Quantification of the Effect of Environmental Factors on Seed Germination and Seedling Growth of Eruca (*Eruca sativa*) Using Mathematical Models

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Abstract

Eruca (*Eruca sativa*; Brassicaceae) is an important industrial crop due to its ability to grow under a wide range of climatic conditions and in poor fertility lands and also for the quality of seed oil and protein. Seed germination (SG) is an important event in plant's life history which can significantly be influenced by several environmental factors such as temperature (T), water potential (ψ), salinity, pH, and burial depth. Therefore, this study aimed (i) to investigate the effects of these environmental factors on SG behavior of Eruca using several mathematical models, (ii) to determine the cardinal Ts and tolerance threshold value for each trait (i.e., 50% reduction than its maximum value) affected by the environmental factor, and (iii) to quantify the response of Eruca seedling growth to each environmental factor. The results indicated that Eruca SG and seedling growth were significantly influenced by these factors ($P < 0.05$). The estimated cardinal Ts were 1 °C for the base T, 30 °C for the optimum T, and 40.8 °C for the ceiling T. The salt and drought tolerance threshold values were 257 mM NaCl and -1.2 MPa for SG and 247 mM NaCl and -1 MPa for the seedling growth, respectively, suggesting that the seedling growth was more sensitive than SG under both salt and drought stresses in Eruca. In addition, the maximum SG and seedling growth were observed at pH 7 and burial depth 1.9 cm. In general, the models used in this study could describe well the response of Eruca SG under different levels of environmental factors and also their parameters could easily be used in Eruca SG simulation models. This information also could help us to better manage the production of this plant under stressful conditions and/or to determine its geographic range expansion in the world.

Keywords Cardinal temperatures · *Eruca sativa* · Germination · Halotime · Hydrothermal time · Tolerance threshold value · Burial depth

Introduction

Eruca (*Eruca sativa*; Brassicaceae) is an important industrial crop due to its ability to grow under a wide range of climatic conditions and in poor fertility lands and its high tolerance to adverse environmental conditions [i.e., drought, salt, and temperature (T)] (Garg and Sharma 2014). It shows a good

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oil and protein concentration (290 and 325 g kg⁻¹ of dry matter, respectively) with high erucic acid ~ 45% (C22:1) and gadoleic acid ~ 8.7% (C20:1) contents (Lazzeri et al. 2004). In addition, its seeds contained high thio-functionalized glucosinolate enzyme as a good biocontrol agent which could be used in integrated pest management (Tacconi et al. 1998).

Seed germination (SG) is the first complex process and the important event in the plant's life cycle (Bewley et al. 2013). Following SG, seedling emergence is also an important phenological event that affects the successful establishment of an annual species (Forcella et al. 2000). In general, the seasonal SG patterns are mostly controlled by environmental factors such as soil temperature, water availability (i.e., water potential or ψ), oxygen deficiency, light quality, salinity, pH, seed burial depth, and their interactive effects

which can determine the speed and extent of SG (Bewley et al. 2013; Baskin and Baskin 2014).

Water potential influenced both the germination rate and the germination percentage within a seed population (Bewley et al. 2013). When water potential becomes more negative (decreased ψ), the rate of seed imbibition and then both germination rate and germination percentage declined (may be completely prevented) resulting of water deficit (Bradford 2002; Bewley et al. 2013). The negative impact of decreasing ψ on SG was previously reported in many species and also several industrial crops such as safflower (*Carthamus tinctorius* L.) (Bidgoly et al. 2018), sugar beet (*Beta vulgaris* L.) (Gummerson 1986), potato (*Solanum tuberosum* L.) (Alvarado and Bradford 2002), zucchini (*Cucurbita pepo* L.) (Atashi et al. 2015) and sesame (*Sesamum indicum* L.) (Bakhshandeh et al. 2017).

Temperature as a major environmental factor can regulate enzyme activities and promote or inhibit the synthesis of hormones that affect SG (Baskin and Baskin 2014). The relationship between germination percentage and T is often a broad maximal range due to it is less sensitive to T compared germination rate. For this reason, germination rate as a parameter which is more sensitive to T can describe well the pattern of SG, particularly for calculating the cardinal Ts (Bewley et al. 2013). Germination rate started to be increased linearly from T_b (the base T often is a single T in a seed population but not always), reached its maximum at T_o (the optimum T, where SG is most rapid and may be a single T and/or a range of Ts) and then decreased with T above T_o (linearly and/or curvilinearly, depending on plant species) until T_c (the ceiling T, where SG is completely inhibited) (Bradford 2002). However, it is important to identify the cardinal Ts for determining the best planting dates for each species (Bakhshandeh et al. 2013). To date, many researchers applied thermal time (TT), hydrotime (HT), and hydrothermal time (HTT) models to quantify the effect of T, ψ, and a combination of both, respectively, on SG of various species (Kebreab and Murdoch 1999; Alvarado and Bradford 2002; Rowse and Finch-Savage 2003; Atashi et al. 2014; Bakhshandeh et al. 2015; Atashi et al. 2015; Bakhshandeh et al. 2017; Bidgoly et al. 2018).

Salinity influences SG either osmotically through decreasing water uptake or ionically through the accumulation of salt ions (i.e., Na^+ and Cl^-) which resulted in an imbalance nutrient uptake and toxicity effect on metabolic processes during SG (i.e., DNA repair and protein synthesis) (Bewley et al. 2013). In contrast, an osmotic adjustment is observed in some species due to ion accumulation in the seeds under low to moderate saline conditions (Seal et al. 2018).

According to previous studies, many plant species can germinate in a wide range of pH (Rezvani and Fani Yazdi 2013; Vahabinia et al, 2019), while for others it could be a limiting factor (Amini et al. 2015). In general, the availability of some micronutrients such as Fe, Mn, Cu, and Zn will be increased at low soil pH, while the availability of P and Mo decreased and Al may indicate a toxic effect on SG (Atwell 2003).

Seed burial depth is also considered as an important factor influencing SG and seedling emergence. In fact, successful seedling emergence depends on the depth at which SG occurs (Javaid et al. 2018; Rezvani and Fani Yazdi 2013; Amini et al. 2015) due to ψ, T, and light exposure in soil which are influenced by seed burial depth (Chachalis and Reddy 2000). Some species show the maximum seedling emergence when the seeds were placed on the soil surface such as tobacco (*Nicotiana glauca* R. Graham) (Florentine et al. 2016), *Cucumis melo* var. agrestis Naud (Xu et al. 2017), and foxtail sophora (*Sophora alopecuroides*) (Nosratti et al. 2018). In addition, seedling emergence decreased at greater depths in many species which could be due to a small amount of seed reserves and/or lower hydration of seeds at greater depths (Dinelli et al. 2013).

Many mathematical models were applied to date, each with strengths and weaknesses, to quantify the response of SG and seedling emergence as functions of measured and estimated environmental factors such as ψ, T, oxygen, light, salinity, pH, seed burial depth, and their interactive effects in various species (Atashi et al. 2014; Bakhshandeh et al. 2015; Bakhshandeh et al. 2017; Nosratti et al. 2018; Javaid et al. 2018; Vahabinia et al. 2019). Therefore, the objectives of this study were (i) to determine the effect of T, ψ, salinity, pH, and burial depth on SG and seedling emergence of Eruca, (ii) to calculate the Eruca SG cardinal Ts using the hydrothermal time model, and (iii) to estimate the tolerance threshold value for each trait (i.e., 50% reduction than its maximum value) affected by different environmental factors using mathematical models. Consequently, a better understanding of the seed ecology of Eruca could help us to better manage the production of this plant under different environmental conditions and/or to determine its geographic range expansion in the world.

Materials and Methods

Seed Description and Germination Test Protocol

Seeds of cultivated Eruca (*Eruca sativa*) were provided by Pakan-Bazr Company (Isfahan, Iran) and then transported to Mazandaran province (Sari city, Iran) in 2017. The seeds were stored in a black plastic bag and maintained in the dark at 5 °C before use (seed viability > 95%). Germination tests were conducted with four replications of 50 seeds for each treatment which were within 80 mm Petri dishes and placed on two sheets of filter paper (Whatman No. 1). Each Petri

dish containing 6 ml of distilled water (control) and/or test solutions (supplemented with 0.1% Tiram fungicide) to provide adequate moisture during the experiment. Petri dishes were placed in thin plastic bags to reduce desiccation and were then randomly placed within the germination incubators with ± 0.5 °C accuracy (IKA-Model KS 4000 ic control, Germany) in the dark, except when recording germination. Seeds were monitored several times daily, depending on the environmental factors (e.g., T, ψ, salinity, and pH) and seeds considered germinated when the radicle protruded 0.2 cm from the seed coat. For all experiments, the germination test was terminated when no further germination has occurred after three consecutive days.

Seedling Test Protocol

Standard germination tests were carried out with four 20-seed samples for each treatment (e.g., ψ, salinity, and pH). For this purpose, rolled papers (i.e., the seed will be germinated between two layers of moist paper) were used (ISTA 2009). Seeds were randomly incubated in the dark in the germinator at 30 °C (i.e., T_o) in all experiments. The number of normal seedlings was measured on the seventh day (the end of standard germination test) and then seven seedlings were randomly selected from each replicate and the length of the radicle and shoot was measured by a ruler in cm. Seedlings were placed in an oven at 70 °C until constant weight and then the dry weight of seedlings was determined by a balance with 0.0001 g precision.

Effects of Temperature and Water Potential

Nine constant temperatures (5, 10, 15, 20, 25, 30, 35, 38, and 40 °C) at each of the following five ψs (0 (Control), − 0.3, − 0.6, − 0.9, and − 1.5 MPa) were used in this experiment. The ψs were prepared using polyethylene glycol (PEG8000, Scharlau, Spain) according to Michel and Radcliffe (1995) formula [$\psi s = 0.13(PEG)^2 T − 13.7(PEG)^2$]. Distilled water was used for control treatment (0 MPa). An osmometer (Model 5100C: Wescor Inc., Logan, UT, USA) was used to re-check the ψ values at each T before starting the experiment and also every 2 days in the germination medium during experiments. The seeds were unable to germinate at − 1.5 MPa across all Ts. In general, treated seeds were placed in the condition as described in the seed germination and seedling test protocols.

Effects of Salinity

To quantify the effect of salt stress on SG and seedling growth of Eruca, eight levels of salinity using solutions including 0 (Control), 50, 100, 150, 200, 250, 300, and 350 mM of sodium chloride (NaCl) were used. Treated seeds were placed in the condition as described in the seed germination and seedling test protocols.

Effects of pH

The effect of pH buffer solutions on SG and seedling growth of Eruca was investigated based on the methods described in Basto et al. (2013). Briefly, citrate–phosphate buffers were used to prepare pH solutions of 2, 3, 4, 5, and 6 [0.1 M citric acid solution + 0.2 M dibasic sodium phosphate solution were combined to make targeted solutions] and by adjusting with 0.1 N HCL solution. A tricine (*N*- Tris (hydroxymethyl) methylglycine) solution was also used to prepare buffered solutions of 8, 9, and 10.5 pH by adjusting with 1 N NaOH solution. The pH 7 was prepared using a 2 mM solution of HEPES [N-(2-hydroxymethyl) piperazine-*N*-2-ethanesulfonic acid)]. Treated seeds were placed in the condition as described in the seed germination and seedling test protocols.

Effects of Burial Depth

Three replicates of 50 seeds for each burial depth were planted in soil in 10-cm-diameter plastic pots (black color and with 17 cm height) at depths of 0.5, 1, 2, 3, 4, 5, 6, and 7 cm. The soil type was loam (45, 25, and 30% of sand, clay, and silt, respectively). Greenhouse T was 28 ± 2 °C during the experiment. The pots were irrigated as required to maintain them at the field capacity during the experiment. Seedling emergence was counted every day and then finished after 2 weeks. Seedling emergence was defined when the two cotyledons could be seen at the soil surface.

Mathematical Models

Thermal time (TT) models were used to quantify the germination time course with T (based on 'heat units') (Bradford 2002). For sub- and supra-optimal Ts, the models can be written as

$$\theta_{T(g)} = (T − T_b)t_g \tag{1}$$

or

$$GR_g = 1/t_g = (T − T_b)/\theta_{T(g)} \tag{2}$$

$$\theta_2 = (T_{c(g)} − T)t_g \tag{3}$$

or

$$GR_g = 1/t_g = (T_{c(g)} − T)/\theta_2, \tag{4}$$

where T, T_b, t_g, $\theta_{T(g)}$, θ_2, and $T_{c(g)}$ are the temperature (°C), the base temperature (°C), the time to a given specific

germination percentage g (h), the thermal time constant at sub-optimal Ts for a specific germination percentage g in the population (°C h), the thermal time constant at supra-optimal Ts (°C h), and the ceiling temperature (°C) (T_c values vary among different seed percentage g in the population), respectively.

At sub-optimal Ts, the TT model (Eqs. 1 and 2) describes that germination rate for a given specific seed percentage g (GR_g) increased linearly at $T > T_b$ with a slope of $1/\theta_{T(g)}$ and also an intercept which defined as T_b. In contrast, the TT model at supra-optimal Ts (Eqs. 3 and 4) predicts that GR_g will linearly decline at $T > T_o$, with a slope of $1/\theta_2$ for all seed percentages and varies intercept which was defined as $T_{c(g)}$. In fact, differences in GR_g for each seed percentage is related to the variation in $T_{c(g)}$ and the TT held constant at supra-optimal T (Bradford 2002).

A hydrotime model (HT; Eqs. 5 and 6) suggested by Gummerson (1986) was used to quantify the response of germination rate to ψ:

$$\theta_H = (\psi - \psi_{b(g)})t_g \tag{5}$$

or

$$GR_g = 1/t_g = (\psi - \psi_{b(g)})/\theta_H, \tag{6}$$

where θ_H, ψ, and $\psi_{b(g)}$ are the hydrotime constant (MPa h), the actual water potential (MPa), and the base water potential or drought tolerance threshold value (MPa, defined for a specific SG fraction).

A hydrothermal time model (Eqs. 7 and 10) was used to simultaneously investigate the effect of T and ψ on SG patterns of Eruca at all Ts and ψs (Rowse and Finch-Savage 2003): For sub-optimal Ts,

$$\theta_{HTT} = (\psi - \psi_{b(g)})(T - T_b)t_g \tag{7}$$

or

$$Probit\ (g) = [(\psi - (\theta_{HTT}/(T - T_b)t_g) - \psi_{b(g)}]/\sigma\psi_b \tag{8}$$

and for supra-optimal Ts,

$$\theta_{HTT} = [\psi - (\psi_{b(g)} + k_T(T - T_d))](T - T_b)t_g \tag{9}$$

or

$$Probit\ (g) = [(\psi - k_T(T - T_d)) - \theta_H/((T - T_b)t_g) - \psi_{b(g)}]/\sigma\psi_b, \tag{10}$$

where θ_{HTT}, T_d, $\sigma\psi_b$, and k_T are the hydrothermal time constant (MPa °C h), T at which $\psi_{b(g)}$ starts to change (°C), the standard deviation of $\psi_{b(g)}$ in the seed population (MPa), and a constant value which is indicating the rate of increase in $\psi_{b(g)}$ per increase in T at supra-optimal T (MPa °C^{-1}), respectively. In fact, in this model, the continuing TT accumulation increases linearly at $T > T_d$ and then increases in germination rate will gradually be offset by the increasing T using the following formula [$\psi - (\psi_{b(g)} + k_T(T - T_d))$] which resulted in a curvilinear shape above T_o (see more details in Rowse and Finch-Savage 2003).

A halotime model (Eqs. 11 and 12) suggested by Seal et al. (2018) was fitted to describe the effect of salt stress on Eruca SG which is as follows:

$$\theta_{Halo} = (NaCl - NaCl_{base(g)})t_g \tag{11}$$

or

$$GR_g = 1/t_g = (NaCl - NaCl_{base(g)})/\theta_{Halo}, \tag{12}$$

where θ_{Halo}, NaCl, and $NaCl_{base(g)}$ are the halotime constant (mM h), the actual NaCl concentration (mM), and the base NaCl concentration or salinity tolerance threshold value (mM, defined for a specific SG fraction).

We also used a three-parameter segmented model (Eq. 13) for describing the response of the final seed germination and normal seedling of Eruca influenced by salt and drought stresses:

$$\begin{aligned} G\ \% &= G_{max} \quad \text{if } x < x_0 \\ G\ \% &= G_{max} + b(x - x_0) \quad \text{if } x \geq x_0 \end{aligned} \tag{13}$$

where G, G_{max}, x_0, and b are the final germination (%) at concentration x, the maximum G (%), the concentration when the linear decrease in G began, and the rate of decrease in G per increase in NaCl (mM) and/or per decrease in ψ (MPa), respectively. In this model, the required concentration of NaCl/ψ for 50% inhibition of G_{max} (i.e., salinity/drought tolerance threshold value) could be calculated by the formula [$x_{50} = ((G_{max}/2)/-b) + x_0$] and also where SG is stopped (no seeds germinated after this point) could be calculated by the formula [$G_0 = (G_{max}/-b) + x_0$]. Based on our knowledge, all parameters estimated by this model (Eq. 13) are easier to understand and also easier to interpret physiologically.

Statistical Analysis

All regression analyses (linear, non-linear, and probit analysis) were done using the statistical analysis system (SAS) ver. 9.4 (SAS Institute 2013) and Excel software to describe the response of Eruca SG under different levels of environmental factors mentioned above. The graphs were drawn by SigmaPlot 11 software. To compare the means of treatments, a two-way analysis of variance by the GLM procedure was used based on the least significant difference (LSD) test at the 0.05 probability level.

Results

T, ψ, salinity, pH, and burial depth significantly influenced the patterns of SG and seedling growth of Eruca ($P \leq 0.05$). The effect of each environmental factor on the SG behavior and seedling growth of Eruca seeds are presented below.

Effects of Temperature

There were linear relationships between germination rates of each percentile ($1/t_g$ for specific germination percentage) when plotted against sub-optimal T, up to 30 °C at 0 to –0.6 MPa and up to 15 °C at -0.9 and -1.5 MPa (data not shown). The estimated T_b was constant (equal to 1 °C) between percentiles at all ψs (Table 1).

Separate TT analysis was done at each of ψ because the SG pattern was different as ψ decreased. Based on the results, the model (Eq. 1) could predict well ($R^2 = 0.97$) the germination time course of Eruca seeds at sub-optimal T (5–30 °C) in water (Fig. 1a, an example at $\psi = 0$ MPa). TT values (1/slope of the line for 50th percentile) increased non-linearly with the decreasing ψ (more negative) in sub-optimal T (Table 1). A similar pattern was also observed in the $\sigma_{\theta T}$ values, which means that the standard deviation of the normal distribution of TT in the seed population increased with a decrease in ψ (Table 1, Fig. 1b, an example at $\psi = 0$ MPa).

We also found that the TT (from 96.15 to 71.42 °C h) and $T_{c(50)}$ (from 40.8 to 32.3 °C) values decreased linearly when ψ declined from 0 to -0.9 MPa (Table 1, Fig. 1d, an example at $\psi = 0$ MPa). On the other hand, the rate of decrease in TT and $T_{c(50)}$ was 27.77 °C h and 9.57 °C per MPa decrease in ψ, respectively (fitted models not shown).

The σ_{Tc} values also showed that there was no significant difference between ψs in terms of this parameter (2.28 °C, averaged for all ψs at supra-optimal T).

Effects of Water Stress

ψ significantly affected SG at each T and also the seedling growth of Eruca at T_o (30 °C). As an example, germination percentage and germination rate significantly declined with decreasing ψ (Fig. 2b). The HT model could describe well ($R^2 \geq 0.87$) the germination time course of Eruca seeds at different levels of ψ when each T was analyzed separately (Table 2). The θ_H values decreased from 70.9 MPa h at 5 °C to 7 MPa h at 40 °C (Table 2). On the other hand, there was no significant difference between the θ_H values at supra-optimal T (~7 MPa h for 35, 38 and 40 °C), but it significantly declined at sub-optimal T when T increased from 5 to 30 °C (i.e., T_o) (Table 2). The $\psi_{b(50)}$ values were also approximately constant at sub-optimal T and then increased linearly at T above T_o until T_c (where SG is equal to zero and ψ is above 0 MPa) (Table 2). In addition, the $\sigma\psi_b$ values ranged from 0.379 to 0.802 MPa which was not significantly affected by T (Table 2).

The results of seedling growth test showed that the percentage of normal seedling remained constant (95%) until -0.54 MPa which means that this trait was not affected by ψ at > -0.54 MPa (Fig. 2c), and then decreased linearly to zero at -1.5 MPa, where the seeds were not able to produce a normal seedling. In the linear phase, normal seedling decreased 94.04% per MPa decrease in ψ (became more negative) (Fig. 2c). Likewise, the same pattern was observed in root length (Fig. 2d). The maximum root length was 1.408 cm which remained constant from zero to -0.67 MPa ($P > 0.05$) and then decreased linearly to zero at -1.5 MPa with the rate of 1.696 cm per MPa decrease in ψ (Fig. 2d). In addition, with the increasing ψ, shoot length decreased

Table 1 Thermal time parameters for the progress of germination of *Eruca sativa* seeds at different water potentials

Water potentials (MPa)	Sub-optimal Ts					Supra-optimal Ts				
	T_b (°C)	$\theta_{T(50)}$ (°C h)	$\sigma_{\theta T}$ (°C h)	Slope	R^2	$T_{c(50)}$ (°C)	θ_2 (°C h)	σ_{Tc} (°C)	Slope	R^2
0	1.00	245.4	175.7	0.00407	0.97	40.83	96.15	2.35	0.01040	0.96
-0.3	1.00	326.6	167.9	0.00306	0.95	38.34	88.49	2.30	0.01130	0.90
-0.6	1.00	449.2	172.6	0.00222	0.90	35.15	79.36	2.26	0.01260	0.94
-0.9	1.00	1057	291.0	0.00094	0.80	32.32	71.42	2.21	0.01400	0.96
-1.5	1.00	9449	356.5	0.00010	0.78	–	–	–	–	–

Parameters were estimated by the models (Eqs. 1 and 3) which are fitted to the germination time course data at each temperature based on a normal distribution of both $\theta_{T(g)}$ and $T_{c(g)}$ in the seed population. The slope of the lines for the 50th percentiles of germination is equal to the inverses of the thermal times to germination ($1/\theta_{T(50)}$), which vary among individual seeds in a normal distribution. The ceiling temperatures for germination ($T_{c(g)}$) also vary among seed percentiles in a normal distribution (see more details in Fig. 1)

Note: T_b, the base temperature for germination; $\theta_{T(50)}$, the sub-optimal thermal time of germination; $\sigma_{\theta T}$, the standard deviation of $\theta_{T(g)}$ distribution; R^2, the coefficient of determination; θ_2, the supra-optimal thermal time of germination; $T_{c(50)}$, the ceiling temperatures for the 50th percentiles of germination; σ_{Tc}, the standard deviation of $T_{c(g)}$ distribution
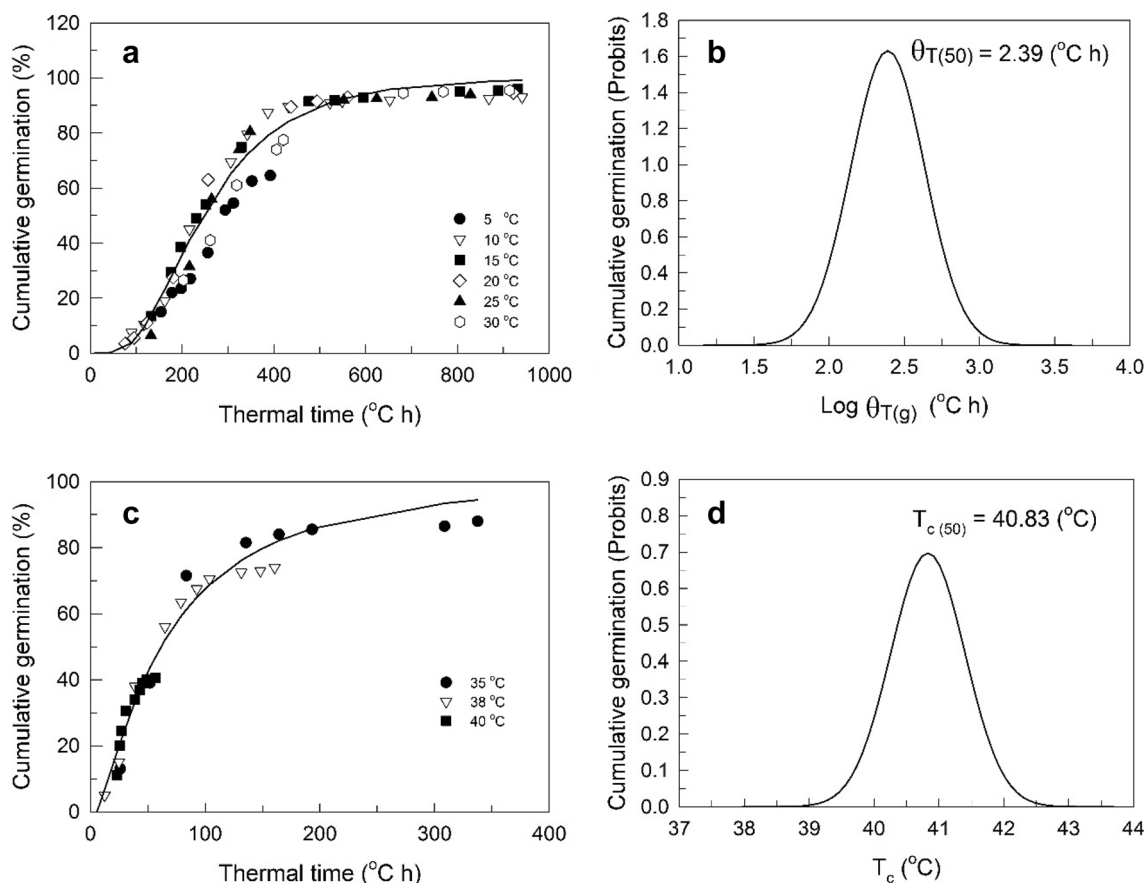
Fig. 1 **a** The relationship between germination and sub-optimal thermal time at the control condition ($\psi = 0$ MPa); **b** $\theta_{T(g)}$ is indicating on a logarithmic thermal time scale based on a normal distribution; **c** the relationship between germination and supra-optimal thermal time at the control condition ($\psi = 0$ MPa); **d** the ceiling temperatures (T_c) for germination among seed population in a normal distribution. The symbols and solid lines are indicating observed and predicted data, respectively. The thermal time parameters are presented in Table 1

rapidly (3.817 cm per MPa) from 4.02 cm at 0 MPa to zero at − 1.1 MPa which is indicating that shoot length was more sensitive to ψ than root length (Fig. 2e). The $\psi_{b(50)}$ value (i.e., drought tolerance threshold value) for SG, normal seedling, root length, and shoot length was − 1.20, − 1.04, − 1.08, and − 0.526 MPa, respectively (Fig. 2a, c, d, e). In addition, the maximum seedling dry weight (SDW) observed at − 0.35 MPa (1 mg plant^{-1}) decreased gradually to zero at –1.1 MPa based on a quadratic model (Fig. 2f).

Effects of Temperature and Water Stress Together

The HTT model (Eqs. 7 and 9) was used to simultaneously quantify the response of Eruca SG at all Ts and ψs. Our findings showed that the model could well quantify these relationships with R^2 of more than 0.93 (Table 3, Fig. 3d). A linear relationship was observed at $T < T_o$, for all ψs, limited to a single T (i.e., T_b) where Eruca seeds were unable to germinate and also at $T > T_o$, for all ψs, where GR_g decreased gradually until T_c (Fig. 3c). T_c varied among ψs

and decreased linearly (9.57 °C per MPa) with the decreasing ψ (data not shown).

In general, the shape of the germination rate response to T is determined by the interplay between θ_H and $\psi_{b(50)}$ values (Fig. 3a and b). In fact, at sub-optimal T, the $\psi_{b(50)}$ values approximately remained constant and so the increasing θ_H values at lower Ts will be the main reason for the linear decrease in germination rate. Inversely, at supra-optimal T, the $\psi_{b(50)}$ values increased linearly as T increased and the θ_H values approximately remained constant at the lowest (~7 MPa h). Therefore, the negative impact of the increasing $\psi_{b(50)}$ was not overcome by the small values of the θ_H in this condition which resulted in a gradually decrease (but not linearly) in germination rate at supra-optimal T (Fig. 3c).

The results showed that the $\psi_{b(50)}$ value was equal to − 1.24 MPa at sub-optimal T and then increased with T at supra-optimal T (with the rate of 0.113 MPa per increase in $T > T_o$ which was defined as k_T). However, the $\psi_{b(50)}$ value reached zero at 40.8 °C (i.e., T_c) the intercept of the linear phase of the model at supra-optimal T
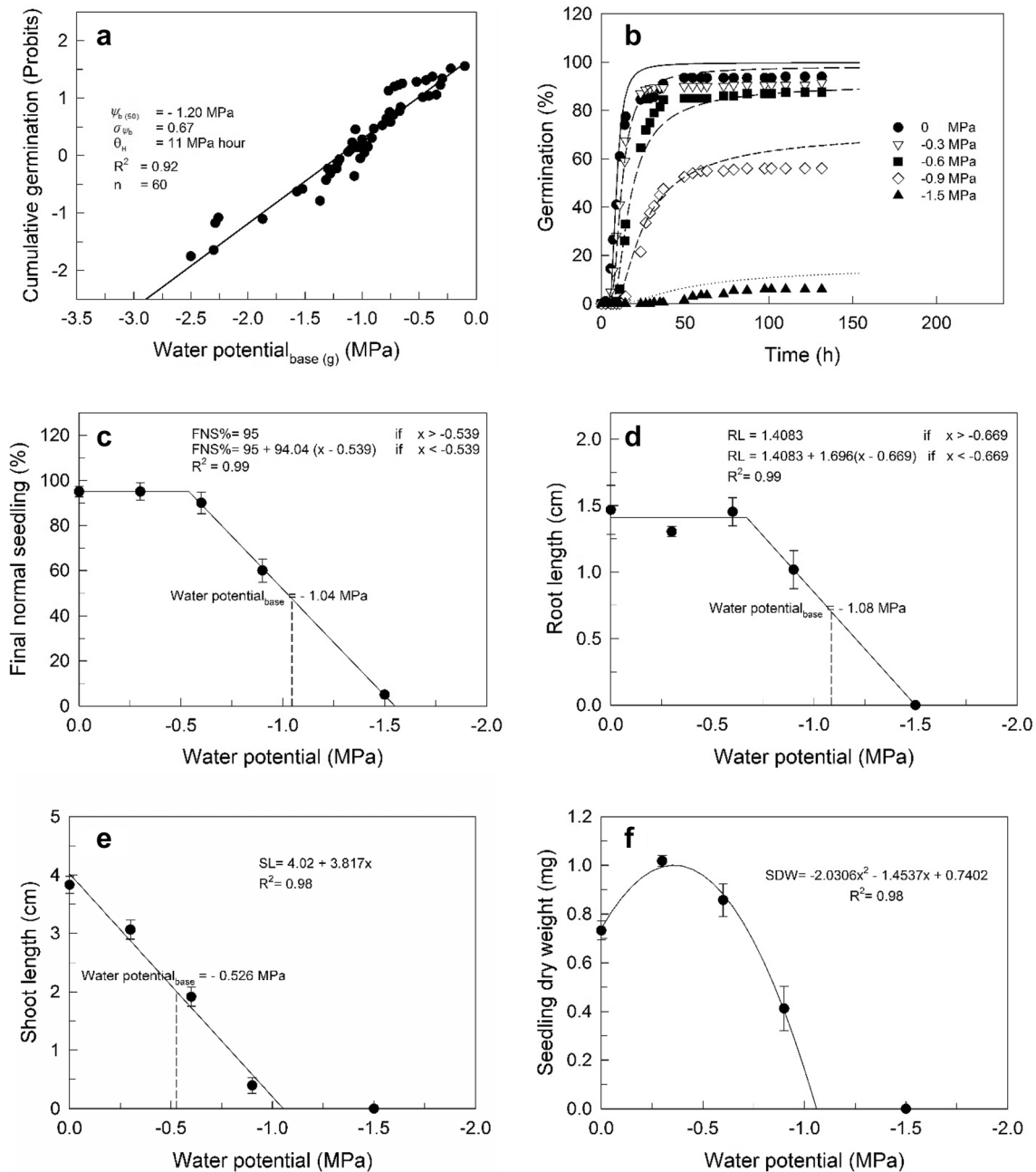
Fig. 2 Effect of the water potential on the germination of *Eruca sativa*. **a** The linear regression using the probit analysis method; **b** the germination time courses at different levels of water potential; **c** the final percentage of normal seedling; **d** root length; **e** shoot length; and **f** seedling dry weight of *Eruca sativa*. The symbols represent observed data and the lines were predicted by the models developed in this study. The vertical bars in parts of **c–f** also represent the mean ± standard error. The data related to − 1.5 MPa were not used when the model fitted in panels **e** and **f**

in water ($\psi = 0$ MPa) (Fig. 3b). The HTT constant was 297.9 MPa °C h after fitting the model (Eq. 7) (Table 3). In general, the HTT model could predict well the germination time courses of Eruca seeds at all Ts and ψs (Fig. 3d). However, the model indicates a small error for the germination time course calculating at supra-optimal

T which can often be expected because it was fitted to all data (combined all Ts and ψs) for describing the full data set (Fig. 3d). Based on the estimated parameters presented in Table 3, the Eruca cardinal Ts were 1, 30, and 40.8 °C for T_b, T_o, and T_c, respectively, in water (Fig. 3c).

Table 2 Estimated parameter values using the hydrotime model (Eq. 5) to describe seed germination of *Eruca sativa* in all temperatures at each of the following different levels of water potential (ψ)

Temperature (°C)	θ_H (MPa h)	$\psi_{b(50)}$ (MPa)	$\sigma\psi_b$ (MPa)	GR (h^{-1})	R^2
5	70.9	− 1.13	0.802	0.01594	0.92
10	31.1	− 1.20	0.522	0.03876	0.87
15	17.0	− 1.11	0.444	0.06521	0.90
20	15.4	− 1.26	0.525	0.08214	0.96
25	11.2	− 1.16	0.444	0.10374	0.92
30	11.0	− 1.20	0.659	0.10860	0.92
35	7.66	− 0.74	0.595	0.09744	0.95
38	7.00	− 0.37	0.379	0.05385	0.87
40	7.00	− 0.07	0.517	0.01054	0.94

Note: θ_H, the hydrotime constant; $\psi_{b(50)}$, the base water potential for the 50th percentile; $\sigma\psi_b$, the standard deviation of $\psi_{b(g)}$ distribution; GR calculated by the model parameters. R^2, the coefficient of determination

Table 3 Estimated Parameter values using the hydrothermal time models (HTT; Eqs. 7 and 9) for describing seed germination of Eruca in all temperature (T) and water potential (ψ) treatments used in the experiment

HTT parameters	*Eruca sativa*
$\psi_{b(50)}$ (MPa)	−1.24
$\sigma\psi_b$ (MPa)	0.481
θ_{HTT} (MPa °C h)	297.9
k_T (MPa °C h)	0.113
T_d (°C)	30.0
Cardinal temperatures	
T_b (°C)	1.00
T_o (°C)	30.0
T_c (°C)	40.8
R^2	0.93

T_c calculated by the extrapolated from the germination rate data at Ts above T_o. R^2 is the coefficient of determination

T_d in Eq. 9 is equal to T_o in the present study

Note: T_b, the base temperature for germination; T_o, the optimum temperature for germination; T_c, the ceiling temperature for germination; $\psi_{b(50)}$, the base water potential for the 50th percentile; $\sigma\psi_b$, the standard deviation of $\psi_{b(g)}$ distribution; HTT; the hydrothermal time constant and k_T; the slope of the line fitted to the $\psi_{b(50)}$ values at $T > T_o$

Effects of Salt Stress

The SG, normal seedling, root length, shoot length, and SDW were affected by the NaCl concentration (Fig. 4). The maximum SG was more than 80% at 0, 50, 100, and 150 mM NaCl ($P \geq 0.05$) and then decreased significantly to 26% (~ 71% lower than the control) at 350 mM NaCl

(Fig. 4b). Also, the seeds germinated more slowly (i.e., higher t_g) under salt stress.

A halotime model (Eq. 11) was fitted to quantify the SG of Eruca at different levels of salt stress at 30 °C (i.e., T_o). In addition, to test the effect of salt ions uptake by the Eruca seeds we first fitted the model to the experimental data and then the NaCl concentrations were converted to ψ values using the formula suggested by Van't Hoff (1887).

The results showed that the estimated NaCl$_{base(50)}$ using the above approach was lower (− 1.47 MPa) than those estimated by the hydrotime model (− 1.20 MPa) when both were presented in MPa. Thus, the amount of osmotic adjustment was calculated to be 18.4% in Eruca seeds [(1−(− 1.20/−1.47))×100 = 18.4] and the model parameters were 2464.9 mM h for the θ_{Halo}, 257 mM for the NaCl$_{base(50)}$, and 141 mM for the standard deviation of NaCl$_{base(g)}$ in the seed population (Fig. 4a).

The maximum value (> 90%) of normal seedling was observed up to 150 mM NaCl, differences were not significant, and then its value decreased linearly as salt stress increased until 355 mM NaCl, where normal seedling was completely inhibited (i.e., G_0) (Fig. 4c). In the linear phase, the amount of decrease in normal seedling was 0.412% per mM increase in salt stress. The results also indicated that normal seedling was more sensitive than SG under salt stress because the salinity tolerance threshold value was estimated to be 257 mM NaCl for SG and 247 mM NaCl for normal seedling (Fig. 4c).

Likewise, root length remained constant (1.40 cm) at salt stress lower than 119 mM NaCl, and then linearly decreased with the rate of 0.00597 cm per mM increase in NaCl concentration until 354 mM NaCl, where root length was completely inhibited (i.e., RL$_0$) (Fig. 4d). In addition, the highest shoot length was 3.65 cm in the control and then linearly declined (0.010 cm per mM) with the addition of salt stress until 339 mM NaCl (i.e., SL$_0$) (Fig. 4e). The salinity tolerance threshold values for root length and shoot length were 236 and 169 mM NaCl, respectively, suggesting that shoot length was more sensitive to salt stress than root length. SDW achieved its maximum value at 85.23 mM NaCl (0.6913 mg plant^{-1}) and then gradually decreased to 345 mM NaCl where SDW was equal to zero (Fig. 4f).

Effects of pH

Eruca seeds germinated well (> 83%) between pH 5 and pH 8, but decreased significantly at pH < 5 and pH > 8 (Table 4). The rate of decrease in SG was the same (~ 76%) for both pH 3 and pH 10.5 when compared to the control (pH 7). Based on the quadratic model parameters, the optimum pH was estimated to be 7 (94%) for this plant and then reached zero at pH < 2 and > 11 (data not shown). The
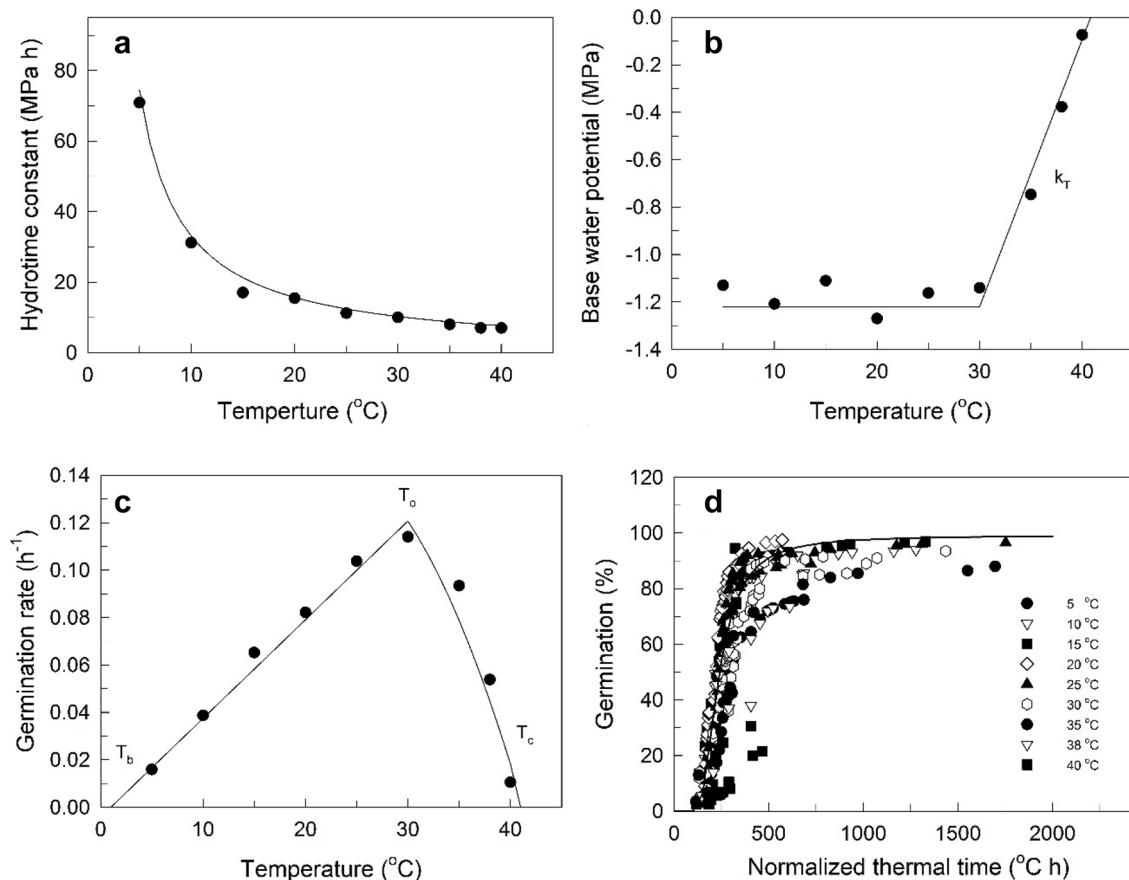
Fig. 3 Changes in the hydrotime constant (**a**), the base water potential (**b**) and the germination rate (**c**) as a function of temperature are presented for *Eruca sativa*. **d** Germination time course data for all Ts and ψs are presented based on a normalized thermal time scale in water, based upon the parameters shown in Table 3. **c** The predicted cardinal temperatures for the 50th percentile in water are shown. The actual and predicted data are shown by the symbols and the lines in the figures

same pattern was observed in the normal seedling when the pH solutions were applied. The maximum normal seedling was observed at pH 7 (81.2%), but significantly decreased by 23 and 81% for pH 8 and pH 9, and by 87, 94, and 94% for pH 6, 5, and 4, respectively, as compared with the control (i.e., pH 7) (Table 4). Eruca seeds were unable to produce a normal seedling at pH values < 3 and > 10, suggesting that the normal seedling was more sensitive to pH solutions than SG in Eruca. This difference between SG and normal seedling suggests that SG (used in many published studies) cannot be an appropriate index to accurately predict seedling establishment of seed lots under natural conditions (i.e., in soil). Root length, shoot length, and SDW, like the normal seedling, showed the same patterns when different levels of pH solutions were applied (Table 4). The highest values were obtained at pH 7 (1.03 and 2.89 cm, and 0.584 mg plant^{-1} for root length, shoot length and SDW, respectively) and/or in alkaline conditions relative to acidic conditions (Table 4).

Effects of Burial Depths

The seedling emergence of Eruca was significantly influenced by burial depth ($P \leq 0.05$). It reached a maximum of 80, 62, 58, 47, and 4% at burial depths of 2, 3, 1, 0.5, and 4 cm, respectively (Fig. 5a). In addition, the time taken for the 50th percentile of seedling emergence was higher at 0.5, 3, and 4 cm (2.5, 2.7, and 3.5 d, respectively), whereas differences were not statistically significant when the seeds were placed at the burial depths of 1 and 2 cm (2.1 and 2 days, respectively) (Fig. 5a). After fitting a quadratic model, the seedling emergence increased from 0.5 to 1.9 cm (equal to the maximum, 80%) and then decreased gradually as the burial depth increased until 4.05 cm, where the seedling emergence completely inhibited (Fig. 5b). Therefore, the best burial depth was 1.9 cm for this plant.
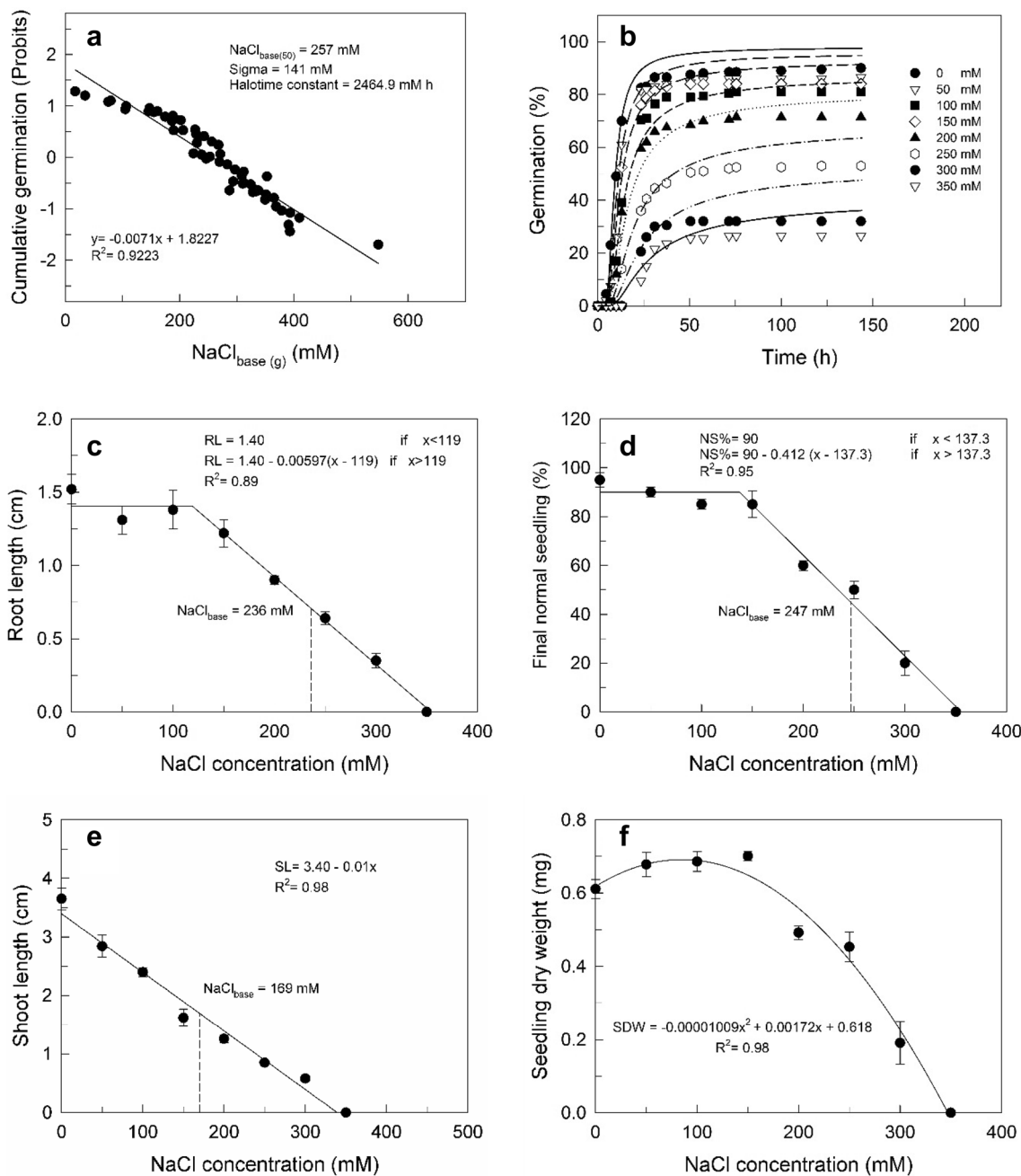
Fig. 4 Effect of the sodium chloride (NaCl) concentration on the germination of *Eruca sativa*. **a** The linear regression using the probit analysis method; **b** the germination time courses at different levels of NaCl concentration; **c** root length; **d** the final percentage of normal seedling; **e** shoot length; and **f** seedling dry weight of *Eruca sativa*. The symbols represent observed data and the lines were predicted by the models developed in this study. The vertical bars in parts of **c**, **d**, **e** and **f** also represent the mean ± standard error

Discussion

Application of mathematical models can be a useful way to quantify the effect of environmental factors on SG in various species (Forcella et al., 2000; Bradford 2002; Bakhshandeh et al. 2013, 2017; Nosratti et al. 2018; Javaid et al. 2018; Vahabinia et al. 2019). To date, the TT, HT, HTT models were successfully used in many studies for quantifying the germination time course at all ψs and Ts (Kebreab and Murdoch 1999; Alvarado and Bradford 2002; Rowse and Finch-Savage 2003; Atashi et al. 2014; Bakhshandeh et al. 2017; Derakhshan et al. 2018; Bidgoly et al. 2018). In addition, other models such as segmented, beta, dent-like, logistic, quadratic, and linear models were used to quantify the effect

Table 4 Analysis of variance and means comparison of the studied traits related to Eruca seed germination under different levels of pH

Sources of variation	Degree of freedom	Seed germination (%)	Normal seedling (%)	Root length (cm)	Shoot length (cm)	Seedling dry weight (mg plant^{-1})
F-test	8	**	**	**	**	**
pH levels						
2		1.00 e	0.00 c	0.0000 d	0.0000 c	0.0000 c
3		22.0 d	0.00 c	0.0000 d	0.0000 c	0.0000 c
4		64.5 c	5.00 c	0.0179 d	0.0179 c	0.0200 c
5		86.0 ab	5.00 c	0.0179 d	0.0179 c	0.0200 c
6		86.0 ab	10.0 c	0.1214 c	0.2143 c	0.0643 c
7		94.5 a	81.2 a	1.0321 a	2.8893 a	0.5786 a
8		83.5 ab	62.5 b	0.4607 b	1.1893 b	0.3643 b
9		70.0 c	15.0 c	0.0500 d	0.2214 c	0.1107 c
10.5		24.5 d	0.00 c	0.0000 d	0.0000 c	0.0000 c

** Significant at 0.01 probability level

CV is the coefficient of variation which was related to overall data

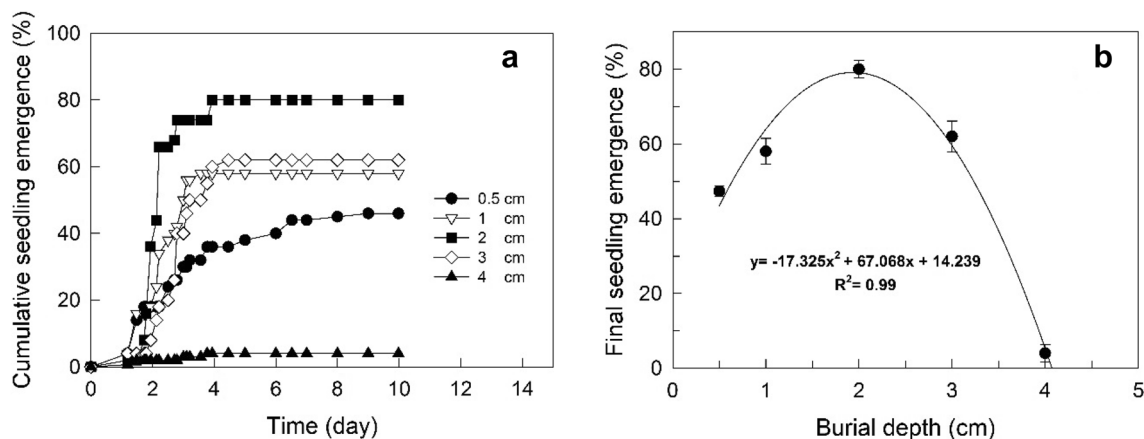† Means with the same letter are not significantly different at the probability level of 0.05

Fig. 5 Effect of burial depth on the seedling emergence time course (**a**) and final percentage of seedling emergence (**b**) in Eruca

of environmental factors on SG in many species in the past (Bakhshandeh et al. 2013; Bidgoly et al. 2018; Bradford 2002; Nosratti et al. 2018). The estimated parameters by the models here can be used as an important input for the prediction models of Eruca SG in the field condition.

Effects of Temperature

In the present study, the estimated T_b (1 °C) was unaffected by ψ. It was similar to those reported by Jalilian and Khalili Aqdam (2015) for Eruca (0.79 °C) and by Andreucci et al. (2016) for cabbage (~0 to 1 °C). The seeds often have a single T_b in the population (Kebreab and Murdoch 1999; Bakhshandeh and Gholamhossieni 2019) which is in agreement with our results, although there were several reports

(often in non-crop species) that indicated this assumption is not always true such as *Orobanche aegyptiaca* (Kebreab and Murdoch 2000) and winterfat (*Eurotia lanata* (Pursh) Moq.) (Wang et al. 2004). This may be due to some genetic variability in the seed population as shown in *Setaria viridis* (Forcella et al. 2000). The TT value non-linearly increased with the addition of ψ at sub-optimal T which means that seeds needed higher TT to complete their germination at lower ψs as a result of slower germination rate in these conditions in comparison with the non-water stress condition (Kebreab and Murdoch 1999; Bidgoly et al. 2018).

The T_c value decreased from 40.8 to 32.3 °C as ψ decreased from zero to − 0.9 MPa which are in accordance with previous studies (Rowse and Finch-Savage 2003; Bakhshandeh et al. 2017; Bidgoly et al. 2018). In fact, the

T_c values are influenced by different levels of ψs in a normal distribution which can be the main reason for decreasing germination rate at supra-optimal T. The θ_{T_c} values decreased linearly with the decreasing ψ until -0.9 MPa, which means that although seeds needed a smaller θ_{T_c} at lower ψ, GR_g will be decreased due to the declining T_c values in these conditions.

Effects of Water Stress

Many previous works showed that the θ_H values significantly declined as T increased which was in agreement with our results (Alvarado and Bradford 2002; Mesgaran et al. 2017; Bakhshandeh et al. 2017; Bakhshandeh and Gholamhossieni 2019). We also found that the $\psi_{b(50)}$ values were constant at sub-optimal Ts and then increased linearly at T above T_o until T_c (Fig. 3b). These findings were similar to the results obtained in other species such as potato (Alvarado and Bradford 2002) and sesame (Bakhshandeh et al. 2017). In contrast, Mesgaran et al. (2017) recently reported that $\psi_{b(50)}$ values increased linearly across all Ts (sub- and super-optimal T) after using a log-logistic distribution in the HT model. In addition, Rowse and Finch-Savage (2003) in carrot and onion indicated that $\psi_{b(50)}$ values increased linearly at $T < T_o$ which it defined as T_d.

$\sigma\psi_b$ is indicating the uniformity of germination within the seed populations based on Bradford and Still's (2004) suggestion. Similarly, Bakhshandeh and Gholamhossieni (2019) in radish and Abdellaoui et al. (2019) in *Retama raetam* indicated that the seeds germinated more uniformly around T_o than $T > T_o > T$. SG and normal seedling were not affected by ψ up to ~ -0.54 MPa which was higher than those reported by Fallahi et al. (2015) who indicated Eruca SG did not decrease until -1 MPa and then its value decreased by 16% at -1.4 MPa as compared with the control. Eruca root length and SDW increased by 30 and 49% until -0.8 MPa and then both remarkably declined (by 83 and 70% compared to the control) when ψ decreased to -1.4 MPa, respectively, which was similar to the results reported by Fallahi et al. (2015). Also, Channaoui et al. (2017) showed that root length of canola increased by 34% until -0.5 MPa and then decreased by 48% until -0.9 MPa when compared with the control.

Fallahi et al. (2015) also reported the amount of decrease in Eruca shoot length was 77% at -1 MPa which was more than the amount of decrease in root length (38%) compared to the control. Kayacetin et al. (2018) in wild mustard reported that shoot length decreased by 90% as ψ decreased up to -1 MPa. In general, decreasing SG and seedling growth with the decreasing ψ can be due to a reduction in water imbibition by seeds during germination which had negatively impact in metabolic processes such as the

reduction in hydrolysis and utilization of the seed reserve (Toosi et al. 2014).

Effect of Temperature and Water Stress Together

The investigation of SG behavior under both T and ψ effects is most important to determine the distribution capacity of species in stressful environmental conditions (Abdellaoui et al. 2019). Therefore, the HTT model as a robust method was used to simultaneously quantify the effect of both T and ψ on SG in recent decades. Similar to the previous results, we observed that the model could describe well ($R^2 < 0.93$) SG behavior of Eruca at all Ts and ψs. The T_b (1 °C) and T_o (30 °C) values estimated in this study were very close to the value reported by Jalilian and Khalili Aqdam (2015) who found that T_b and T_o for Eruca SG were 0.79 °C and 16.5–32.5 °C, respectively, while the estimated T_c value (40.8 °C) in this study was lower than those reported by them (47.5 °C).

In fact, the HTT is explaining how biological and environmental factors interact to regulate SG behavior in a seed population. Indeed, it considers that at a given T, germination rates in a seed population are proportional to the amount by which T and ψ exceed their threshold values for these environmental factors and are controlled by the difference between a physiologically determined ψ threshold and ψ of the seed. Thus, the HTT analysis can offer several indices about seed quality, stress tolerance, speed, and uniformity of germination (Bradford 2002; Bakhshandeh and Gholamhossieni 2018).

Effects of Salt Stress

Plant sensitivity to salt stress depends on plant species and their developmental stage (Prado et al. 2000). Our findings agree with the results of Fallahi et al. (2015) who reported that Eruca SG was not significantly affected by salt stress up to 100 mM NaCl and then sharply decreased by increasing NaCl concentration (60% at 200 mM NaCl than the control). In other study, Jamil et al. (2005) reported that with the increasing salt stress until 14.1 ds m^{-1} (~ 141 mM NaCl) SG significantly declined by 43.5, 88, and 77% in canola, cabbage, and cauliflower (*Brassica oleracea botrytis* L.), respectively, suggesting that Eruca seeds could be germinated at higher levels of salt stress compared to other brassicaceae species.

Both root and shoot, as the most important plant components, can significantly affect the response of the plant to salt stress (Jamil et al. 2005). Roots absorb water from the soil and shoot supply it to the plant. Fallahi et al. (2015) in Eruca showed both root and shoot length significantly decreased with the increasing salt stress and reached zero at 300 mM NaCl for root length and 200 mM NaCl for shoot length,

which were lower than those obtained in this study (354 and 345 mM NaCl, respectively).

SDW increased with the addition of salt stress until a maximum (0.6913 mg plant^{-1} at 100 mM NaCl) and then gradually declined at higher salt stress which is in agreement with the results found by Ashraf (1994) who reported that *Eruca sativa* Mill. had a greater SDW under lower salt stress compared to the control condition as a result of higher soluble sugars, proline, and free amino acids in the tissues particularly in the leaves. In general, exclusion of Na$^+$, high K/Na selectivity, and high Ca^{+2} uptake along with a higher amount of sugars, amino acids, and proline in the leaves were considered as the main reasons for enhancing salt tolerance in plants (Shannon and Grieve 1998).

However, salt stress influenced SG and seedling growth either osmotically through decreasing water uptake which is often observed in halophyte crops or ionically through the accumulation of sodium and chloride which resulted in imbalanced nutrient uptake and toxicity effect on metabolic processes (i.e., DNA repair and protein synthesis) which is often observed in non-halophyte crops (Bewley et al. 2013). The decline in SG under salt stress may be due to an osmotically enforced "seed dormancy" under this condition as an adaptive strategy of seeds to inhibit germination and the growth in stressful environments (Gill et al. 2003). Moreover, salt stress can possibly reduce the activity of phosphorolytic enzymes (i.e., acid phosphatase) which resulted in a decrease in SG (Nasri et al. 2016).

In agreement with the results presented in this study, Seal et al. (2018) reported that Na$^+$ accumulation in *Suaeda maritime* seeds leads to higher seed moisture. Therefore, the predicted NaCl$_{base}$ value by the model may be higher in seeds with a permeable seed coat (salt ion includes, i.e., *S. maritime*) than those with non-permeable seed coat (salt ion excluders). Consequently, the ability of the halotime model will depend on differences between species in term of their ability to include and/or exclude one of the sodium and chloride ions into the seed (Seal et al. 2018).

Effects of pH

Many researchers to date have investigated the effect of hydrogen ion concentration (pH) on SG of various crops such as canola and wheat (Baquy et al. 2017), field muskmelon (Xu et al. 2017), and Dame's Rocket (*Hesperis matronalis*) (Susko and Hussein 2008) but not on seedling growth. pH values < 4 and > 8 have been reported to prevent SG in many plant species such as canola and wheat (Baquy et al. 2017) and *Rumex confertus* (Kołodziejek and Patykowski 2015), while other reports indicated that SG may be uninfluenced by pH 4–10 such as African mustard (Chauhan et al. 2006), field muskmelon (Xu et al. 2017), and Dame's Rocket (Susko and Hussein 2008). An optimum

pH in many species has been reported to be 7 (Honarmand et al. 2016; Amini et al. 2015) which is in agreement with our results in Eruca. For example, pH was not limited for SG of white horehound (*Marrubium vulgare* L.) and the seeds were able to germinate at a range of pH from 5 to 10 with the highest SG at pH 7 (99%), and then severely declined (~ 90%) in acidic or alkaline conditions (Javaid et al. 2018). In general, decreasing SG may be due to the negative effects of pH on several biological systems during SG, damaging organic compounds, organelles, and/or physical structure of seed (Basto et al. 2013).

Effects of Burial Depth

Seed burial depth is another factor influencing SG and seedling growth due to it is effectiveness from the soil moisture, soil temperature, light, physical properties of the soil, and/or the physical limitations of the seedling in this condition (Chachalis and Reddy 2000; Xu et al. 2017). Based on our results, the seedling emergence declined significantly with the increasing burial depth which is in accordance with the results obtained in canola and wild mustard (Soltani et al. 2014) and cabbage (Shanmuganathan and Benjamin 1992).

Our findings also agree with the study demonstrating that African mustard seeds were able to emerge in soil surface (29%), but lower than those placed at 1 and 2 cm (51 and 44%, respectively) and the seedling emergence completely stopped at 5 cm depth (Chauhan et al. 2006). Xu et al. (2017) indicating that an increase in burial depth leads to higher t_{50} values in field muskmelon, similar to the results presented here. Moreover, many reports showed that light may be a requisite for SG such as tobacco (Florentine et al. 2016) and foxtail sophora (Nosratti et al. 2018), but we found that Eruca seeds were able to germinate in the dark and light was not a prerequisite for this plant. The main reason for decreasing the seedling emergence percentage at deeper burial depth (> 2 cm) can be due to insufficient seed reserves of Eruca seeds (as small-seed species; each seed had approximately ~1.61 mm diameter and 0.0022 mg weight), because seeds usually required higher reserves to reach the soil surface (Baskin and Baskin 2014).

Conclusion

SG and seedling growth of Eruca were significantly affected by environmental factors such as T, ψ, salt stress, pH, and burial depth. The cardinal Ts were 1 °C for T_b, 30 °C for T_o, and 40.8 °C for T_c. The salinity and drought tolerance threshold value for 50% reduction was 257 mM NaCl and − 1.2 MPa for SG and 247 mM NaCl and − 1 MPa for seedling growth, respectively, suggesting that seedling growth was more sensitive than SG (used in many previously

studies) to both salt and drought stresses in Eruca. In addition, the maximum SG and seedling emergence were observed at pH 7 and burial depth 1.9 cm. The models used in this study could describe well the response of Eruca germination under different levels of environmental factors and also their parameters could easily be used in Eruca SG simulation models. This information also could help us to better manage the production of this plant under different environmental conditions and to determine its geographic range expansion in the world.

Compliance with Ethical Standards

Conflict of interest All authors declared that they have no conflict of interest.

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