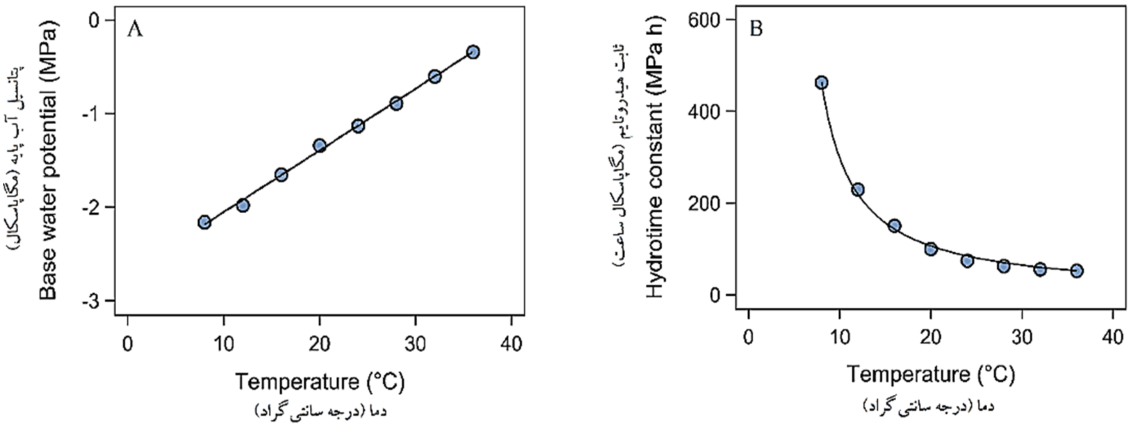
Results and discussion

While $\Psi_{b(g)}$ showed a linear increase in the temperature range between T_b (base temperature) and $T_{m(g)}$, the hydrotime constant (θ_H) decreased nonlinearly in response to increasing temperature. Based on the relationship between $\Psi_{b(g)}$ and θ_H, the shape of the germination rate ($GR_{(g)}$) response to temperature in the hydrothermal time model was curvilinear. The model estimated the values of θ_{HT} (hydrothermal time constant), T_b, Ψ_{base} (base water potential at T_b), and K_T (slope of the $\Psi_{b(g)}$ response to temperature) as 1800.04 MPa °C h, 4.20 °C, -2.46 MPa, and 0.064 MPa °C^{-1}, respectively. Both $T_{o(g)}$ and $T_{m(g)}$ decreased proportionally with increasing drought intensity and became cooler for higher germination percentiles. For example, the estimated $T_{o(50)}$ (optimal temperature for the median) for *M. parviflora* seeds germinated under no water stress (Ψ=0 MPa) was 23.38 °C but dropped to 15.59 °C as water availability became minimum (Ψ=-1.0 MPa). Similarly, it was estimated that 50% of seeds would be able to germination at (or below) 42.55 °C form zero osmotic potential ($T_{m(50)}$ at Ψ=0 MPa) but to attain the same germination level at -1.0 MPa, temperature should never exceed 26.99 °C ($T_{m(50)}$ at Ψ=-1.0 MPa).

Conclusion

The hydrothermal time model not only gave good fits to germination data but also showed some adaptive properties of *M. parviflora* seeds to different temperature and moisture environments. With the increasing severity drought, the $T_{o(g)}$ and $T_{m(g)}$ shifted to cooler values, which mean that the seeds were able to germinate at a narrower temperature range under drought conditions.

***Keywords*:** Base temperature; Base water potential; Germination rate; Thermoinhibition; Weibull distribution



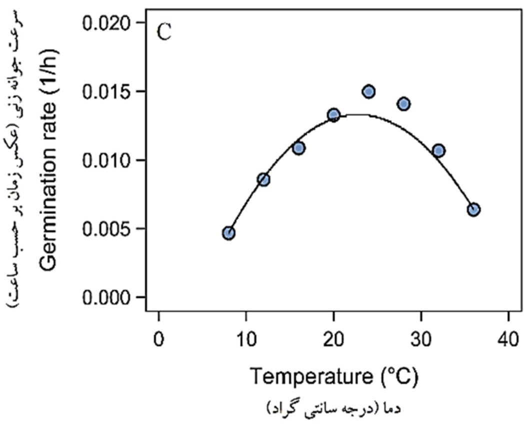


Fig. 1. Changes in median base water potential ($\Psi_{b(50)}$) (A), hydrotime constant (θ_H) (B) and germination rate (GR_{50}) (C) as a function of temperature for *Malva parviflora*. The GR_{50} curve is determined by using the equation $GR_{(50)} = -\Psi_{b(50)} / \theta_H$ as a function of $\Psi_{b(g)}$ and θ_H

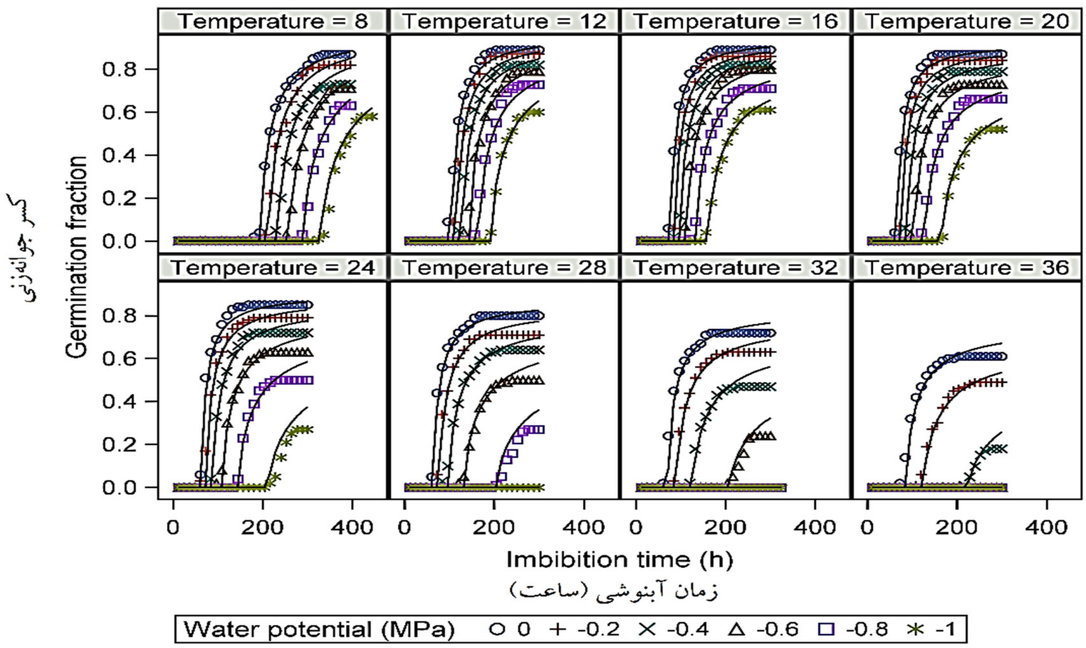


Fig. 2. Cumulative germination of *Malva parviflora* seeds at various temperatures and water potentials. The lines represent the germination time course predicted by the hydrothermal time model and symbols are the observed values

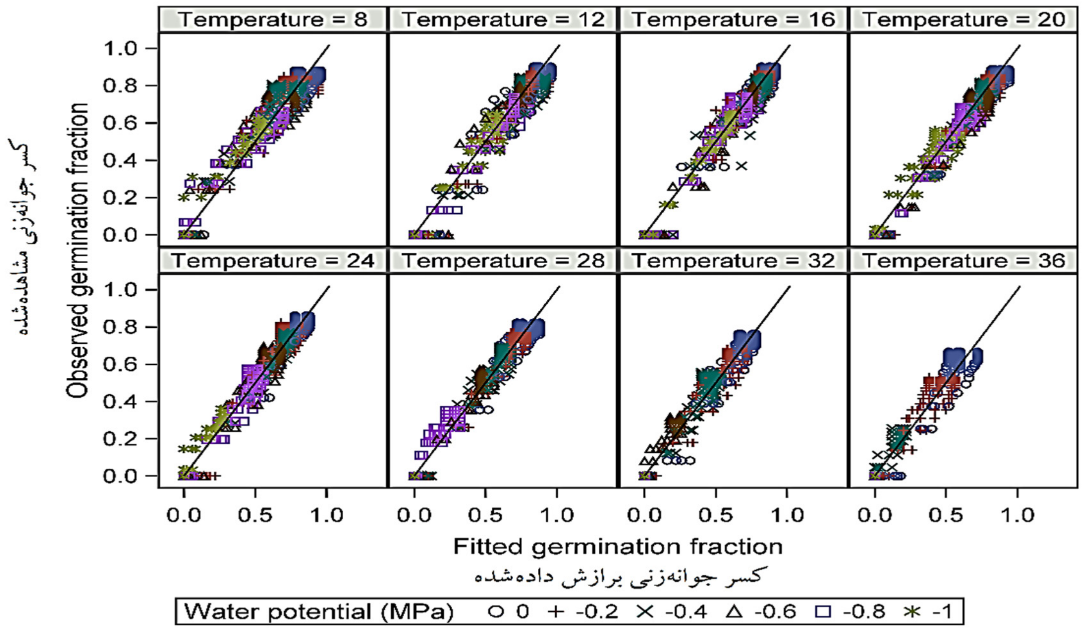


Fig. 3. Observed versus fitted germination fraction for *Malva parviflora* seeds at various temperatures and water potentials.

Table 1. Estimation of the parameters of the hydrothermal time model fitted to germination data of *Malva parviflora* seeds at different temperatures and water potentials.

Parameters†	Estimate	Standard error
θ_{HT} (MPa °C h)	1800.04	7.35
Ψ_{base} (MPa)	-2.464	0.003
K_T (MPa °C^{-1})	0.064	0.000
T_b (°C)	4.198	0.047
β (MPa)	0.401	0.003
α	0.665	0.006
RMSE (%)	5.23	0.05

† θ_{HT}, Hydrothermal time constant; Ψ_{base}, The value of base water potential at $T=T_b$; K_T, The slope of the $\Psi_{b(g)}$ response to temperature; T_b, Base temperature; β, The scale parameter of $\Psi_{b(g)}$ distribution; α, The shape parameter of $\Psi_{b(g)}$ distribution; RMSE, Root Mean Square Error.

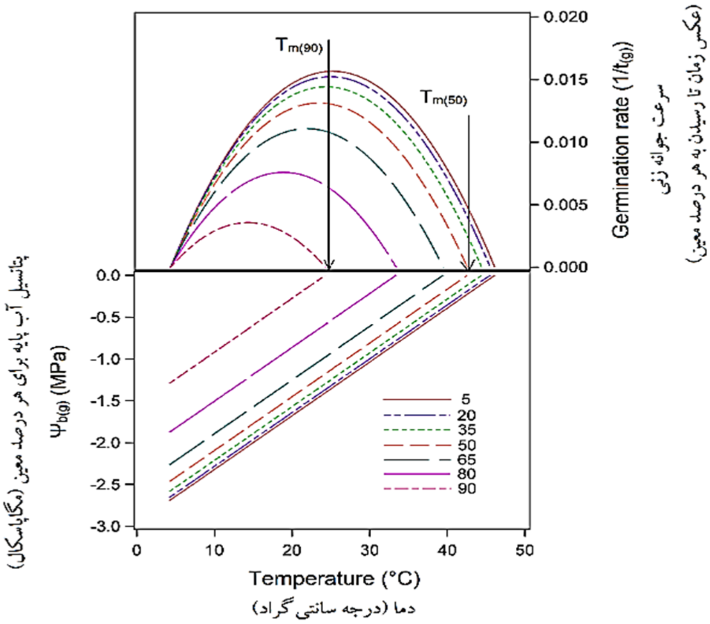


Fig. 4. The effect of temperature on germination rate (GR) and base water potential (Ψ_b) for different germination percentiles (g) of *Malva parviflora* seeds. Base temperature (T_b) was constant among germination percentiles, but optimal temperature (T_o; curvilinear peak) and ceiling temperature (T_m; shown by arrows) were not the same among germination percentiles. T_m for a given germination percentage is the temperature at which the line of $\Psi_{b(g)}$ vs. temperature reaches zero.

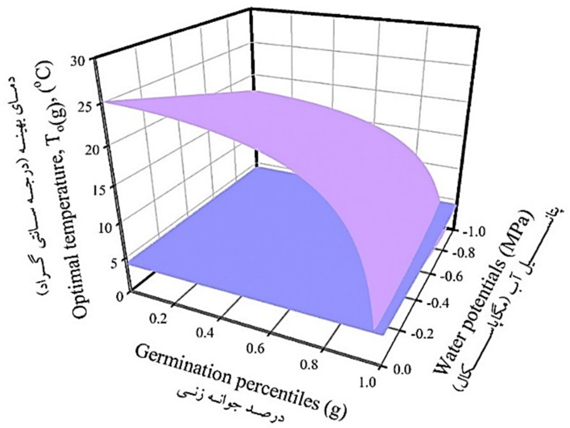


Fig. 5. Predicted changes in optimal temperature (T_o) among germination percentiles (g) at various water potentials for *Malva parviflora*.

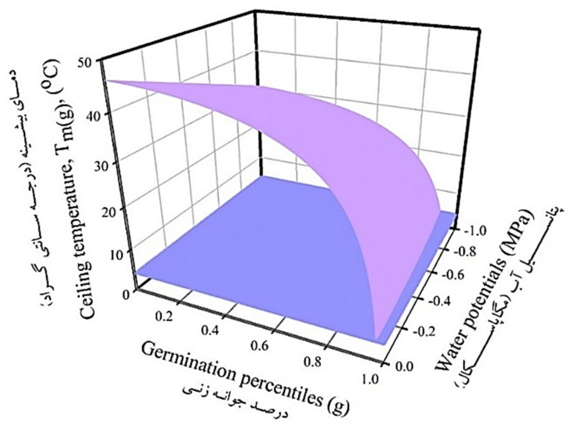


Fig. 6. Predicted changes in ceiling temperature (Tm) among germination percentiles (g) at various water potentials for *Malva parviflora*.