



Modeling seed germination of quinoa (*Chenopodium quinoa* Willd.) at different temperatures and water potentials

Hedayatollah Karimzadeh Soureshjani¹ · Mahmoud Bahador² · Mahmoud Reza Tadayon² · Ayoub Ghorbani Dehkordi³

Received: 18 February 2021 / Revised: 11 May 2022 / Accepted: 26 August 2022 / Published online: 3 September 2022
© The Author(s) under exclusive licence to Franciszek Górski Institute of Plant Physiology, Polish Academy of Sciences, Kraków 2022

Abstract

Seed germination is one of the most critical plant growth stages regulated by temperature (T) and water potential (Ψ). This experiment was conducted to quantify the seed germination response of two quinoa (*Chenopodium quinoa*) cultivars (Sajama and Titicaca) to T and Ψ using hydro time (HT) and hydrothermal time (HTT) models. The results showed that T , Ψ , and their interaction significantly affected the maximum germination percentage (MGP) of both cultivars. Based on the results of the segmented model fit at $\Psi=0$ MPa, the minimum (T_b), optimum (T_o), and maximum T (T_c) in Sajama was estimated at 6.9, 21.9 and 34.9 °C, respectively and in Titicaca were estimated 8.0, 21.8 and 33.6 °C, respectively. While using the HTT model at different T and ψ the T_b was estimated by 8.28 and 8.39 °C for Sajama and Titicaca, respectively, the T_o also estimated 26.96 for Sajama and 27.21 °C for Titicaca. Also, using the modified HTT model, the T_o estimated 27.46 for Sajama and 27.31 °C for Titicaca. There was an increase in hydro time constant (θ_H) when T increased at supra-optimal T_s (from 17 to 70 MPa h⁻¹) as well as when the T decreased at sub-optimal T_s (from 17 to 79 MPa h⁻¹). Also, it was observed that change of the T from T_o to T_b and T_c increased base Ψ (ψ_b) so that for each degree Celsius decrease of T at sub-optimal T_s , the ψ_b increased by 0.032 and 0.034 MPa in Sajama and Titicaca, respectively. Each degree Celsius increase of T at supra-optimal T_s also increased ψ_b by 0.021 MPa in Sajama and 0.020 MPa in Titicaca. Using HT and HTT to predict germination rate for the 50% of germination (GR50) revealed that they had acceptable accuracy (HT, $R^2=0.97$, and $=0.99$ for Sajama and Titicaca, respectively; HTT, $R^2=0.87$ for Sajama and $=0.90$ for Titicaca). The results of this experiment provide data for future simulating models of quinoa growth and development.

Keywords Base water potential · Cardinal temperatures · Germination rate · Hydro time model (HT) · Hydrothermal time model · Simulation

Abbreviations

T_b	Base (minimum) temperature	θ_{HTT}	Hydrothermal time constant
T_c	Ceiling (maximum) temperature	θ_T	Thermal time constant
T_o	Optimum temperature	$\sigma\psi_b$	Standard deviation of base water potential
t_g	Time to a given germination percentage	ψ_b	Base water potential
θ_H	Hydro time constant	GR	Germination rate
		HT	Hydro time
		HTT	Hydrothermal time
		MGP	Maximum germination percentage
		MPa	Megapascal
		T	Temperature
		TT	Thermal time
		Ψ	Water potential

Communicated by A. Gniazdowska-Piekarska.

✉ Hedayatollah Karimzadeh Soureshjani
karimzadeh.he@gmail.com

¹ Research Center for Plant Science, Ferdowsi University of Mashhad, Mashhad, Iran

² Department of Agronomy, Shahrekord University, Shahr-e Kord, Iran

³ Department of Horticulture, Gorgan University of Agricultural Science and Natural Resources, Gorgan, Iran

Introduction

Quinoa (*Chenopodium quinoa* Willd.) is considered a pseudo-grain, and due to its protein quality, has been known as a complete food (Ando et al. 2002). Its nutritional value is due to its protein content (15%) and its great amino acid balance (Aluko and Monu 2003). Quinoa contains minerals, vitamins, and other beneficial compounds such as flavonoids, phytosterols, and polyphenols (Abugoch et al. 2008; James 2009). The Andean region has been cultivating this plant since 5000 years ago (Vega-Gálvez et al. 2010). Quinoa's strong nutritional content has given it new life as an alternative crop to cereals in recent (Pellegrini et al. 2018).

Seed germination is the most critical step in the life cycle of a grain plant (Karimzadeh Soureshjani et al. 2019). Temperature (T), water potential (Ψ), light, nitrate, and other environmental conditions have varying effects on a seed lot germination (Alvarado and Bradford 2002; Watt et al. 2011). Non-dormant germination of the seed potential is heavily influenced by temperature (Alvarado and Bradford 2002; Bakhshandeh et al. 2017). The T range for seed germinate of a particular species are described by three cardinal T_s (T_b ; base or minimum T , T_o ; optimum T and T_c ; ceiling or maximum T) (Bewley and Black 1994). T_b is lowest germination, T_o is the most rapid germination, and T_c is the highest T germination (Vegis 1964).

Germination rate (GR) and germination time (T) have long been the subject of numerous mathematical theories (e.g., Garcia-Huidobro et al. 1982; Covell et al. 1986; Ellis et al. 1986; Ellis and Butcher 1988). The various models that have been used by different researchers had some strengths and weaknesses, and each of them is more suitable in the specific condition (Soltani et al. 2001; Kamkar et al. 2008; Atashi et al. 2015; Karimzadeh Soureshjani et al. 2019).

The thermal time (TT) concept (or heat unit) can be used to describe the germination timing for sub-optimal T_s (from T_b to T_o) (Bierhuizen and Wagenvoort 1974). Based on the thermal time concept for each germination percentage, time to that germination percentage (t_g) multiplied by the T above T_b is constant and equal to the thermal time constant ($\theta_T(g)$), (Eqs. 1 and 2):

$$\theta_T(g) = (T - T_b)t_g, \quad (1)$$

$$GR_g = 1/t_g = (T - T_b)/\theta_{T(g)}. \quad (2)$$

A linear relationship between the rate of germination and T above T_b are predicted using this model, where (GR_g or $1/t_g$) has a slope of $1/\theta_{T(g)}$. The changes of T_b among seeds of a specific species is minimal except when the seeds have a dormancy (Garcia-Huidobro et al. 1982; Covell et al. 1986; Grundy et al. 2000; Kebreab and Murdoch 2000; Batlla and Benech-Arnold 2015; Batlla and Agostinelli 2017).

There is a comparable model for germination rates at higher than optimum T_s (from T_o to T_c). The germination rate reduces linearly with T increment above T_o and reaches zero at T_c (Labouriau 1970; Garcia-Huidobro et al. 1982). It was also observed that generally, the T_c values of a seed population's different fractions are not the same (Ellis and Butcher 1988). Equations 3 and 4 can explain the variation in T_c in different fractions of seed germination (Covell et al. 1986; Ellis et al. 1986; Ellis and Butcher 1988):

$$\theta_2 = (T_{c(g)} - T)t_g, \quad (3)$$

$$GR_g = 1/t_g = (T_{c(g)} - T)/\theta_2. \quad (4)$$

In which θ_2 presents the thermal time constant, and $T_c(g)$ donates that T_c values change in in the seed population among different germination fractions (g).

Although the thermal time model can accurately predict the germination timing at both sub- and supra-optimal T_s , it is unable to explain why the germination rate is reduced at supra-optimal T_s (Alvarado and Bradford 2002). To eliminate such defects, the hydro time (HT) model was introduced by Gummerson (1986) and Bradford (1990). Equations 5 and 6 are used in this model to explain the connection between germination rate (GR) and water potential (Ψ):

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

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

In which θ_H indicates the constant of hydro time, ψ represents the water potential, and $\psi_{b(g)}$ donates the base or threshold Ψ to prevent germination fraction of seed population. For each T a probit regression (Eq. 7) analyses can also estimate HT parameters at different Ψ (Bradford 1990; Dahal and Bradford 1990):

$$\text{Probit}(g) = [\psi - (\theta_H/t_g) - \psi_b]/\sigma\psi_b. \quad (7)$$

The hydrothermal time (HTT) model describes the time of seed germination at different Ψ and T at both sub- (Gummerson 1986) and supra-optimal T_s (Alvarado and Bradford 2002). The HTT equation at sub-optimal T_s can be written as Eq. (8).

$$\theta_{HTT} = (\psi - \psi_{b(g)})(T - T_b)t_g, \quad (8)$$

where θ_{HTT} , $\psi_{b(g)}$, and t_g are hydrothermal time constant, base Ψ , and time to germination fraction, respectively. In this model, $\psi_{b(g)}$ changes among seeds in the population, while θ_{HTT} and T_b are assumed to be constant (Gummerson 1986). In sub-optimal T_s (assuming θ_{HTT} and T_b are constant), the probit regression (Eq. 9) can also be used to quantifying seed

germination response to Ψ and T (Dahal and Bradford 1994; Bradford 2002):

$$\text{Probit}(g) = [(\psi - (\theta_{\text{HTT}}/(T - T_b)t_g) - \psi_b)]/\sigma\psi_b, \quad (9)$$

where ψ_b shows the base Ψ of the 50th percentile and $\sigma\psi_b$ presents the standard deviation of ψ_b among the seed population. In the supra-optimal T_s , Eqs. (8) and (9) cannot predict the reduction of germination rate (Alvarado and Bradford 2002). Many studies have shown the Ψ and T interaction in the supra-optimal T_s (Alvarado and Bradford 2002; Rowse and Finch-Savage 2003; Watt et al. 2011; Bakhshandeh et al. 2015). In all of these studies, it was reported that in supra-optimal T_s with an increment of T , ψ_b was increased (become more positive). It was suggested that these changes of ψ_b might be the reason for seed germination inhibition in supra-optimal T_s (Alvarado and Bradford 2002). Hence Alvarado and Bradford (2002) modified Eqs. (8) and (9) and written them as Eqs. (10) and (11) for supra-optimal T_s :

$$\theta_{\text{HTT}} = [\psi - \psi_{b(g)}] - (K_T(T - T_o))(T - T_b)t_g, \quad (10)$$

$$\text{Probit}(g) = [(\psi - (K_T(T - T_o)) - \theta_{\text{HTT}}/((T - T_b)t_g)) - \psi_b]/\sigma\psi_b. \quad (11)$$

Full details on these strategies can be found in Alvarado and Bradford (2002) and Bradford (2002). True potato seeds (*Solanum tuberosum* L.) and watermelon (*Citrullus vulgaris*) were among the many crops studied using the HTT model to determine the germination response to and T . Other crops studied included lemon balm (*Melisa officinalis* L.), sesame (*Sesamum indicum* L.) and zucchini (*Cucurbita pepo* L.) as well as carrots (*Daucus carota*) and onions.

Quinoa cultivation occurs mainly in marginal lands where such limitations such as temperature stress and water stress are inevitable. Also, there is very little research that quantifies seed germination of quinoa (*Chenopodium quinoa* Willd.) in the literature. On the other hand, considering the efficiency of HT and HTT models for predicting germination time and percentage at different temperatures and water potentials in the field and laboratory conditions, this study was carried out aiming to quantify the germination response of two cultivars of quinoa (Sajama and Titicaca) to Ψ and T using HT and HTT models.

Materials and methods

The seeds of two quinoa varieties (Sajama and Titicaca) were used in the present study. At 25 °C, 50 seeds of each cultivar were tested for viability in three replications. The viability of Sajama and Titicaca was 98.6 and 97.5%, respectively. The experiment was conducted in 2020 using a germinator at Shahrekord University, Shahrekord, Iran.

Eight constant T_s (5–40 °C by 5 °C intervals) were used to incubate the seeds of each cultivar at each following water potentials (0, -0.3, -0.6, and -0.9 MPa). However, the seeds did not germinate in 5 and 40 °C, and the data of those constant T_s were not statistically analyzed. Polyethylene glycol (PEG 6000, Merck, Germany) was used for the water potential treatments, as described by Michel and Kaufmann (1973). Additionally, distilled water was used as a control (0 MPa). For each treatment, the potential of the desired solution determined via a vapor pressure osmometer (Model 5100C: Wescor Inc., Logan, UT, USA).

In a 9 cm diameter Petri dish with 10 ml of distilled water or PEG solutions, 50 seeds were germinated between two Whatman filter paper layers Cat. No. 1001-150. There also were three replications for each T at each water potential treatment. The Petri dishes were then randomly placed in the germinator for each T in darkness except at the time of recording germination. The quantity of germinated seeds was counted multiple times per day (depending on the T and). The radicle length of two mm was the germination criteria (Soltani et al. 2006; Karimzadeh Soureshjani et al. 2019). The seed germination record was completed when no new seeds germinated for three days in a row (Bakhshandeh et al. 2015, 2017).

To estimate cardinal T_s of both cultivars, a segmented model (Eq. 12) was fitted to germination data at $\Psi=0$ MPa (Karimzadeh Soureshjani et al. 2019). Based on the results of this fit, the T_b , T_o and T_c in Sajama were estimated at 6.9, 21.9, and 34.9 °C, respectively, and in Titicaca were estimated 8.0, 21.8, and 33.6 °C, respectively. Hence to fit the HT and HTT models, T_s below 22 °C were considered as sub-optimal T_s , and T_s above 22 °C were considered supra-optimal T_s :

$$\begin{aligned} f(T) &= \frac{T - T_b}{T_o - T_b} \quad \text{If } T_b < T < T_o \\ f(T) &= 1 - \left(\frac{T - T_o}{T_c - T_o} \right) \quad \text{If } T_o \leq T < T_c \\ f(T) &= 0 \quad \text{If } T \leq T_b \text{ or } T \geq T_c, \end{aligned} \quad (12)$$

$f(T)$ donates the temperature function as a reduction factor, which ranges from 0 at the base and ceiling T to one at optimum T ; temperature, T_b ; base T , T_o ; optimum T , T_c ; ceiling T .

The NLIN procedure in SAS environment software was used to fit the HT and HTT models to germination data (SAS 9.4). The Coefficient of determination (R^2) and root mean square error (RMSE) were used to compare the parameters estimated by the two models and evaluate the model's goodness of fit using R^2 and RMSE, respectively. Analysis of variance was also performed in SAS 9.4 environment, using GLM procedure:

$$R^2 = 1 - \frac{SSR}{SST} \tag{13}$$

In which, SSR is the sum of squares of residuals and SST shows the total sum of squares:

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (O_i - S_i)^2} \tag{14}$$

In which, n shows number of samples, O_i donates the observed value, and S_i represents the predicted values.

Results

The results showed that the T , Ψ , cultivar, and interaction of $T*\Psi$ significantly affected the percentage of maximum germination (MGP) (Fig. 1). Mean MGP averaged over all germination conditions was significantly higher in Titicaca, so that, mean MGP of Titicaca and Sajama was 56 and 54.5%, respectively. The quinoa cultivar response to T depended on Ψ . In each T level, the highest MGP was observed in $\Psi=0$ MPa and, decreasing of Ψ caused a significant reduction of MGP (Fig. 1). The results also showed that the highest MGP was recorded in 20 and 25 °C for all levels of Ψ (Fig. 1). In other words, with the T exceeding 25 °C and the T decreasing from 20 °C, the MGP reduced in both cultivars. It was also observed that in all T levels, the MGP of both

cultivars did not reach 50% in $\Psi=-0.9$ MPa, and it did not exceed 60% in $\Psi=-0.6$ MPa.

The HT and HTT models were fitted to germination data of both quinoa cultivars to quantify quinoa germination, and the parameters were estimated (Tables 1, 2). Results showed that the HT model had high accuracy in predicting germination results so that except for Sajama in 10 °C ($R^2=0.79$), in the other cases, it had an R^2 greater than 0.90 (Table 1). The lowest θ_H was observed in 20 and 25 °C T_s and T greater than 25 °C or lower than 20 °C increased θ_H . In sub- and supra-optimal T_s $\sigma\psi_b$ was relatively constant, but ψ_b increased by changing the T from T_o to T_b and T_c (Table 1).

The use of the HTT model makes it possible to estimate the T_b and T_o in different Ψ in addition to the parameters of the HT model. Using this model, the T_b was estimated by 8.28 and 8.39 °C for Sajama and Titicaca, respectively. The T_o also was estimated by 26.96 and 27.21 °C for Sajama and Titicaca, respectively. Estimated parameters were not different for the two cultivars, and the θ_{HTT} was also lower in sub-optimal T_s (Table 2). The HTT model had acceptable accuracy for both cultivars at sub-optimal T_s (R^2 greater than 0.90), while at high T_s , its accuracy was reduced (R^2 lower than 0.80).

To compare these two models, the predicted germination rate (for the 50% of germination, GR50, using parameters presented in Tables 1 and 2) of both cultivars were plotted versus observed germination rate (Fig. 2). It was

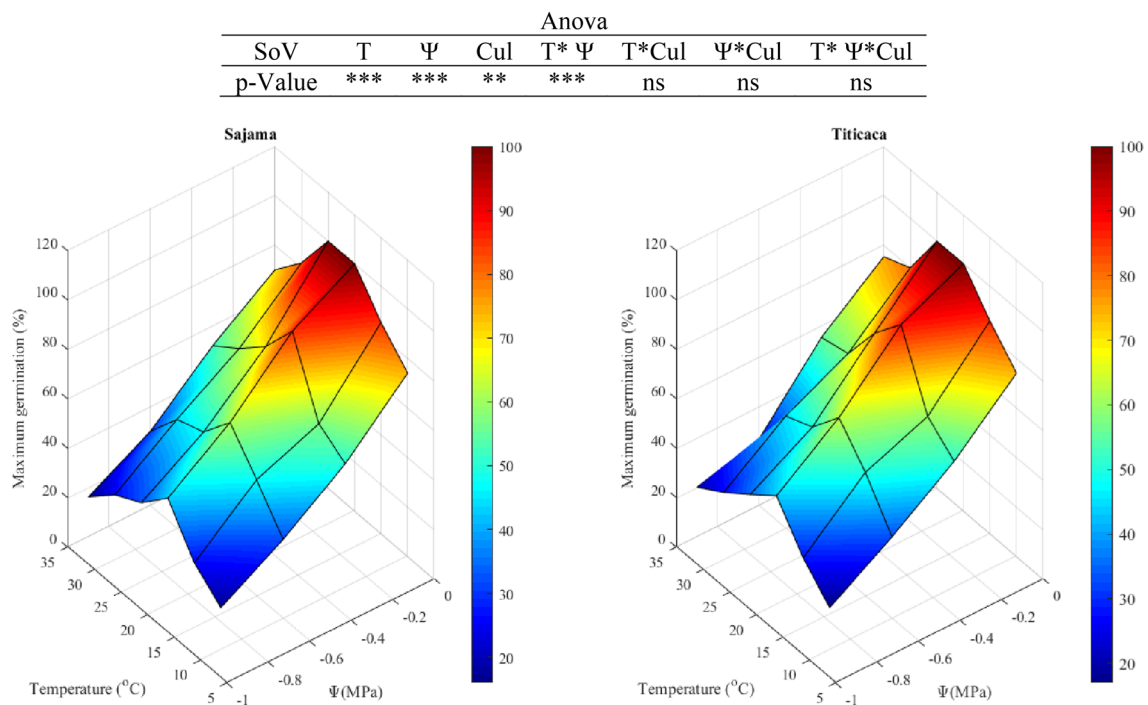


Fig. 1 Analysis of variance and maximum germination percentage (MGP) of two quinoa cultivars affected by different temperatures (T) and water potentials (Ψ) (ns, ** and ***; non-significance differ-

ence, Significant difference at $P \leq 0.01$ and Significant difference at $P \leq 0.001$, respectively)

Table 1 Hydrotime model parameters, characterizing germination of two quinoa cultivar seeds at four water potentials (0, -0.3, -0.6 and -0.9 MPa) at sub- (10, 15 and 20 °C) and supra-optimal (25, 30 and 35 °C) temperatures

Temperature	Cultivar	ψ_b (MPa)		$\sigma\psi_b$ (MPa)		θ_H (MPa h ⁻¹)		R^2
		Amount	SE	Amount	SE	Amount	SE	
10	Sajama	-0.59	0.03	0.55	0.03	78.87	4.86	0.79
	Titicaca	-0.57	0.04	0.57	0.04	76.80	6.26	0.93
15	Sajama	-0.70	0.02	0.53	0.02	20.57	0.74	0.99
	Titicaca	-0.73	0.02	0.54	0.02	21.12	0.73	0.99
20	Sajama	-0.91	0.05	0.45	0.04	17.56	1.63	0.94
	Titicaca	-0.91	0.03	0.44	0.02	15.12	0.85	0.98
25	Sajama	-0.74	0.03	0.42	0.03	17.19	1.20	0.95
	Titicaca	-0.78	0.04	0.39	0.03	15.98	1.25	0.93
30	Sajama	-0.76	0.03	0.58	0.03	42.39	2.59	0.98
	Titicaca	-0.77	0.03	0.65	0.03	45.33	2.43	0.98
35	Sajama	-0.54	0.02	0.54	0.02	69.97	3.06	0.98
	Titicaca	-0.57	0.02	0.52	0.02	68.03	3.32	0.97

The hydrotime model was fitted to data from four Ψ (0, -0.3, -0.6 and -0.9 MPa) at each T

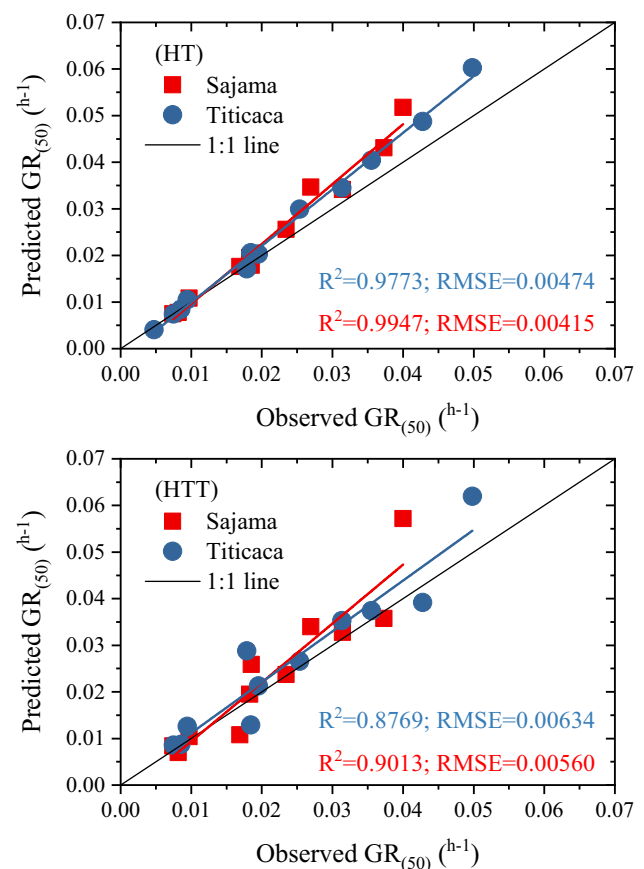
Table 2 Hydrothermal time model parameters, characterizing germination of two quinoa cultivar seeds at four water potentials (0, -0.3, -0.6 and -0.9 MPa) at sub- (10, 15 and 20 °C) and supra-optimal (25, 30 and 35 °C) temperatures

	Parameters	Sajama		Titicaca	
		Amount	SE	Amount	SE
Sub-optimal T	$\psi_{b(50)}$	-0.74	0.03	-0.76	0.03
	$\sigma\psi_b$	0.51	0.02	0.51	0.02
	T_b	8.28	0.10	8.40	0.09
	θ_{HTT}	151.60	10.00	141.80	9.00
	R^2	0.92		0.93	
Supra-optimal T	$\psi_{b(50)}$	-0.74	0.03	-0.76	0.03
	$\sigma\psi_b$	0.54	0.04	0.54	0.04
	T_o	26.96	0.69	27.22	0.69
	θ_{HTT}	433.50	43.77	414.40	44.25
	K_T	0.08	0.01	0.08	0.01
	R^2	0.78		0.76	

The sub-optimal hydrothermal time model was fitted to data from four Ψ (0, -0.3, -0.6 and -0.9 MPa) across all three sub-optimal T , and supra-optimal hydrothermal time model was fitted to data from four Ψ (0, -0.3, -0.6 and -0.9 MPa) across all three supra-optimal T

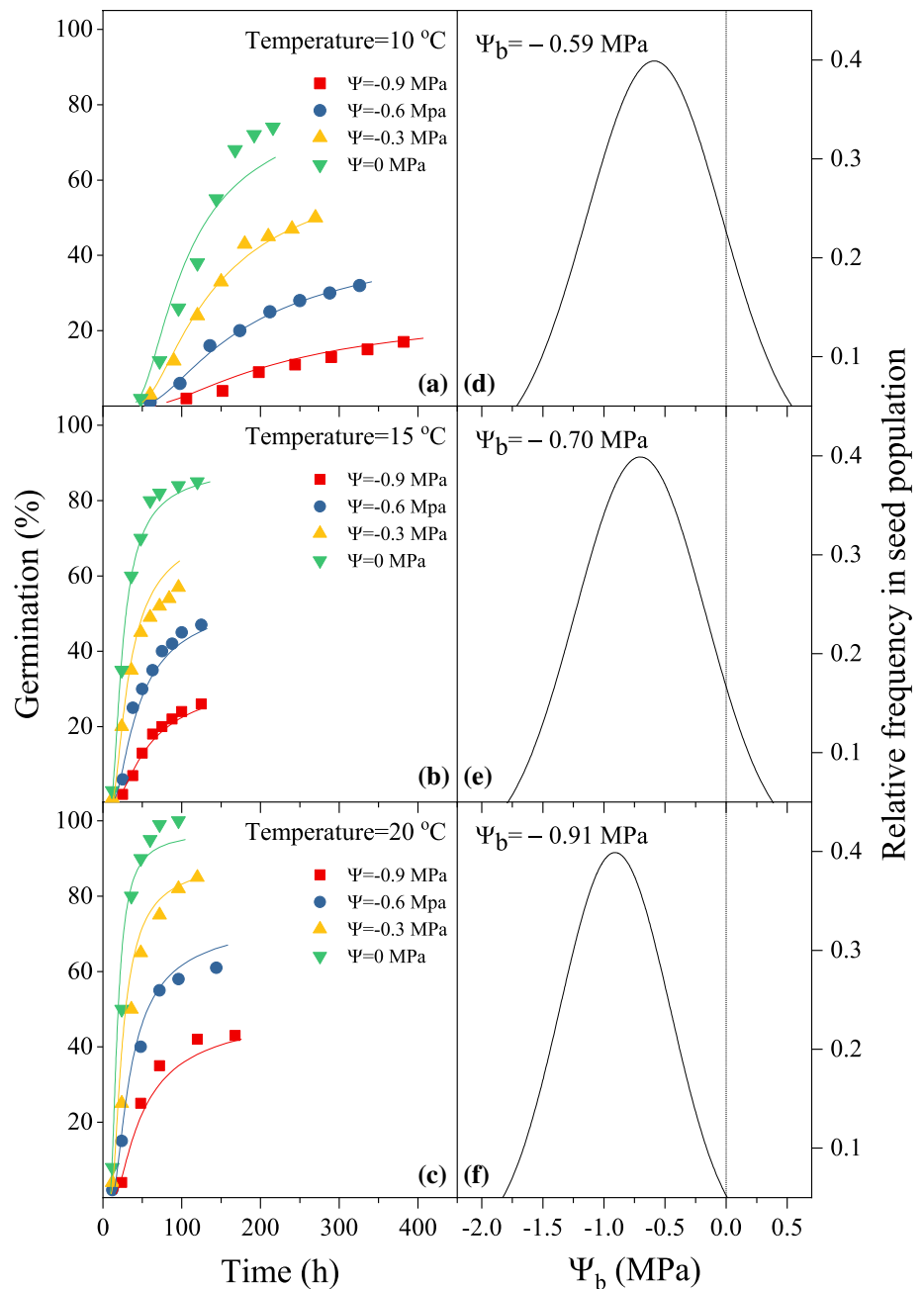
observed that at the highest germination rate (T_o), the predicted amounts of GR50 were slightly higher than observed GR50. However, the HT model had a higher R^2 and a lower RMSE than the HTT model; therefore, it is more accurate in predicting the germination rate.

The predicted (using the HT model) and observed cumulative germination percentage of Titicaca and Sajama are shown in Figs. 3 and 4, respectively, for sub-optimal T_s using parameters presented in Table 1. The germination of both cultivars' seeds at sub-optimal T_s was increased with T increasing (Figs. 3, 4a-c). Therefore, at each T , MGP and

**Fig. 2** Predicted GR50 (predicted by HT and HTT models) vs observed GR50 of two quinoa cultivars affected by different temperatures (T) and water potentials (Ψ)

germination rates were reduced by reduction of Ψ . In other words, MGP and germination rate was increased caused by Ψ increment at each sub-optimal T . The normal distribution

Fig. 3 Germination time courses of Sajama seeds at sub-optimal temperatures. **a–c** Germination time courses at 10, 15 and 20 °C and 0, –0.3, –0.6 and –0.9 MPa. The symbols are the actual data, and the lines are the time courses predicted by the hydrotime model using the values shown in Table 1. **d–f** Normal distributions showing the relative frequencies of Ψ_b values at each temperature. The median or Ψ_b values are shown (see Table 1)



of ψ_b was plotted at each T using Table 1 parameters. The increment of T from T_b to T_o resulted in ψ_b increases at sub-optimal T_s (Figs. 3, 4d–f). In other words, the seeds can germinate at more negative ψ_b at T_o , and the time to germination reduced at this condition for all Ψ .

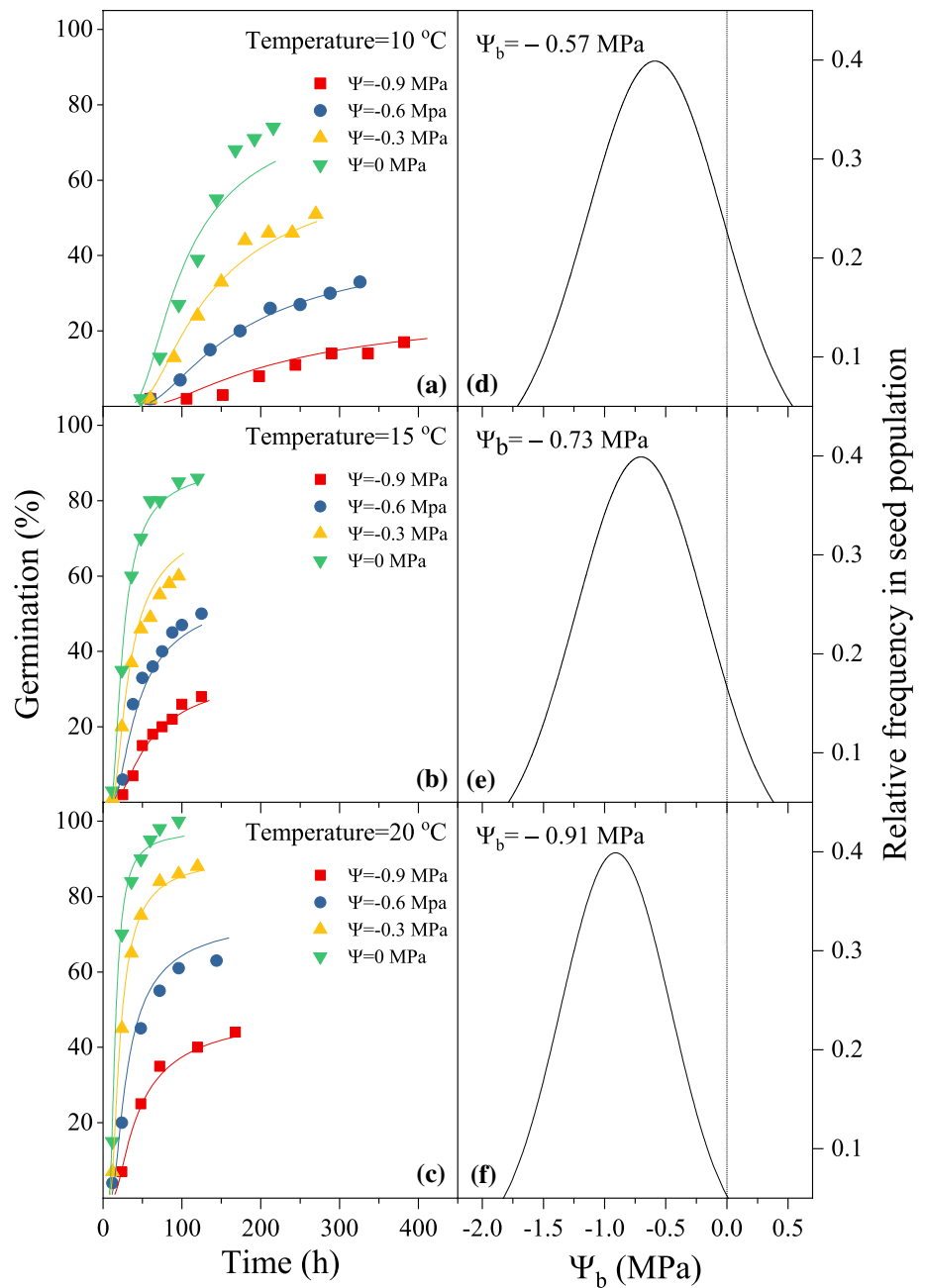
At supra-optimal T_s also the MGP and germination rates were decreased in both cultivars due to T increment from T_o to T_c (Figs. 5, 6a–c). The reduction of Ψ at each supra-optimal T also reduced MGP and germination rates of both cultivars. The results also showed that the increase of T from T_o to T_c caused the seeds to need a more positive ψ_b for germination (Figs. 5, 6d–f). It seems as the T rises above the

T_o , the seeds cannot absorb water at more negative Ψ . In this condition, the time to germination was increased for all Ψ .

Discussion

The current experiment results showed that T , Ψ , cultivar, and their interaction had a significant effect on MGP. In general, reduction of Ψ and change of T from T_o to T_b and T_c reduced MGP of both cultivars. Other plants, such as watermelon (Bakhshandeh et al. 2015), sesame (Bakhshandeh et al. 2013), and potato (Alvarado and Bradford 2002) have

Fig. 4 Germination time courses of *Triticaca* seeds at sub-optimal temperatures. **a–c** Germination time courses at 10, 15 and 20 °C and 0, –0.3, –0.6 and –0.9 MPa. The symbols are the actual data, and the lines are the time courses predicted by the hydrotime model using the values shown in Table 1. **d–f** Normal distributions showing the relative frequencies of Ψ_b values at each temperature. The median or Ψ_b values are shown (see Table 1)

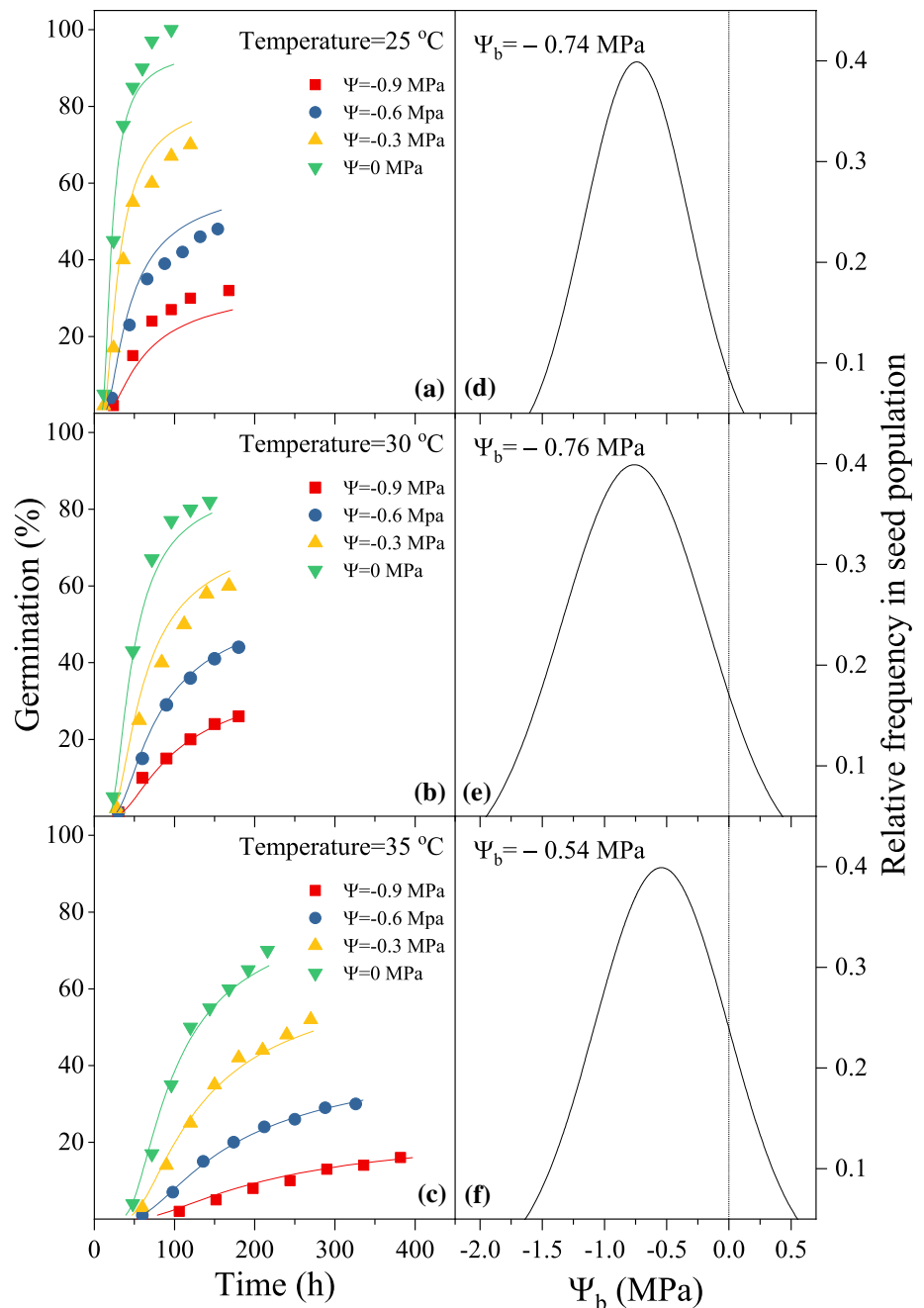


shown reduced germination percentages and rates due to a decrease in Ψ . In the present study, not only MGP was reduced by T increment from T_o to T_c or T reduction from T_o to T_b but also the water potential at which growth is initiated is increased.

Since the thermal time model cannot predict the germination reduction (germination percentage and rate) at supra-optimal T_s (Alvarado and Bradford 2002; Rowse and Finch-Savage 2003), the uses of HT and HTT models can compensate for this defect. These two models explain how the difference of Ψ in inside the seed and the surrounding environment controls germination of a seed batch at a

certain T (Gummerson 1986; Alvarado and Bradford 2002). Although, shifts in the ψ_b thresholds and shifts in response to multiple factors, including dormancy level and temperature that are more likely physiologically controlled by the seeds, have effects on germination reduction at supra-optimal T_s . The results of this study showed that the lowest estimation of θ_H was observed at T_o , and it increased with T increment over T_o or T reduction from T_o . The increase in θ_H due to T reduction (from T_o to T_b) was reported in many plants such as tomato (Dahal and Bradford 1994), potato (Alvarado and Bradford 2002), winterfat (Wang et al. 2005). As a result, θ_H can be utilized as a measure of seed vigor and physiological

Fig. 5 Germination time courses of Sajama seeds at supra-optimal temperatures. (a–c) Germination time courses at 25, 30 and 35 °C and 0, –0.3, –0.6 and –0.9 MPa. The symbols are the actual data, and the lines are the time courses predicted by the hydrotime model using the values shown in Table 1. **d–f** Normal distributions showing the relative frequencies of Ψ_b values at each temperature. The median or Ψ_b values are shown (see Table 1)

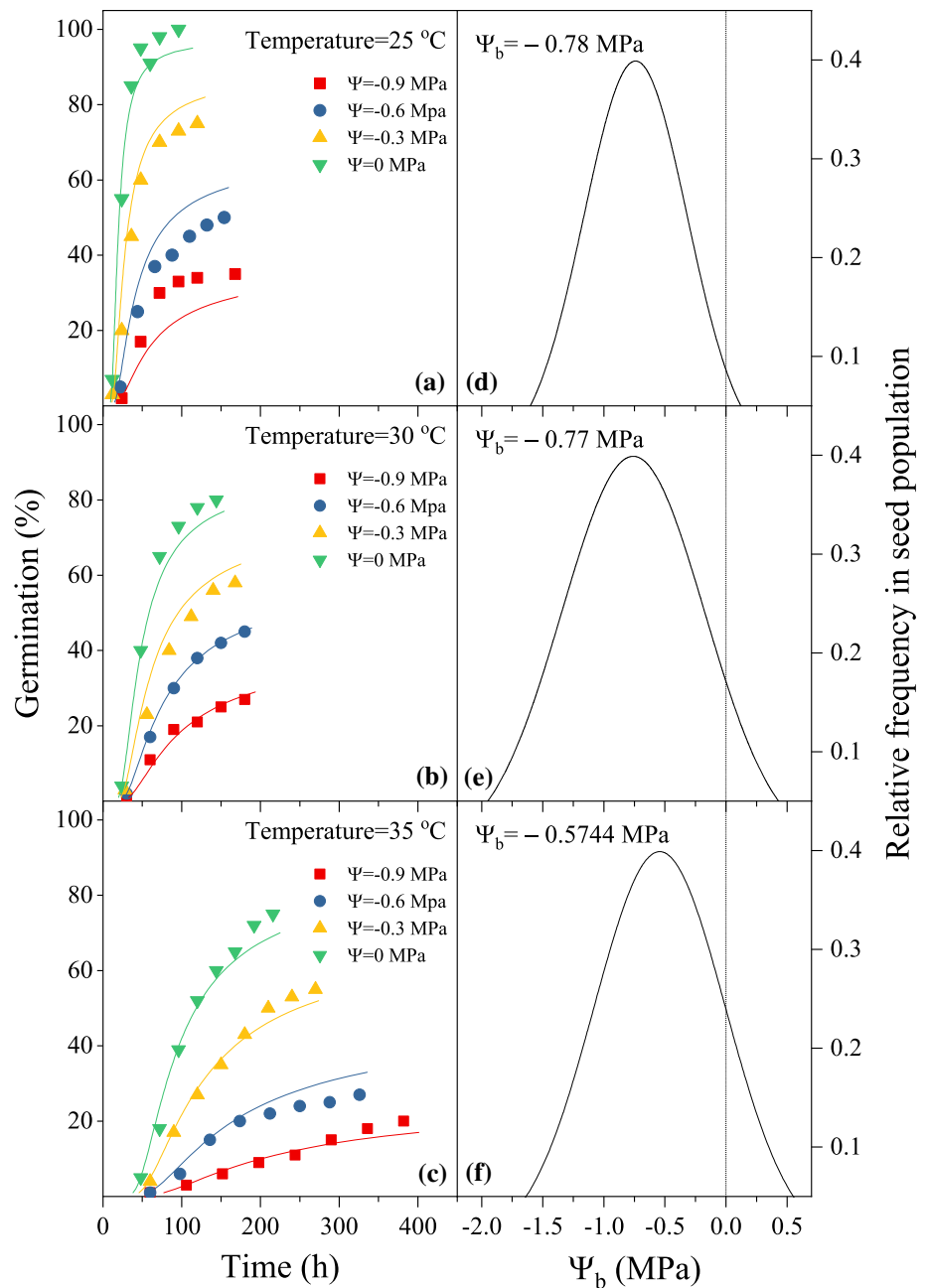


quality in seed lot (Dahal and Bradford 1990). The amount of θ_H in large seeds was found to be lower than that in small seeds, especially at lower T_s (Wang et al. 2005).

It has long been recognized that germination of seeds occurs in the range of cardinal T_s , including minimum (T_b), optimum (T_o), and maximum (T_c) (Bewley and Black 1994; Alvarado and Bradford 2002). The T_b of quinoa was estimated at 8.28 °C for Sajama and 8.39 °C for Titicaca in the current work. T_o also was 26.96 and 27.21 °C for Sajama and Titicaca, respectively. González et al. (2017) used a binomial model to estimate cardinal T_s of quinoa. They observed

that the T_o of quinoa was lower than 33 °C. Mamedí et al. (2017) also studied the effect of different T_s on quinoa's seed germination. They reported that T_o ranged between 18 to 36 °C. As can be seen, the range of T data estimated in these studies is extensive. However, in the present study, the cardinal T_s (T_b and T_o) have been accurately estimated using the HTT model. As Alvarado and Bradford (2002) reported, if thermal time accumulation stopped at T_o , as in the present study (Fig. 7), the modified HTT model can be used in which $(T_o - T_b)$ is placed instead of $(T - T_b)$ in Eq. 10. Using the modified HTT resulted in more accurate parameter

Fig. 6 Germination time courses of Triticaca seeds at supra-optimal temperatures. **a–c** Germination time courses at 25, 30 and 35 °C and 0, –0.3, –0.6 and –0.9 MPa. The symbols are the actual data, and the lines are the time courses predicted by the hydrotime model using the values shown in Table 1. **d–f** Normal distributions showing the relative frequencies of Ψ_b values at each temperature. The median or Ψ_b values are shown (see Table 1)



estimation in both genotypes so that θ_{HTT} in Sajama and Titicaca were estimated by 496.8 and 484.7, respectively. T_o was also estimated 27.46 in Sajama and 27.73 in Titicaca. $\sigma\psi_b$ was 0.53 and 0.52 in Sajama and Titicaca, respectively, while K_T was equal (0.07) in both genotypes. Also, R^2 in Sajama and Titicaca were estimated by 0.84 and 0.83, respectively.

The variations in mean Ψ_b values that occurred as a result of a reduction in T and an increase in T were observed in the current investigation. The seeds could not absorb water at a higher negative Ψ when they were farther away from T_o . Seeds just can germinate at more positive Ψ in this

condition. At low temperatures, prior studies found that Ψ_b remained constant. The germination rate and germination percentage were found to be reduced at supra-optimal T_s because of a linear increase in b , which was found to increase with T (Dahal and Bradford 1994; Alvarado and Bradford 2002; Rowse and Finch-Savage 2003; Atashi et al. 2014). However, our results showed that not only Ψ_b was less negative with T increment at supra-optimal T_s , but also it was less negative with T reduction at sub-optimal T_s . In other words, increasing the Ψ_b in addition to supra-optimal T_s , at sub-optimal T_s , is also the reason for the decrease in germination rate and percentage. Similar to our result, the

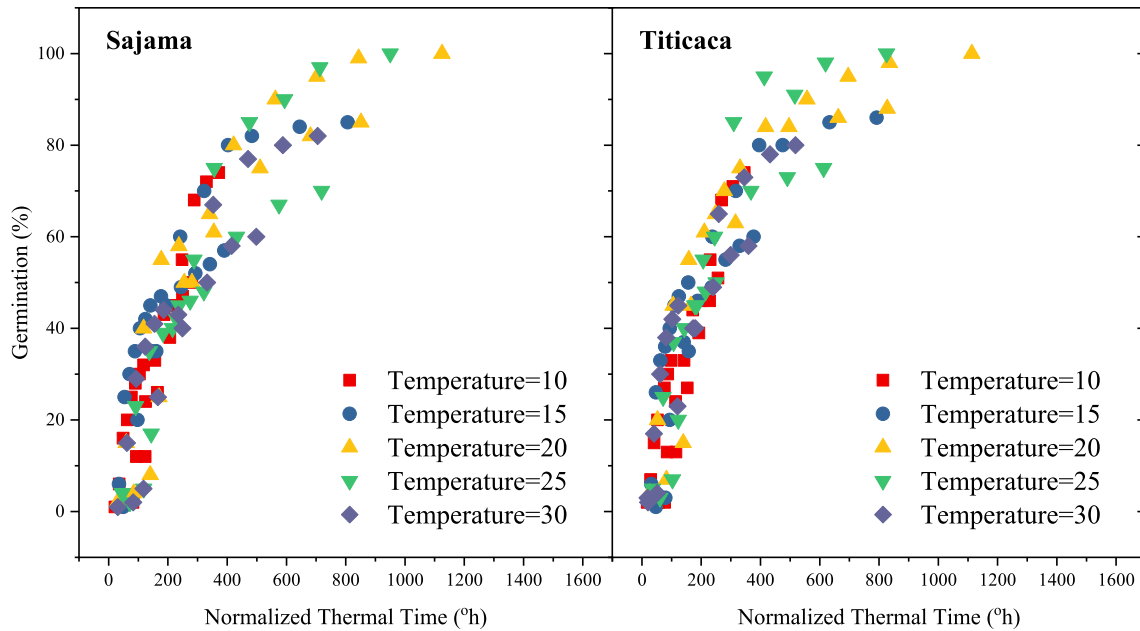


Fig. 7 Cumulative germination (%) vs. normalized thermal time in Sajama and Titicaca at sub- and supra optimal temperatures. A normalization factor $[1 - (\frac{\Psi}{\Psi_{b(g)}})]t_g$, was used for the normalization of germination time courses across a range of Ψ

reduction of T from T_0 to T_b increased Ψ_b of watermelon (Bakhshandeh et al. 2015) and winterfat (Wang et al. 2005). The current study results showed that for each degree Celsius decrease of T at sub-optimal T_s , the Ψ_b increased by 0.032 and 0.034 MPa in Sajama and Titicaca, respectively (Fig. 8). Each degree Celsius increase of T at supra-optimal T_s also increased Ψ_b by 0.021 MPa in Sajama and 0.020 MPa in Titicaca (Fig. 8).

Conclusion

In conclusion, T and Ψ affected MFP and germination rates of both quinoa cultivars. To quantify quinoa's germination response to T and Ψ , we used HT and HTT. The results showed that these models could accurately predict the germination (percentage and rate) changes under varying T and Ψ . Using these models can also help us to estimate cardinal T_s and threshold (Ψ_b) water potential for seed germination of quinoa. The results of this experiment provide data for future simulating models of quinoa growth and development.

Author contribution statement HKS: designed and performed experiment, analyzed data and wrote the paper. MB: performed experiment and collected the data. MRT: provided essential materials and equipment. AGD: performed experiment and collected the data. HKS wrote the first draft of the manuscript and all authors commented on previous

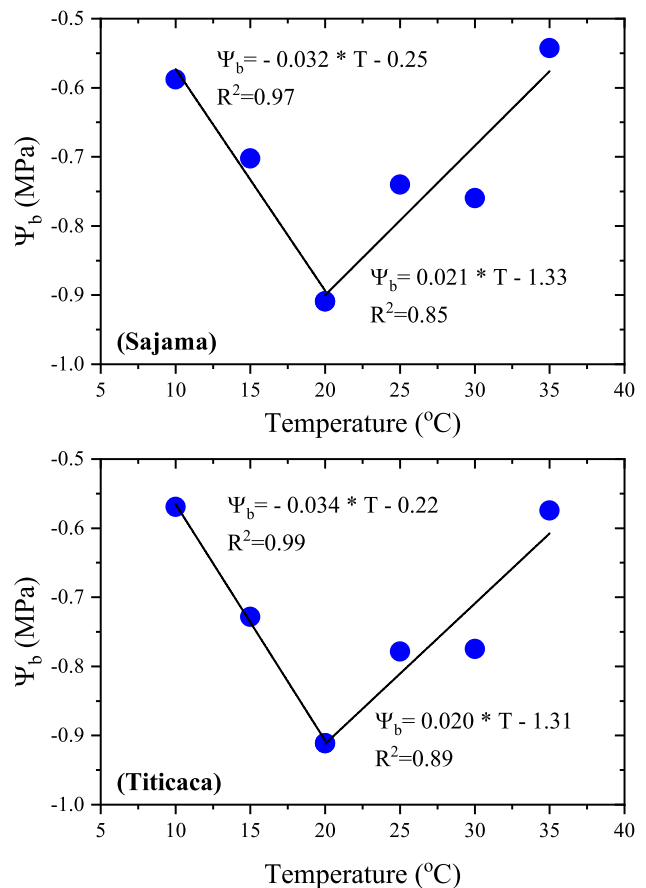


Fig. 8 Relationship between temperature (T) and base water potential (Ψ_b) of two quinoa cultivars

versions of the manuscript. All authors read and approved the final manuscript.

Acknowledgements The authors appreciate the advice and information offered by Prof. Kent J. Bradford, Department of Plant Science, University of California, Davis, USA.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

- Abugoch LE, Romero N, Tapia CA et al (2008) Study of some physicochemical and functional properties of quinoa (*Chenopodium quinoa* Willd.) protein isolates. *J Agric Food Chem* 56:4745–4750
- Aluko RE, Monu E (2003) Functional and bioactive properties of quinoa seed protein hydrolysates. *J Food Sci* 68:1254–1258
- Alvarado V, Bradford KJ (2002) A hydrothermal time model explains the cardinal temperatures for seed germination. *Plant Cell Environ* 25:1061–1069
- Ando H, Chen Y, Tang H et al (2002) Food components in fractions of quinoa seed. *Food Sci Technol Res* 8:80–84
- Atashi S, Bakhshandeh E, Zeinali Z et al (2014) Modeling seed germination in *Melisa officinalis* L. in response to temperature and water potential. *Acta Physiol Plant* 36:605–611
- Atashi S, Bakhshandeh E, Mehdipour M et al (2015) Application of a hydrothermal time seed germination model using the Weibull distribution to describe base water potential in zucchini (*Cucurbita pepo* L.). *J Plant Growth Regul* 34:150–157
- Bakhshandeh E, Atashi S, Hafez-Nia M, Pirdashti H (2013) Quantification of the response of germination rate to temperature in sesame (*Sesamum indicum*). *Seed Sci Technol* 41:469–473
- Bakhshandeh E, Atashi S, Hafeznia M et al (2015) Hydrothermal time analysis of watermelon (*Citrullus vulgaris* cv. ‘Crimson sweet’) seed germination. *Acta Physiol Plant* 37:1738
- Bakhshandeh E, Jamali M, Afshoon E, Gholamhossieni M (2017) Using hydrothermal time concept to describe sesame (*Sesamum indicum* L.) seed germination response to temperature and water potential. *Acta Physiol Plant* 39:250
- Batlla D, Agostinelli AM (2017) Thermal regulation of secondary dormancy induction in *Polygonum aviculare* seeds: a quantitative analysis using the hydrotime model. *Seed Sci Res* 27:231–242
- Batlla D, Benech-Arnold RL (2015) A framework for the interpretation of temperature effects on dormancy and germination in seed populations showing dormancy. *Seed Sci Res* 25:147–158
- Bewley JD, Black M (1994) Seeds physiology of development and germination, 3rd edn. Plenum Press, New York, p 445
- Bierhuizen JF, Wagenvoort WA (1974) Some aspects of seed germination in vegetables. 1. The determination and application of heat sums and minimum temperature for germination. *Sci Hortic (amsterdam)* 2:213–219
- Bradford KJ (1990) A water relations analysis of seed germination rates. *Plant Physiol* 94:840–849
- Bradford KJ (2002) Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Sci* 50:248–260
- Covell S, Ellis RH, Roberts EH, Summerfield RJ (1986) The influence of temperature on seed germination rate in grain legumes: I. A comparison of chickpea, lentil, soyabean and cowpea at constant temperatures. *J Exp Bot* 37:705–715
- Dahal P, Bradford KJ (1990) Effects of priming and endosperm integrity on seed germination rates of tomato genotypes: II. Germination at reduced water potential. *J Exp Bot* 41:1441–1453
- Dahal P, Bradford KJ (1994) Hydrothermal time analysis of tomato seed germination at suboptimal temperature and reduced water potential. *Seed Sci Res* 4:71
- Ellis RH, Butcher PD (1988) The effects of priming and ‘natural’ differences in quality amongst onion seed lots on the response of the rate of germination to temperature and the identification of the characteristics under genotypic control. *J Exp Bot* 39:935–950
- Ellis RH, Covell S, Roberts EH, Summerfield RJ (1986) The influence of temperature on seed germination rate in grain legumes: II. Intraspecific variation in chickpea (*Cicer arietinum* L.) at constant temperatures. *J Exp Bot* 37:1503–1515
- Garcia-Huidobro J, Monteith JL, Squire GR (1982) Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.) I. Constant temperature. *J Exp Bot* 33:288–296
- González JA, Buedo SE, Bruno M, Prado FE (2017) Quantifying cardinal temperatures in quinoa (*Chenopodium quinoa*) cultivars. *Lilloa* 179–194
- Grundy AC, Phelps K, Reader RJ, Burston S (2000) Modelling the germination of *Stellaria media* using the concept of hydrothermal time. *New Phytol* 148:433–444
- Gummerson RJ (1986) The effect of constant temperatures and osmotic potentials on the germination of sugar beet. *J Exp Bot* 37:729–741
- James LEA (2009) Quinoa (*Chenopodium quinoa* Willd.): composition, chemistry, nutritional, and functional properties. *Adv Food Nutr Res* 58:1–31
- Kamkar B, Ahmadi M, Soltani A, Zeinali E (2008) Evaluating nonlinear regression models to describe response of wheat emergence rate to temperature. *Seed Sci Biotechnol* 2:53–57
- Karimzadeh Soureshjani H, Bahador M, Tadayon M, Gorbani Dehkordi A (2019) Modelling seed germination and seedling emergence of flax and sesame as affected by temperature, soil bulk density, and sowing depth. *Ind Crops Prod* 141:111770
- Kebreab E, Murdoch AJ (2000) The effect of water stress on the temperature range for germination of *Orobanche aegyptiaca* seeds. *Seed Sci Res* 10:127–133
- Labouriau LG (1970) On the physiology of seed germination in *Vicia graminea* Sm. 1. *An Acad Bras Cienc* 42:235–262
- Mamedi A, Tavakkol Afshari R, Oveisi M (2017) Cardinal temperatures for seed germination of three quinoa (*Chenopodium quinoa* Willd.) cultivars. *Iran F Crop Res* 48:89–100
- Michel BE, Kaufmann MR (1973) The osmotic potential of polyethylene glycol 6000. *Plant Physiol* 51:914–916
- Pellegrini M, Lucas-Gonzales R, Ricci A, Fontecha J, Fernández-López J, Pérez-Álvarez JA, Viuda-Martos M (2018) Chemical, fatty acid, polyphenolic profile, techno-functional and antioxidant properties of flours obtained from quinoa (*Chenopodium quinoa* Willd.) seeds. *Ind Crops Prod* 111:38–46
- Rowse HR, Finch-Savage WE (2003) Hydrothermal threshold models can describe the germination response of carrot (*Daucus carota*) and onion (*Allium cepa*) seed populations across both sub- and supra-optimal temperatures. *New Phytol* 158:101–108
- Soltani A, Khooe FR, Ghassemi-Golezani K, Moghaddam M (2001) A simulation study of chickpea crop response to limited irrigation in a semiarid environment. *Agric Water Manag* 49:225–237
- Soltani A, Robertson MJ, Torabi B et al (2006) Modelling seedling emergence in chickpea as influenced by temperature and sowing depth. *Agric for Meteorol* 138:156–167
- Vega-Gálvez A, Miranda M, Vergara J et al (2010) Nutrition facts and functional potential of quinoa (*Chenopodium quinoa* willd.), an ancient Andean grain: a review. *J Sci Food Agric* 90:2541–2547

- Vegis A (1964) Dormancy in higher plants. *Annu Rev Plant Physiol* 15:185–224
- Wang R, Bai Y, Tanino K (2005) Germination of winterfat (*Eurotia lanata* (Pursh) Moq.) seeds at reduced water potentials: testing assumptions of hydrothermal time model. *Environ Exp Bot* 53:49–63
- Watt MS, Bloomberg M, Finch-Savage WE (2011) Development of a hydrothermal time model that accurately characterises how thermos-inhibition regulates seed germination. *Plant Cell Environ* 34:870–876

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.