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Germination response of *Apocynum venetum* seeds to temperature and water potential

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Summary

Apocynum venetum (commonly known as luobuma or rafuma) is a shrub that is native to Eurasia. It is economically important for sand fixation, forage production, honey production, and for the production of medicine, fiber and fuel. Rapid and uniform seed germination is critical for successful crop establishment and vegetation restoration. The purpose of this study was to determine the germination responses of *A. venetum* seeds to temperature and water availability using hydrotime, thermal time and hydrothermal model analysis. Seed germination was relatively high for *A. venetum* from 25 °C to 30 °C. The base (T_b), optimum (T_o) and ceiling temperatures ($T_c(50)$) of *A. venetum* seed germination were 16.6, 27.0 and 45.9 °C, respectively. Values of base water potential ($\Psi_b(g)$) shifted to zero with increasing temperature, which was reflected in the greater effect of low Ψ on germination for temperatures above 30 °C. Hydrotime analysis suggested that T_b may not be independent of Ψ , and $\Psi_b(g)$ may change as a function of temperature at temperatures below 30 °C. The interaction effects of Ψ and temperature reduced the ability of the hydrothermal time model to predict germination performance across temperature and Ψ conditions.

Introduction

Apocynum venetum is a perennial semi-shrub species that is widely distributed in the temperate regions of Asia and Europe, and is found in Iran, Afghanistan, India, Russia and China. It commonly grows in barren saline soil, desert edges, riverbanks, alluvial plains and areas surrounding reservoirs and is well adapted to desert climates (THEVS et al., 2012). *A. venetum* is of economic importance and is used in sand fixation and a forage, tea, medicine, and fiber. However, wild populations of this species are currently in danger of being over-exploited (THEVS et al., 2007; WESTERMANN et al., 2008). Previous research on *A. venetum* has been conducted covering fiber extraction from its stems (GONG and FU, 2001) and processing tea and medicine from its leaves (MA et al., 2003). Seed germination is critical for its use in sand fixation and crop production. *A. venetum* can be propagated from seeds or cuttings; however, propagation by cuttings limits its use compared to propagation by seeds. Studies have shown that sowing seeds in a nursery and transplanting the saplings after the second year is the best way to propagate this species (TANG, 2008). Temperature and soil water content are critical factors that influence seed germination in both greenhouse and field environments. In arid environments, the water required for germination is only available for short periods. Consequently, successful crop establishment depends not only on rapid and uniform seed germination, but also the seed's ability to germinate under low water availability (FISCHER and TURNER, 1978; WINDAUER et al., 2012). Knowledge of the influence of water and temperature on seed germination in *A. venetum* is fundamental for its use in crop production and sand stabilization. Previous research was shown that seed germination of *A. venetum*

is difficult under conditions of high soil water content, whereas high temperatures can increase its germination (LIU, 2010). ZHANG et al. (2007) found that low concentrations of NaCl (≤ 50 mmol/L) promote seed germination in *A. venetum*, whereas high NaCl concentrations (≥ 200 mmol/L) reduce germination. However, limited research has been conducted on the interaction affects of water and temperature on the germination and seedling establishment of this economically species.

Population-based threshold models have been used to model the ecophysiological responses of seed germination to environmental factors (FINCH-SAVAGE and LEUBNER-METZGER, 2006). Seed germination attributes can be quantified using the thermal time model (θ_T) (GARCIA-HUIDOBRO et al., 1982), hydrotime model (θ_H) (GUMMERSON, 1986) and hydrothermal time model (θ_{HT}) (GUMMERSON, 1986). Seed germination responses to temperature can be characterized using three cardinal temperatures (BEWLEY and BLACK, 1994): a base temperature (T_b) below which germination of the seed lot does not proceed, an optimal temperature (T_o) at which the process occurs with the highest speed and a maximum (ceilings) temperature (T_c) over which the germination process does not proceed. When temperature remains constant, but water is suboptimal, progress towards the completion of germination can be quantified in hydrotime (FINCH-SAVAGE and LEUBNER-METZGER, 2006). In addition, the thermal and hydrotime models can be combined to produce a hydrothermal time (HTT) model (GUMMERSON, 1986; ALVARADO and BRADFORD, 2002).

The objective of this study was to characterize the germination responses of *A. venetum* seeds to temperature and water availability using thermal time, hydrotime and hydrothermal time analysis to test the validity of these models to *A. venetum* seeds.

Materials and methods

Seed

Seeds of *A. venetum* were collected during October 2009 in a desert environment (41.08°N, 85.97°E, 878 m asl) of the middle Tarim River in southern Xinjiang, China. Seeds were cleaned and stored at 4 °C in a sealed glass bottle until needed for experimentation (March 2010). The mass of 1000 seeds of *A. venetum* used in our study was 0.36 g.

Germination assays

Germination assays were conducted in the Forage and Turf Grass Seed Laboratory at the Grassland Science Department, China Agricultural University, Beijing, China. Seeds were sterilized for 5 min with 10% NaClO and then washed with distilled water. Seeds were placed on two layers of filter paper saturated with distilled water or polyethylene-glycol (PEG) solution in glass Petri dishes (90-mm inner diameter). Four replicates per treatment with 50 seeds each were placed in a growth chamber under 8 h light and 16 h dark at constant temperatures of 20, 25, 30 and 35 °C (± 1 °C).

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The water potential (Ψ) of the germination medium was controlled by different solutions of polyethylene-glycol 6000 (PEG 6000) and prepared according to MICHEL and KAUFMANN (1973) so that Ψ was -0.3, -0.6, -0.9, -1.2 and -1.5 MPa at the respective temperature. The actual Ψ at all temperatures was measured using a vapour pressure osmometer (Wescor, Inc., Logan, Model 5100C). Seeds incubated on solutions containing PEG were transferred to fresh solutions every 2 d to maintain constant water potential in the germination medium. The germination (radicle protrusion) was scored daily, and the germinated seeds were removed. Germination experiments were terminated when no new germination for three consecutive days was recorded in the four replicates of a treatment.

Germination analysis

Germination rates were calculated as the inverse of the time to radicle emergence. Germination times for specific percentiles of the seed population (GR50) were calculated by interpolation using curves fit to the time course data. To determine the optimal germination temperature, germination rates at 30 and 35 °C were compared. If germination at 30 °C was significantly greater than germination at 35 °C, the optimal temperature was assumed to be 30 °C. The germination time course data were analyzed using repeated probit regression analysis, as described by BRADFORD (1990) and DAHAL and BRADFORD (1990, 1994). Probit analyses were conducted using the PROC PROBIT routine of the SAS statistical package, which employs a maximum-likelihood weighted regression method (SAS 9.2).

Thermal time

In the sub-optimal temperature range (i.e., between T_b and T_o), the thermal time to germination at fraction g ($\theta_{T1}(g)$) can be characterized using the following thermal time (θ_{T1} , °C d) equation:

$$\theta_{T1}(g) = (T - T_b)t_g \quad (1)$$

where T is the germination temperature, T_b is the base temperature and t_g is the germination time of fraction g . This equation indicates that for a given seed fraction g , $\theta_{T1}(g)$ is constant at all sub-optimal temperatures when expressed on a thermal time basis as the degrees in excess of T_b multiplied by the actual time to germination. Values of T_b and θ_T were determined through repeated probit regression analysis (GARCIA-HUIDOBRO et al., 1982) by regressing all observed germination percentages on a probit scale versus log thermal times $\log\theta_{T1}(g)$ to germination, varying the value of T_b until the best fit was obtained, according to the equation:

$$\text{probit}(g) = \{\log[(T - T_b)t_g] - \log[\theta_{T1}(50)]\} / \sigma_{\theta_{T1}} \quad (2)$$

Where probit (g) is the probit transformation of cumulative germination percentage g , $\theta_{T1}(50)$ is the median thermal time to germination, and $\sigma_{\theta_{T1}}$ is the standard deviation in $\log\theta_{T1}$ among individual seeds in the population.

Above T_o , the germination rate decreases almost linearly until T_c is reached, which is also known as thermoinhibition (HILLS and VAN STADEN, 2003). Thus, in the supra-optimal temperature range, the equation used is as follows (ELLIS and BUTCHER, 1988):

$$\theta_{T2} = [T_c(g) - T]t_g \quad (3)$$

Germination time courses (θ_{T2} , T_c) in the supra-optimal temperature range can be predicted in a similar way to those in the sub-optimal temperature range (Equation 4); however, the germination rate decreases with temperature, and $T_c(g)$ varies among fractions, while the thermal time to radical protrusion is constant for all seeds:

$$\text{Probit}(g) = [\log(T + \theta_{T2}) / t_g - \log T_c(50)] / \sigma_{\theta_{T2}} \quad (4)$$

Where probit (g) is the probit transformation of cumulative germination percentage g , $T_c(50)$ is the median ceiling temperature to germination, and $\sigma_{\theta_{T2}}$ is the standard deviation in $\log T_c(50)$ among individual seeds in the population.

Hydortime

The germination response to reduced Ψ was analyzed by the hydrotime model (BRADFORD, 1990; FINCH-SAVAGE and LEUBNER-METZGER, 2006) according to the equation:

$$\theta_H = [\Psi - \Psi_b(g)]t_g \quad (5)$$

where θ_H is the hydrotime (MPa d) of the seeds required for germination, Ψ is the actual water potential of the germination medium (MPa), $\Psi_b(g)$ is the theoretical threshold or base water potential that will just prevent the germination of fraction g and t_g is the germination time (d) of fraction g . The model assumes that Ψ_b varies among fractions of a seed population following a normal distribution with mean $\Psi_b(50)$ and standard deviation σ_{Ψ_b} . θ_H is considered constant for a seed population (BRADFORD, 1990). The parameters in the hydrotime model were estimated according to the equation:

$$\text{Probit}(g) = [(\Psi - \theta_H / t_g) - \Psi_b(50)] / \sigma_{\Psi_b} \quad (6)$$

where $\Psi_b(50)$ is the median Ψ_b , and σ_{Ψ_b} is the standard deviation in Ψ_b among seeds within population. The parameters from the hydrotime model can be used to normalize germination time courses for the effects of reduced Ψ . Germination time course at any Ψ can be normalized to the time course that would occur in water (0 Mpa) for the seed population by multiplying the actual time to germination $t_g(\Psi)$ by the factor $[1 - (\Psi / \Psi_b(g))]$ (BRADFORD, 1990). This normalization can evaluate the ability of the model to describe the germination behavior (BRADFORD, 1995). All normalized data from all temperatures were normalized on a common thermal time scale, using the estimated T_b at 0 Mpa.

Hydrothermal time

The thermal and hydrotime models were combined to produce a hydrothermal time (HTT) model to describe germination rates when temperature and Ψ both varied. The HTT model at the sub-optimal temperature where θ_{HT} is the HTT constant (MPa °C d) was calculated according to the equation:

$$\theta_{HT} = (T - T_b) [\Psi - \Psi_b(g)]t_g \quad (7)$$

This equation describes germination time courses at any combination of sub-optimal temperature and Ψ (ALVARADO and BRADFORD, 2002). The following modified hydrothermal time model was proposed by ALVARADO and BRADFORD (2002) to describe the germination timing and percentages across all T from T_b to T_c :

$$\theta_{HT} = \{\Psi - \Psi_b(g) - [K_T(T - T_o)]\}(T - T_b)t_g \quad (8)$$

where $[K_T(T - T_o)]$ applies only when $T > T_o$ and in this supra-optimal range of T ; the value of $\Psi_b(g)$ is set equal to $\Psi_b(g)T_o$ and $T - T_b$ is set equal to $T_o - T_b$. The values of K_T , T_b , T_o and θ_{HT} in this model can be obtained by repeated probit regressions using germination time course data according to the equation:

$$\text{Probit}(g) = [(\Psi - \theta_{HT} / (T_o - T_b)t_g) - K_T(T - T_o) - \Psi_b(50)] / \sigma_{\Psi_b} \quad (9)$$

The values of K_T and T_o were varied for germination time courses at $T > T_o$ until a fit was obtained that resulted in θ_{HT} , $\Psi_b(50)$ and σ_{Ψ_b} values close to those obtained at or below T_o (ALVARADO and BRADFORD, 2002).

Results

Germination responses to temperature and water potential

The cardinal temperature of *A. venetum* seeds was determined by germination in distilled water at different constant temperatures. Germination of *A. venetum* seeds in water progressed more rapidly as T increased within the sub-optimal range (20–30 °C). In contrast, the final germination percentage in water decreased between 30 and 35 °C. The final germination percentage in the temperature range of 25 to 30 °C was relatively high with the values of Ψ used in our study, which ranged from 70 to 89%, respectively (Fig. 1a). The germination rate increased with temperature in the range of 20 to 30 °C, and decreased above 30 °C. The germination rate (1/t₅₀) was highest for seeds incubated at 30 °C (Fig. 1b). As a result, the effect of the PEG solutions was tested at temperatures of 20 and 25 °C, considered as sub-optimal temperatures, and 30 and 35 °C considered as supra-optimal temperatures.

Thermal time analysis

Accumulated daily germination percentages at 20 and 25 °C for distilled water were transformed to probit and regressed on $\log\theta_{T1}(g)=\log[(T-T_b)t_g]$. The number of degree days necessary for 50% of the seeds to germinate in the sub-optimal temperature range was 29.4 °C d (θ_{T1}) ($R^2=0.65$). The value of T_b that produced the best fit was 16.6 °C, which was taken as the minimum temperature for germination of *A. venetum* seeds. In the supra-optimal temperature range, the value of probit (g) was related to $\log T_c(g)=\log[(T+\theta_{T2}/t_g)]$, and the best fit was obtained with $T_c(50)=45.9$ °C ($R^2=0.87$) (Tab. 1). In the supra-optimal interval, the value of $\theta_{T2}=43.2$ °C d was assumed to be constant, and the limiting factor for germination would be the distribution of T_c (g) within the population. The value of T_c varies among fractions of a seed population, following a normal distribution with mean T_c (50) and standard deviation (σ_{Tc}). Similar analyses of germination data under of -0.3, -0.6, -0.9, -1.2 and -1.5 MPa were also performed (Tab. 1). The R^2 values indicated that the thermal model for sub-optimal temperatures occurred at lower values of Ψ ($R^2=0.69-0.90$), but T_b was underestimated and $\theta_{T1}(50)$ was overestimated. T_b decreased with decreasing Ψ , especially below -0.6 MPa.

Hydrotime analysis

The hydrotime model accounted for most of the variation in germination time at reduced Ψ values at various temperatures ($R^2=0.93-0.95$) (Tab. 2). The predicted germination time courses at the various Ψ values (Fig. 2) generally fit the observed data well, except for some cases in which the predicted response deviated

Tab. 1: Parameter estimates of the thermal time model describing seed germination across a range of water potentials.

Water potential (MPa)	T_b (°C)	$\theta_{T1}(50)$ (°d)	$\sigma_{\theta_{T1}}$ (°d)	R^2
Temperature at 20, 25 Probit(g)={log[(T-T _b)t _g]-log[$\theta_{T1}(50)$]}/ $\sigma_{\theta_{T1}}$, $\theta_{T1}(g)=(T-T_b)t_g$				
0	16.6	29.4	0.51	0.65
-0.3	15.9	42.6	0.57	0.69
-0.6	16.1	50.2	0.64	0.76
-0.9	12.9	89.1	0.45	0.90
-1.2	2.4	466.0	0.86	0.77
-1.5	0.3	773.1	0.90	0.86
Temperature at 30, 35 Probit(g)={log[(T+ θ_{T2})/t _g]-logT _c (50)]/ $\sigma_{\theta_{T2}}$, $\theta_{T2}=[T-T_c(g)] t_g$				
Water potential (MPa)	θ_{T2} (°d)	$T_c(50)$ (°C)	σ_{Tc} (°d)	R^2
0	43.2	45.9	0.12	0.87
-0.3	65.7	45.7	0.19	0.95
-0.6	103.5	48.4	0.19	0.98
-0.9	78.6	40.2	0.19	0.97
-1.2	70.0	31.5	0.20	0.95
-1.5	64.6	29.4	0.16	0.99

T_b , base temperature; $\theta_{T1}(50)$, thermal time to germination of 50% at sub-optimal T; θ_{T2} , thermal time constant at supra-optimal T; $T_c(50)$, ceiling temperature to germination of 50%; $\sigma_{\theta_{T1}}$, standard deviation for $\theta_{T1}(50)$; σ_{Tc} , standard deviation for T_c (50). R^2 , coefficient of determination.

considerably from actual germination. Estimated values of θ_H , $\Psi_b(50)$ and σ_{Ψ_b} for various germination temperatures are shown in Tab. 2. θ_H decreased from 14.2 MPa d at 20 °C to 4.0, 3.1 and 3.1 MPa d at 25, 30 and 35 °C, respectively. In addition, the values of $\Psi_b(50)$ increased as temperature increased from 20 °C to 35 °C, becoming less negative; at 35 °C, $\Psi_b(50)$ was -0.8 MPa. The predicted responses in Fig. 3 are based upon the $\psi_{b(g)}$ threshold distributions from the hydrotime model. In general, the predicted responses described the distributions of the observed cumulative germinations percentage relatively well for the treatments at 20, 25 and 35 °C and -0.3, -0.6 and -0.9 MPa, whereas the predicted values showed poor agreement with the observations at water potentials of

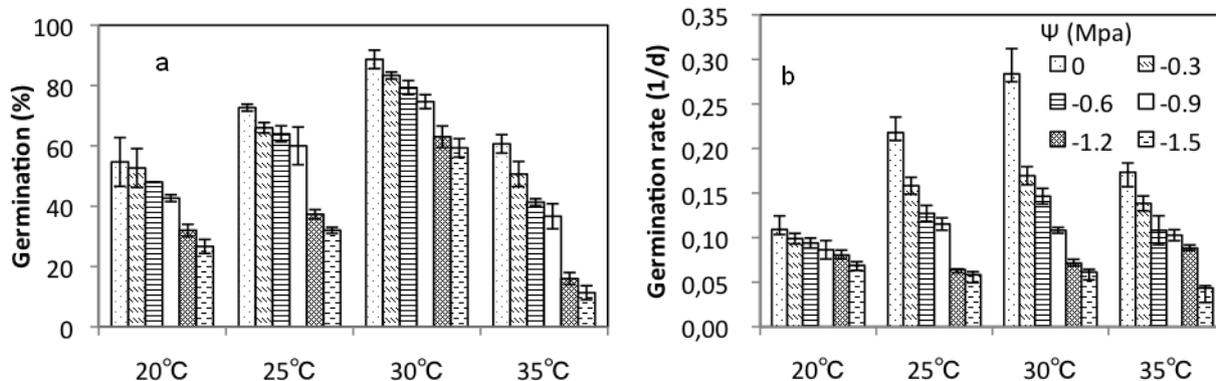


Fig. 1: Effect of temperature on the final germination (a) and germination rate (b) for *A. venetum* seeds incubated at various water potentials (Ψ) (0–1.5MPa).

Tab. 2: Parameter estimates of the hydrotime model ($\text{Probit}(g)=[(\Psi-\theta_H/t_g)-\Psi_b(50)]/\sigma_{\Psi_b}$, $\theta_H=(\Psi-\Psi_b(g))/t_g$) describing seed germination.

Temperature (°C)	θ_H (MPa d)	$\Psi_b(50)$ (MPa)	σ_{Ψ_b} (MPa)	R^2
20	14.2	-1.76	1.95	0.93
25	4.0	-1.32	1.15	0.95
30	3.1	-1.19	1.01	0.93
35	3.1	-0.80	1.23	0.94

θ_H , hydrotime; $\Psi_b(50)$, base water potential for 50% seed germination; σ_{Ψ_b} , standard deviation for $\Psi_b(g)$; R^2 , coefficient of determination.

-1.2 and -1.5 MPa. Predicted σ_{Ψ_b} varied considerably from 1.01 to 1.95 MPa.

The normalized germination curves for the hydrotime model (Fig. 4) showed that the observations from various values of Ψ at the various experimental temperatures merged into a common curve. When the interaction between temperature and Ψ_b was taken into account using individual estimates of $\Psi_b(50)$ and σ_{Ψ_b} at sub-optimal temperatures, the observations normalized more consistently into a common curve, whereas distinct groupings of observations remained at sub-optimal temperatures (Fig. 4a). However, the normalized curves revealed that observations fell into a distinct group at 35 °C, at which temperature the germination time was long and final germination values were low (Fig. 4b). This indicated that the hydrotime estimates interacted with temperature, and consequently, the grouping of observations was the most profound in the seed population with the largest shift in Ψ_b with temperature (Tab. 2).

Hydrothermal time analysis

The hydrothermal model of each sub-optimal temperature at different Ψ was regressed on $\theta_{HT}=(\Psi-\Psi_b(g))(T-T_b)t_g$, which described the germination responses at constant sub-optimal temperatures in the Ψ range of 0 to -0.6 MPa well. The values producing the best fit are presented in Tab. 3. According to the hydrothermal model, T_b and $\Psi_b(50)$ were 16.6 °C and -1.30 MPa, respectively, at sub-optimal temperatures. In the supra-optimal temperature interval, $\theta_{HT}=32.2$ MPa d, predicted by the hydrothermal time model (Tab. 3), was used to fit the germination data across various Ψ at each T (30, 35 °C).

Because the distributions of Ψ_b for various temperatures were pooled into one common distribution in the hydrothermal time model, estimates of $\Psi_b(50)$ and σ_{Ψ_b} in the hydrothermal time model (Tab. 3) generally agreed with estimates of the hydrotime model at sub-optimal temperatures. However, the estimated values were not consistent with those of the hydrotime model at supra-optimal temperatures.

Discussion

In the present study, we used *A. venetum* seeds stored for approximately 10 months, which generally exhibit a lower germinability than newly collected seeds (95%) (HU et al., 2002b). The germination of our *A. venetum* seeds was 88%, which was similar to those of HU et al. (2002a) who found that germination decreased to 81-85% after 6 months of storage and then remained stable for more than 10 years at room temperature under sealed conditions.

Many studies have shown that responses of seed germination to temperature are related to the geographical and ecological distribution of the particular species studied (GRIME et al., 1981; SCHÜTZ

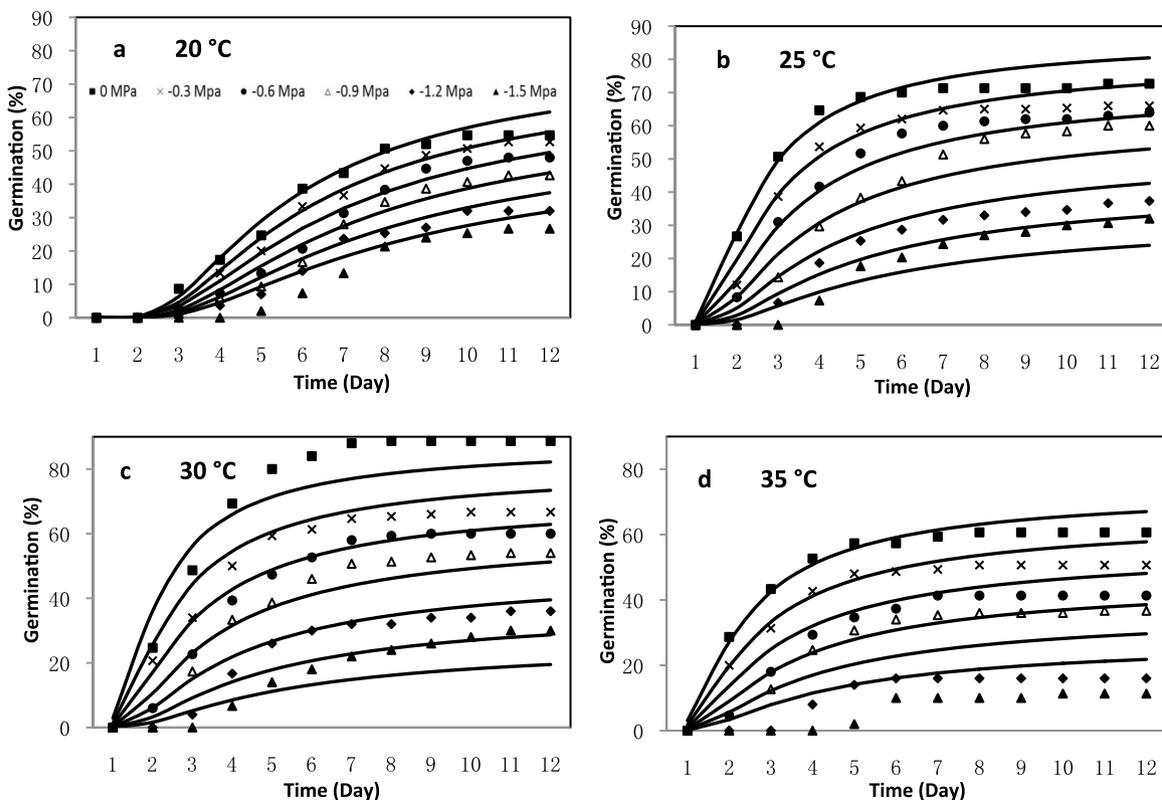


Fig. 2: Germination time course of *A. venetum* seeds for a range of water potentials at various constant temperatures. Symbols indicate actual data, and lines indicate values predicted by probit analysis.

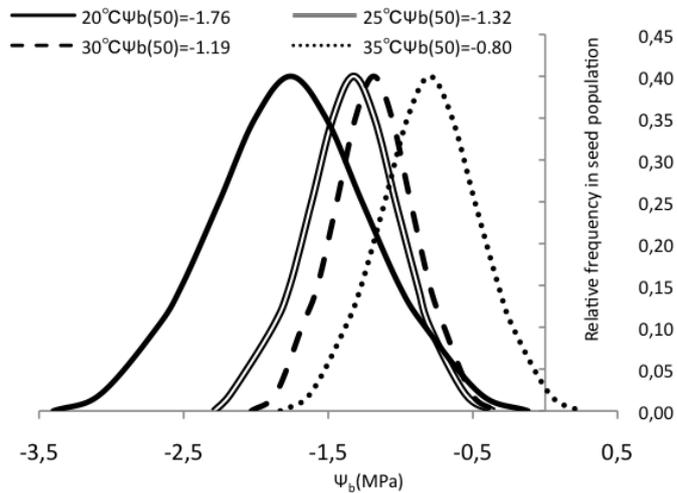


Fig. 3: Distribution of the base water potential of *A. venetum* seeds at various temperatures.

Tab. 3: Parameter estimates of the hydrothermal time model describing seed germination.

Sub-optimal temperature (20, 25 °C):					
Probit(g)=[Ψ-(θ _{HT})/(T-T _b)t _g]-Ψ _b (50)/σ _{Ψ_b} , θ _{HT} =(Ψ-Ψ _b (g))/(T-T _b)t _g					
T _b (°C)	θ _{HT} (MPa d)	Ψ _b (50) (MPa)	σ _{Ψ_b} (MPa)	R ²	
16.6	32.2	-1.31	1.19	0.93	
Supra-optimal temperature (30, 35 °C):					
Probit(g)=[Ψ-(θ _{HT})/(T _o -T _b)t _g -K _T (T-T _o)-Ψ _b (50)]/σ _{Ψ_b} , θ _{HT} ={Ψ-Ψ _b (g)-[K _T (T-T _o)]}/(T _o -T _b)t _g					
T _o (°C)	θ _{HT} (MPa d)	Ψ _b (50) (MPa)	σ _{Ψ_b} (MPa)	K _T (MPa °C ⁻¹)	R ²
27.0	32.2	-1.54	1.07	0.10	0.89

T_o, optimal temperature; θ_{HT}, hydrothermal time constant; Ψ_b(50), base water potential for 50% seed germination; σ_{Ψ_b}, standard deviation for Ψ_b(g); R², coefficient of determination.

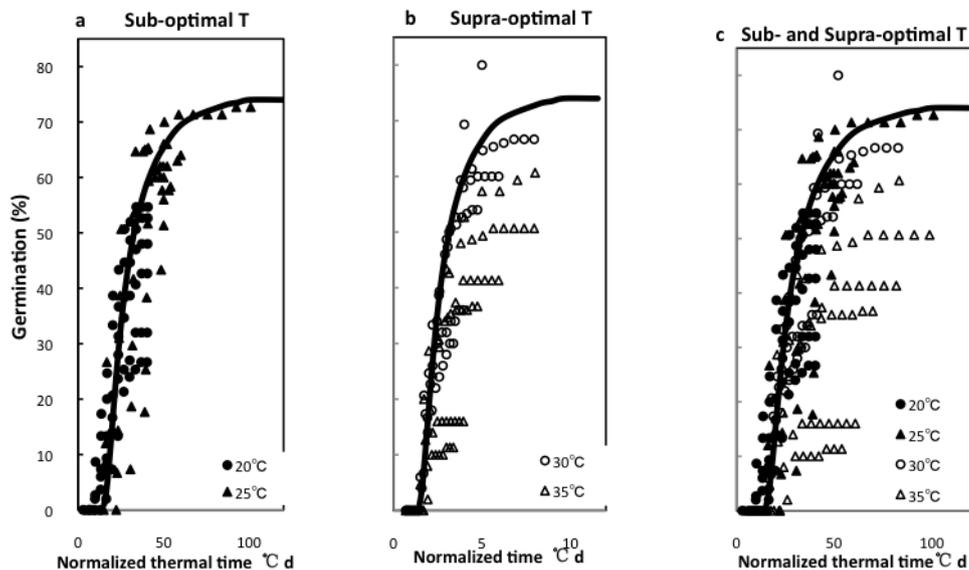


Fig. 4: Normalized time courses of the hydrothermal time model at sub-optimal temperatures (a), supra-optimal temperatures (b) and all temperatures combined (c).

and RAVE, 1999; LIU et al., 2011). The thermal requirement of seed germination also was related to the life history strategy of the species (PROBERT, 2000). *A. venetum* grows in Central Asia and is adapted to desert climates, surviving even under extremely arid conditions (<50 mm mean annual precipitation) by exploiting groundwater to meet its water demands (CHEN et al., 2007; THEVS et al., 2012). In our study, temperature had a marked effect on the germination of *A. venetum* at Ψ studied, and the effect was described by the thermal time model using probit analysis (Tab. 1). *A. venetum* seeds germinated in a relatively narrow temperature range with the final germination reaching 70-88% in the interval of 25-30 °C. The estimated T_b and θ_{T1} were 16.6 °C and 29.4 °C d in distilled water, respectively, corresponding to a relatively high T_b and low accumulated temperature during seed germination. This is consistent with some

studies reporting a negative relationship between T_b and θ_{T1} (ANGUS et al., 1981; TRUDGILL et al., 2000). Species originating from tropical regions have higher T_b and lower θ_{T1} (TRUDGILL et al., 2005). T_c was high in our study, which indicated that seeds of *A. venetum* are able to tolerate quite high temperatures. This germination characteristic of *A. venterum* is important for desert environments, which have highly variable temperatures, precipitation and soil water availability.

The thermal time model did not fit the data at lower Ψ (e.g., -1.2 MPa and -1.5 MPa). The low estimate of T_b and considerably high θ_{T1} (50) at low values of Ψ are probably not biologically significant. The thermal time analysis in our study failed to describe germination response at the later phases of germination. One possible reason could be that maximal germination was not possible during

the 15 days used in our study. According to HU et al. (2002a), the storage of *A. venetum* seeds led to lengthening the germination time period at lower temperatures, which in their study was 21 days.

The parameters from the thermal time analysis can be used for production conditions for *A. venetum*. First, T_b was estimated to be 16.6 °C; this value is quite high and precludes the sowing of these seeds in soils where the temperature does not exceed 16.6 °C. Secondly, germination rate (GR50) was found to be the highest at 30 °C, demonstrating that maximum germination rate would be attained at soil temperatures approaching this value. However, our analysis also revealed that final germination percentage decreased sharply at temperatures higher than 30 °C.

Results from the hydrotime analysis indicated that the θ_H constant was reduced from 14.2 to 3.1 MPa d when the incubation temperature increased to 30 °C and then remained stable at 35 °C. Seed germination was relatively low even at 20 °C, the germination rate was faster at higher temperatures (25, 30 and 35 °C), with seed germination beginning on the third day. The hydrotime analysis also indicated that $\Psi_b(50)$ were less negative at 30 and 35 °C than at 20 and 25 °C. According to hydrotime theory, the $\Psi_b(50)$ value of a seed population gives an indication of its ability to avoid stress. Less negative values of $\Psi_b(50)$ at supra-optimal temperatures result in declines of both seed germination rate and percentage germination, eventually reaching zero at a ceiling temperature.

Several studies documented that changes in the dormancy state are related to changes in Ψ_b (MEYER et al., 2000; ALVARADO and BRADFORD, 2002; ROWSE and FINCH-SAVAGE, 2003), with $\Psi_b(50)$ increasing with rising temperatures. Many native species in central Asia apparently have no pronounced dormancy or lack deep dormancy with species following an opportunistic strategy that allows them to germinate whenever physical conditions become suitable (WESCHE et al., 2006). Soil water availability is critical for seed germination with higher temperatures inducing thermoinhibition (HILLS and STADEN, 2003). When the distribution of Ψ_b overlaps with 0 MPa, the proportion of seeds with Ψ_b larger than 0 MPa is inhibited at the given temperature (LARSEN et al., 2004; WATT et al., 2011). In our study, Ψ_b values above 0 MPa were observed at 35 °C (Fig. 3), which is consistent with a reduction in maximum final germination percentages with temperature.

At value of less than -0.6 MPa at 25 and 30 °C, values of the θ_H constant and σ_{Ψ_b} increased. A similar response was reported by DAHAL and BRADFORD (1994) for tomato seeds, who ascribed this effect to physiological changes produced by prolonged exposure to the osmoticum. Because 30 °C was found to be optimal for seed germination (i.e., GR50 was highest at this temperature), some seeds within the population probably germinated so quickly that they escaped the water stress effect of this temperature. The hydrotime model has been effective at explaining the cardinal temperatures for seed germination in potato seeds (ALVARADO and BRADFORD, 2002) to investigate the effect of fluctuating temperatures on the termination of dormancy (BENECH-ARNOLD et al., 2000). From a crop production standpoint, the $\Psi_b(50)$ values (-1.86 to -0.80 MPa) determined in our analysis suggest that seeds of *A. venetum* have a strong tolerance to water stress.

According to ALVARADO and BRADFORD (2002), the decrease of germination rate and percentage in the supra-optimal temperature range is due to an increase (less negative values) in the $\Psi_b(g)$ thresholds for germination. When T exceeded T_o , the $\Psi_b(50)$ of the seed population shifted to -0.8 MPa d, which was the highest value observed in our study. Values of σ_{Ψ_b} ranged from 1.01 to 1.95 MPa d, which was higher than values reported in other studies and indicates that seed germination time varied substantially. This may be a survival adaptation to harsh desert environments. The extended germination time for *A. venetum* may avoid mass germination following suitable environment conditions by allowing a few seeds to rapidly

germinate under initial favorable temperature and soil water availability, and then wait a bit longer for confirmation of safe germination conditions before the remaining seeds germinate (BATLLA et al., 2009; WATT et al., 2011).

Conclusion

This study characterized *A. venetum* seed responses to temperature and water availability through the application of thermal time, hydrotime and hydrothermal models. Interactions between Ψ and temperature affected the ability of the hydrothermal time model to predict germination responses across temperature and Ψ conditions. Results also revealed some possible limitations in seed germination that need to be considered in working with *A. venetum* for crop production. The narrow thermal range for seed germination and non-uniform germination in response to Ψ and temperature variation are the most important characteristics during *A. venetum* seed germination. These factors might sufficiently delay or even prevent germination in arid and semi-arid environments. Plant breeding and selection in *A. venetum* may be useful in modifying these responses.

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Conflict of interest

None.

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