Predicting Seed Germination of Winterfat (*Eurotia lanata*), a Native Forage Species

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Abstract

The timing of seed germination plays a critical role in the survival of plants in natural ecosystems. Population-based models for the prediction of seed germination as the function of temperature and water potential have been developed, which can also be used in predicting field emergence. We used winterfat (*Eurotia lanata*) to test variations in parameters of the thermal time and hydrothermal time model among seed mass classes and germination conditions. Germination rates (GR) of subpopulations were estimated from germination time courses over a water potential range from 0 to –1.33 MPa at 2, 5, 10, 15, 20, and 25 ^{o}C. Estimated base temperature (T_b) was lower in the large seed mass class (-4.5 ^{o}C) than the small seed mass class (-3.5 ^{o}C). The $\zeta_{b(50)}$ was lowest at intermediate temperatures between 10 to 15 ^{o}C. A linear increase of hydro time (ρ_H) with subpopulation was found at lower temperatures, especially at 2 ^{o}C. There were no significant differences in $\zeta_{b(50)}$ between large and small seeds, but significant differences were observed in hydrothermal time requirement ($\rho_{HT(50)}$), which was lower at intermediate temperatures than at either lower or higher temperatures. The predictability of the thermal and hydrothermal time model was improved when parameters were allowed to change with seed size and germination conditions. Variations in T_b among seed mass classes favor large seeds, which accumulate more thermal time at a given temperature. This is particularly important for species such as winterfat, which germinates early in the season and early-emerged seedlings have better chance to establish and survive.

Introduction

The timing of germination plays a critical role in seedling establishment in natural ecosystems as well as agricultural cropping systems, and plants have evolved specific mechanisms to optimize germination time to enhance seedling survival. Since the seedling stage usually has the highest mortality rate in the plant life cycle (Fenner, 1987; Booth, 1992), and mechanisms such as delaying germination and spreading germination in time may result in better seedling establishment (Probert, 1992). Population-based threshold models, such as thermal time and

hydrothermal time models, have considerable potential for characterizing and quantifying the effects of thermal and hydro environment on seed germination and seedling emergence (Forcella *et al*., 2000; Bradford, 2002). These models have been applied successfully to predict field seedling emergence of crops (Finch-Savage and Phelps, 1993), forages (Hardegree and Van Vactor, 1999) and weed species (Roman *et al*., 2000).

Temperature is the primary environmental factor regulating both seed dormancy and germination (Roberts, 1988). Thermal time, the heat unit accumulation above a temperature threshold, is not only a firmly established developmental principle for plants including germination, but also an essential component in germination modeling. One basic assumption of the thermal time model is that base temperature (T_b) is constant within a seed population (Garcia-Huidobro *et al*., 1982; Gummerson, 1986). Unless dormancy is present (Welbaum and Bradford, 1991), T_b generally is believed to have little variation among individual seeds within a seed lot (Ellis and Barrett, 1994; Dahal *et al*., 1990; Steinmaus *et al*., 2000). Other reports, however, have shown that T_b changes with water potential (Fyfield and Gregory, 1989; Kebreab and Murdoch, 1999), priming treatments (Hardegree, *et al.,* 2002), and germination stages (Fyfield and Gregory, 1989; Lisson *et al.,* 2000). More complex models have been suggested for seed germination behaviour at temperatures near T_b (Kebreab and Murdoch, 1999). Base temperature may be an adaptation characteristic for species and a species that normally germinates at cool temperatures has a relatively low T_b (Steinmaus *et al*., 2000). T_b can be below 0 ^oC in rangeland species (Trudgill, *et al.,* 2000) and even in crop species (Squire *et al*., 1997). Species with low or subzero T_b that germinate and emerge earlier in cold temperature may have a competitive advantage for survival and establishment (Hou and Romo, 1998).

Hydrothermal time (ρ_{HT}) quantifies the combined effects of temperature and water potential on the progress of seed germination, which includes both the thermal time accumulation above the thermal threshold (base temperature, T_b) and the hydro time accumulation above the hydro threshold (base water potential, ζ_b) towards seed germination. Base temperature varies little among individual seeds or subpopulations and the thermal time (ρ_T) is normally distributed within a seed population in the thermal time model (reviewed by Bradford, 1995; 2002). Base water potential in the hydrothermal time model differs among individual seeds and hence must be defined according to a particular germination fraction (g), while hydro time (ρ_H) and ρ_{HT} are assumed constant (Bradford, 1995; Gummerson, 1986). Hydro time is based on the effect of water availability on the germination rate of subpopulations (Gummerson, 1986). Water has more complicated effects on germination compared to temperature, especially at low water potentials. When ζ is lower than -0.5 MPa, physiological adjustment occurs (Ni and Bradford, 1992), and when ζ is below the threshold of radicle emergence, metabolic advancement or priming effect is observed (i.e., Hardegree *et al.,* 2002).

Larger or heavier seeds usually germinate faster than smaller or lighter seeds of the same species (i.e. Humara, *et al*., 2002). Because thermal time modeling is based on germination rates of subpopulation, it is reasonable to hypothesize that parameters in the thermal time model vary among different portions. Therefore, the testing and validation of common assumptions in

thermal time modeling will help improve modeling accuracy and provide insight to the mechanisms that plants have developed to cope with their environment.

Winterfat (*Eurotia lanata* (Pursh) Moq.) was selected to test the effect of seed size on thermal time and hydrothermal model parameters. Winterfat is a small shrub native to the Great Plains of North America (Romo *et al.*, 1995) with superior forage quality (Smoliak and Bezeau 1967). Seeds of winterfat are capable of germinating at or near 0 ^{o}C (Booth, 1987). Hydrated winterfat seeds survived temperature below –30 ^{o}C even after the occurrence of the low temperature exotherm (Bai *et al*., 1998). Different metabolic responses to temperature have also been found among ecotypes (Thygerson *et al*., 2002). We hypothesized that the parameters of thermal time and hydrothermal time model are influenced by seed size and the independency of T_b and ζ_b on germination condition are affected by temperature and water potential. Specific objectives were: 1) to construct thermal and hydrothermal time model for two seed size classes and two collections of winterfat; 2) to test assumptions of thermal and hydrothermal time model, such as the constancy of ρ_H and ρ_{HT} and the independence of thermal and hydro thresholds on temperature and water potential; and 3) to analyze the variations in parameters of the model between seed size classes and seed collections.

Materials and Methods

Seed sources and characteristics

Two collections of winterfat seed (diaspores), Cela-01 and #63, were purchased from Wind River Seed (Manderson, Wyoming, USA). Both collections originated from Utah. Fruits were stored in a warehouse for approximately 7 months after harvesting in October 2001. They were air-dried at room temperature for at least one week after purchase, and then cleaned by rubbing, fanning and passing serial sieves and blowers. Cleaned seeds were separated into two classes using a seed blower based on seed mass and hereafter were referred to seed mass classes as seed size classes (large and small). Seed moisture content was similar between large and small classes within each collection. Cleaned and classified seeds were then sealed in plastic bags and stored at –18 ^{o}C until use. Please see Wang *et al.* (2004) for details regarding characteristics of the two seed collections.

Germination at various temperature and water potential regimes

Water potential gradients were created using polyethylene glycol (PEG-6000, EM Science, Germany) solutions (Michel, 1983; Hardegree *et al.,* 1990). Designated water potentials of PEG solution were 0, -0.25, -0.50, -0.75, -1.0, -1.25, and -1.5 MPa. The actual water potentials of PEG solutions were measured using a vapor pressure osmometer (Model 5100C, Wescor Inc., Logan, UT). The measurement was taken 30 min after PEG solutions penetrated into two layers

of filter papers (Whatman No. 1) in a Petri dish as suggested by Hardegree *et al.* (1990) to take the effect of filter paper on water potential into consideration. The value of water potential was adjusted according to each germination temperature for modeling.

A randomized complete block design (RCBD) with five replicates was used and there was a 7-day interval between replicates. Seeds, 50/unit, were carefully sprinkled in 9 cm Petri dishes with distilled water or PEG solutions on top of two layers of filter papers (Whatman No.1), and Petri dishes were randomized within each chamber block (shelf). Five mL of PEG solution or distilled water were added initially to each Petri dish and an extra 2 mL were added after 24 h and periodically as required. Clear plastic bags were used to seal Petri dishes to reduce water evaporation.

Parameter estimation for the hydrothermal time model

In order to estimate the germination rate of subpopulations ($GR_{(g)}$), germination time courses of each temperature, water potential, and replicate were fitted separately using probit analysis procedures as described in Wang *et al.* (2004). The base temperature for the 50% subpopulation ($T_{b(50)}$) was estimated using the linear function of $GR_{(50)}$ on temperature at the suboptimal temperature range for each water potential (Dahal and Bradford, 1994). Thermal time for subpopulations of 10, 20, 30, 40, 50, 60, and 70 % was estimated as the inverse of slopes of linear regression lines.

According to the thermal time model (Garcia-Huidobro *et al*., 1982),

$$GR_{(g)}=1/t_{(g)}=(T-T_b)/\rho_{T(g)} \qquad (1)$$

germination rate ($GR_{(g)}$), the reciprocal of germination time (t_g) to a given germination percentile (g), is linearly related to temperature (T) within the range between base temperature (T_b) and optimal temperature for non-dormant seeds. The linear relationship between $GR_{(g)}$ and T varies among subpopulations in the slope of the linear regression line, which is equal to the reciprocal of thermal time ($\rho_{T(g)}$).

The linear function of $GR_{(50)}$ on water potential was used to estimate $\zeta_{b(50)}$ at each germination temperature, which is the x-intercept of the linear regression line. Similarly, the linear functions of a specific *g* fraction on ζ for subpopulation 10, 20, 30, 40, 50, 60, and 70% were used for ρ_H estimation. The inverse of the each regression slope was ρ_H (Bradford, 1995) for each subpopulation at a given temperature. Data were pooled from all replicates and the regression lines were disregarded when they were not significant ($P > 0.05$).

Comparison of models predictability

The basic hydrothermal time model was based on Gummerson (1986) and Dahal and Bradford (1990, 1994):

$$\rho_{HT} = (T - T_b) (\zeta - \zeta_{b(g)}) t_g \qquad (2)$$

According to the assumptions of the hydrothermal time model, germination progress can be described by the normal distribution of $\zeta_{b(g)}$ within a seed population (Dahal and Bradford, 1994):

$$\text{Probit (g)} = [\zeta - (\rho_{HT} / (T - T_b) t_g) - \zeta_{b(50)}] / \tau_{\zeta b} \qquad (3)$$

The hydrothermal time for 50% subpopulation ($\rho_{HT(50)}$) was used in the hydrothermal time model for simplification even though variations existed among subpopulations. The predictability of the hydrothermal time model (Equation 3) based on assumptions: $\rho_{HT(50)}$ was allowed to change with temperature and estimated using Equation (2). The model fit was tested using modified R^2, which was 1 minus the ratio of the sum square of residuals, the difference between observed and predicted values, and the sum of squares of observed values and observed means (Wang *et al.*, 2004).

Results

Germination percentage and germination rate as affected by water potential and temperature

Both water potential and temperature affected the final germination percentage of winterfat, which was reduced especially when $\zeta < -0.50$ MPa and $T < 5\ ^{o}C$ (Fig. 1). The final germination percentage was more sensitive to changes in water potential than temperature. Both water potential and temperature and their interactions significantly influenced the final germination percentage ($P < 0.001$ to 0.01). Large seeds of both collections had higher final germination percentage than small seeds at all combinations of T and ζ, and the differences between seed size classes increased with decreasing water potentials and temperatures. About 54 % of viable large seeds germinated at –0.89 MPa, 2 ^{o}C; only 37 % for the small seeds under the same condition of collection #63; and 31 % and 24 % germinated for the large and small seeds of collection Cela-01, respectively.

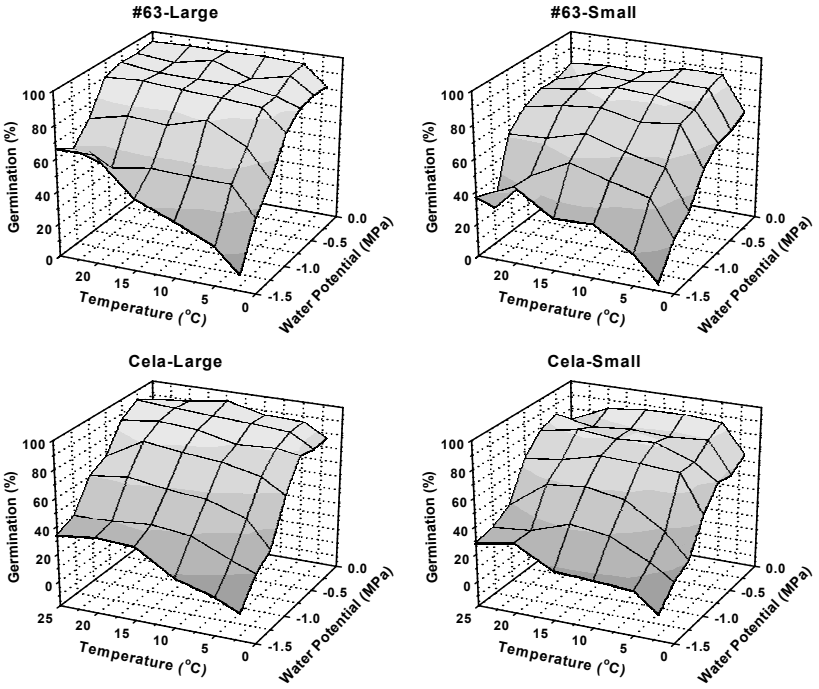

Fig 1. Effects of water potential and temperature on the final germination percentage of two seed size classes and two collections of winterfat.

Seed germination rate as measured by GRI was different between seed size classes and seed collections at various temperatures and GRI was dependent on incubation temperature (Fig. 2). The large seeds germinated faster than small seeds in both collections ($P < 0.05$) and collection #63 had faster germination than collection Cela-01 ($P < 0.05$) when all data were analyzed together. Large seeds germinated faster than small seeds at all temperatures for the #63 collection and at 2 and 25 ^{o}C for the Cela-01 collection ($P \leq 0.05$).

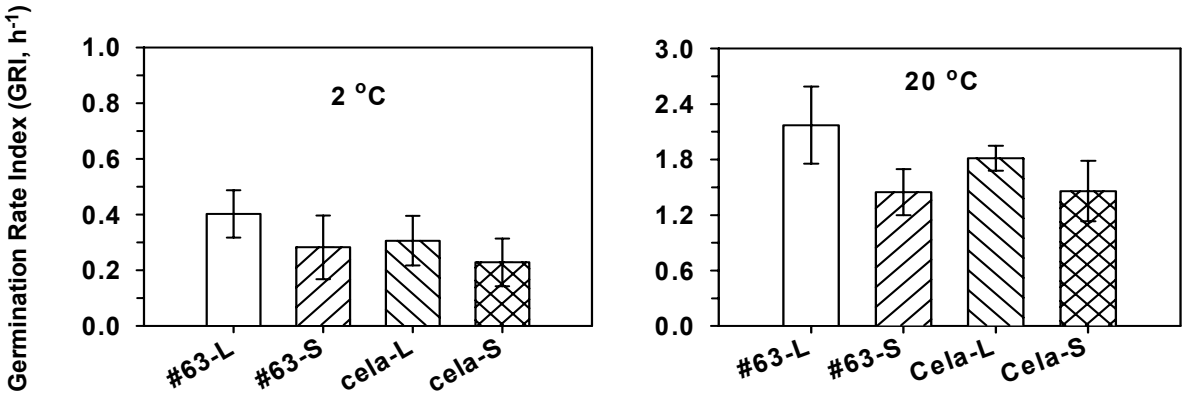

Fig 2. Germination rate index (GRI) of two seed size classes and two seed collections of winterfat incubated at temperatures 2 and 20 ^{o}C. Values are means ± SE. L: Large seed; S: Small seed

Parameter estimation and accuracy of thermal time model

Germination rates ($GR_{(g)}$) of subpopulations calculated from the predicted germination time course correlated strongly with temperature ($R^2 > 0.90$) at the suboptimal temperature range (Fig. 3). Optimum temperatures varied among subpopulations between 20 and 25 ^oC with lower optimum temperature in more slowly germinating subpopulations.

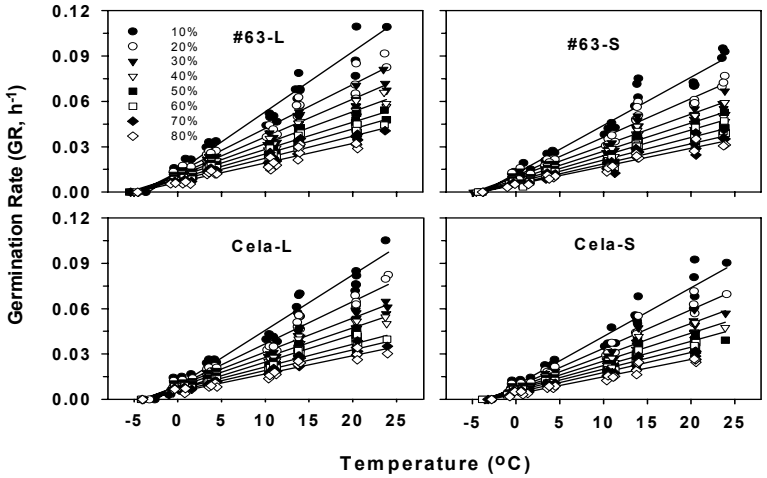

Fig 3. Germination rate ($GR_{(g)}$) within the range of suboptimal temperatures as a function of temperature and sub-population in two seed size classes and two seed collections of winterfat. L: Large seed, S: Small seed.

T_b was below 0 ^oC for both seed collections, and was significantly different between seed size classes and between collections (Table 1). T_b for collection #63 (-4.48 ^oC) was about 1 ^oC lower than that of Cela-01 (-3.53 ^oC). Large seed class (-4.28 ^oC) had lower T_b than small seed class (-3.74 ^oC), the difference between seed size classes was more than 0.5 ^oC for the two collections, and was greater in Collection #63. T_b was significantly different among subpopulations in collection Cela-01 (P／ 0.05), but not in collection #63 (data not shown). There were no significant differences either in $\rho_{T(50)}$ or in $\tau_{\rho T}$ between collections and seed size classes.

Table 1.
Estimated parameters for the thermal time model in two seed size classes and two collections of winterfat. Means with the same letter within a parameter are not significantly different at P ≤ 0.05 using FPLSD among treatments of seed collections and seed size classes.

Seed collection	Seed size	Tb (±C)	ρY!)61∗ (±C h)!	τρY!!(±C h)!
#63	Large	-4.80 a	549.0 a	253.8 a
	Small	-4.18 b	571.1 a	247.0 a
Cela-01	Large	-3.77 b	567.0 a	262.9 a
	Small	-3.29 c	614.4 a	274.3 a
LSD		0.45	92.3	44.7

Thermal time models were constructed separately for each seed size class and collection using parameters in Table 1. Original germination data at temperatures between 2 and 20 ^{o}C were used to test the accuracy of the thermal time models. R^2 values were generally high and were mostly > 0.80 for both collections and seed size classes.

Effects of temperature on $\zeta_{b(g)}$ and ρ_H

The estimated $\zeta_{b(50)}$ was curvilinearly correlated to temperature in both collections and seed size classes except for small seeds of Cela-01 which exhibited large variability among temperatures (Fig. 4). The value of $\zeta_{b(50)}$ was lowest at intermediate temperatures (10-15 ^{o}C) and the difference in $\zeta_{b(50)}$ between temperatures can be more than 0.5 MPa.

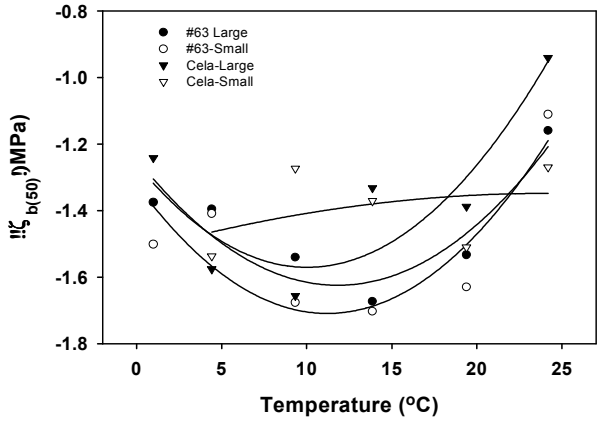

Fig. 4. Variations of the base water potential of the 50 % subpopulation ($\zeta_{b(50)}$) with temperature in two seed size classes and two collections of winterfat. The value of $\zeta_{b(50)}$ was estimated by the linear function of $GR_{(50)}$ on water potential at each temperature.

Hydro time (ρ_H), estimated from the inverse of the slope of the linear function of $GR_{(g)}$ on water potential, was not always constant among subpopulations, and the constancy varied with temperature (Fig. 5). Hydro time was relatively constant among subpopulations when temperatures were above 10 ^{o}C, but it increased with increasing germination fractions or subpopulation when temperature was lower than 10 ^{o}C, especially at 2 ^{o}C. Generally, ρ_H increased with decreasing temperature for a given subpopulation. Therefore, the assumption of ρ_H being constant in the hydrothermal time model was invalid at low temperatures for winterfat seeds. In general, large seeds had less ρ_H requirement than that of small seeds and differences in ρ_H between seed size classes were greater at low temperatures. Small seeds of collection #63 required about 60 MPa h more hydro time than large seeds at 2 ^{o}C. Collection #63, which originated from a dryer site, required less ρ_H than Collection Cela-01, especially at low temperatures.

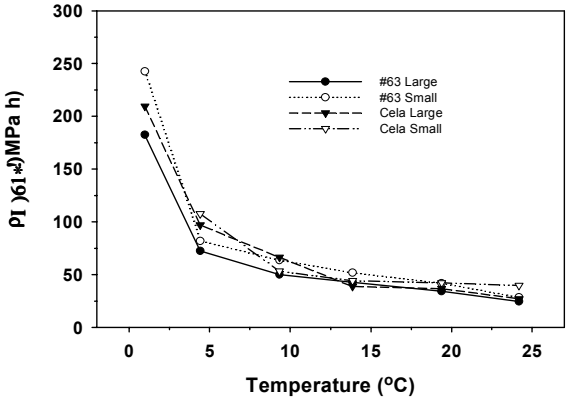

Fig. 5. Effect of temperature on hydro time of the 50% subpopulation ($\rho_{H(50)}$) of two seed size classes and two collections of winterfat. The value of $\rho_{H(50)}$ was estimated from the slope (ρ_H=1/slope) of linear function of $GR_{(50)}$ on water potential.

When ρ_{HT} was allowed to vary with temperature, model predictability was improved at the low temperature and high water potential range, indicating that changes in ρ_{HT} with temperature have an important impact on model predictability in winterfat (data not show).

Discussion

It is not surprising to find that seeds of large size class germinated faster than that of small size class because the ability of large seeds to provide higher energy and nutrients (Vaughton and Ramsey, 1998) for greater germination capacity (Humara *et al.,* 2002). However, whether the faster germination rate is the result of less thermal time requirement, lower base temperature, or less variation in thermal time among subpopulations remains unknown. The base temperature, however, was significantly lower in large seed classes than that in small seed classes, allowing large seeds to accumulate more thermal time units than small seeds under the same temperature and subsequently to germinate faster. Furthermore, T_b was significantly different between seed collections for a given size class. T_b is believed to have little variation among individual seeds within a seed lot (Garcia-Huidobro *et al*., 1982; Dahal *et al*., 1990), or among genotypes (Ellis and Barrett, 1994) or seed lots (Cheng and Bradford, 1999) of the same species. It is considered as a stable trait of crop cultivars (Bradford, 1995; Cheng and Bradford, 1999) or species (e.g. Ellis and Butcher, 1988). However, the similar results as here, there have been reports that T_b along with other parameters in the thermal time model did not appear stable for non-crop species (Forcella *et al*., 2000) due to distinct genetic variability within the population (Wang *et al*., 1995).

Reduced water potential lowered both germination rate and final germination percentage in winterfat, similar to other species (Fyfield and Gregory, 1989; Shrestha *et al.,* 1999). The interactive effect of water potential and temperature on germination rate and percentage of

winterfat has also been reported in other species (Ni and Bradford, 1992; Kebreab and Murdoch, 1999; Shrestha *et al.,* 1999). The hydrothermal time model assumes a fixed set of model parameters under any germination condition in a seed population (Gummerson, 1986). This approach simplifies the modeling process with relative constant germination responses under varied environmental conditions. However, these parameters were found variable with germination conditions (i.e., Kebreab and Murdoch, 1999; Alvarado and Bradford, 2002). Bradford (2002) illustrated the parameter adjustment for the hydrothermal time model according to seed physiological status, priming effects and germination initiators. The present study demonstrated parameters of the hydrothermal time model were highly variable not only with germination conditions, but also with seed sizes within a seed collection in winterfat. Estimated hydro thresholds for seed germination of winterfat shifted with temperature, an interactive effect of temperature and water potential also influenced the variation of these parameters. Therefore the basic assumption of the hydrothermal time model, constant thresholds, is invalid in winterfat. The quantification of $\zeta_{b(g)}$ shifting with temperature was developed at supraoptimal temperature range in potato (*Solanum tuberosum* L.) seed (Alvarado and Bradford, 2002), and carrot and onion (Rowse and Finch-Savage, 2003).

Also ρ_H was found not constant among subpopulations at low temperatures in winterfat, indicating the altering of water relations at low temperature. Hydro time determines germination rate at a given temperature, which is a temperature specific parameter (Kebreab and Murdoch, 1999). Large increase ρ_H with decreasing temperature was reported in many other species (Dahal and Bradford, 1994; Kebreab and Murdoch, 1999; Alvarado and Bradford, 2002). However, the variation of ρ_H was not only associated with decreasing temperature, but also with subpopulations in winterfat. The ρ_H for late subpopulations was generally high at low temperatures, which may lead to the failure of achieving high germination percentage at low water potential and low temperature. The ρ_H can be an indicator of seed physiological quality or vigor in a seed lot and genetic differences among genotypes where $\zeta_{b(g)}$ is not changing markedly (Dahal and Bradford, 1990). Physiological advancement of priming treatment was due primarily to a smaller ρ_H requirement, and aged tomato seeds have a higher ρ_H value than freshly harvested seeds (Dahal and Bradford, 1990). Low ρ_H requirement, especially at low temperature in the large seed of winterfat, shows advantages of large seeds to germinate under lower temperatures.

Species adapted to wild and unpredictable conditions are more likely able to adjust germination response to their environment than crop species that are under optimal cultivation conditions. Adjustment and modification of model parameters according to germination conditions improved the predictability of the hydrothermal time model at reduced water potential. The adjustment of ρ_{HT} to temperature had a large impact and improved the model predictability. Dahal and Bradford (1994) used two sets of parameters for higher or lower water potentials, respectively and obtained a better model fit, which showed that ρ_{HT} was not constant for any combination of temperature and water potential.

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