Base water potential for germination of radiata pine and buddleia seeds adjusts in response to time, seed-bed water potential and supra-optimal temperatures

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Abstract

Hydrothermal germination models are mathematical models which predict germination time of seeds for a specified seed-bed temperature (T) and water potential (Ψ). In this paper, the commonly observed decline in seed germination at supra-optimal temperatures is investigated by fitting a hydrothermal time model to germination data from two unrelated plant species (*Buddleia davidii* and *Pinus radiata*). For both these species, reduced germination rates and germination percentages above optimum temperatures (20°C and 25°C for *P. radiata* and *B. davidii*, respectively) were successfully modelled by an upward shift in the seeds' base water potential (Ψ_b) during germination. The upwards shift in Ψ_b was shown to be an asymptotic function of time to germination, but with the rate increased by higher temperatures and moister seed-bed conditions. The physiological and ecological implications of this proposed model of the observed decline in germination at supra-optimal temperatures are discussed.

Keywords: hydrothermal, model, *Pinus radiata*, *Buddleia davidii*

Introduction

In hydrothermal time (HTT) models, time to germination and percentage germination of seeds are explained by seed population characteristics and by the water potential (Ψ) and temperature (T) of the seed's environment. The HTT model was first proposed by Gummerson (1986) and can be specified mathematically as:

$$t(\mathrm{G}) = \frac{\theta_{HT}}{[\Psi - \Psi_b(\mathrm{G})](T - T_b)} \qquad (1)$$

where $t(\mathrm{G})$ is the time for the G$^{\mathrm{th}}$ percentile of the seed population to germinate, θ_{HT} is a hydrothermal time constant that has a unique value for the population and $\Psi_b(\mathrm{G})$ and T_b are respectively the base water potential and base temperature for germination.

The model specifies that base temperature has a common value for all percentiles (T_b) but each seed percentile G has a unique value for its base water potential, $\Psi_b(\mathrm{G})$. This means that for a specific water potential, each seed percentile will accumulate hydrothermal time at a different rate to other percentiles; therefore it is the variation in $\Psi_b(\mathrm{G})$ that results in a spread of seed germination times within that population (Bradford 2002; Finch-Savage 2004).

HTT models for supra-optimal temperatures

For most seed plants there is an optimum temperature (T_o) for germination, where both the seed germination rate and percentage germination reach a maximum. Above T_o both germination rate and percentage germination decline, eventually reaching zero at a ceiling temperature (T_c).

A mechanistic explanation for this decline in germination is that firstly an upwards shift in seed base water potential ($\Psi_b(\mathrm{G})$) has been linked to increased resistance of tissues surrounding the embryo to radicle elongation, so that seeds with more resistant tissues require higher turgor pressures in the radicle in order to emerge (Bradford 1995; Bradford 2002); and secondly supra-optimal temperatures induce physiological processes (mediated by abscisic acid (ABA)) within the seed that increase endosperm resistance (Tamura *et al.* 2006). Therefore supra-optimal temperatures effectively raise the value of Ψ_b towards zero leading to reduced accumulation of hydrothermal time and inhibited germination.

The HTT model specified in Equation 1 applies only at sub-optimal temperatures, because it implies that germination rate will increase indefinitely with increasing T, i.e., if the term $(T - T_b)$ becomes larger and if θ_{HT} is a constant, then $t(G)$ must become smaller. To account for the decline in germination rate at supra-optimal temperatures, additional terms must be included in the model. Alvarado and Bradford (2002) and Rowse and Finch-Savage (2003) have proposed a HTT model which accounts for declining germination rate and germination percentage above T_o. As specified by Rowse and Finch-Savage (2003), the model achieves this using Equation 2 to calculate the increase in seed base water potential at supra-optimal temperatures:

$$\Psi_b(G)_{supra} = \Psi_b(G) + k[T - T_d]. \qquad (2)$$

Here $\Psi_b(G)_{supra}$ and $\Psi_b(G)$ are the base water potentials at supra-optimal and sub-optimal temperatures respectively, k is a constant, T is supra-optimal temperature, and T_d is the temperature at which the upwards shift in water potential commences.

Equation 2 can be checked by calculating deviations of $\Psi_b(G)_{supra}$ from sub-optimal $\Psi_b(G)$ and plotting these against germination temperature. Deviations $(\Delta\Psi_b(G))$ are specified by rearranging Equation 2:

$$\Delta\Psi_b(G) = \Psi_b(G)_{supra} - \Psi_b(G) = k[T - T_d] \qquad (3)$$

If Equation 3 holds true, then firstly plots of $\Delta\Psi_b(G)$ versus T should be linear with a slope = k; and secondly plots of $\Delta\Psi_b(G)$ versus $t(G)$ should not show any dependency on time to germination, as the model proposed by Rowse and Finch-Savage (2003) ignores any effect of time on the upwards shift in $\Psi_b(G)$.

The next two sections present results from germination studies using seed from radiata pine (*Pinus radiata* D. Don) (Bloomberg *et al.* 2009) and buddleia (*Buddleia davidii* Franch.). For both of these studies the aim was to test the Rowse and Finch-Savage (RFS) model of germination (Equation 2) at supra-optimal temperatures.

Methods

Germination data were measured for a commercial radiata pine seed lot (seed lot number 075/780, Proseed NZ Ltd) and buddleia seeds collected from wild plants growing at Rotorua, New Zealand (38.2°S, 176.3°E, elevation 285 m above sea level).

Seeds were incubated under constant factorial combinations of temperature and water potential (Table 1). Water potentials were established using appropriate strengths of polyethylene glycol 6000 and 8000 (PEG) osmotic solutions made up according to Hardegree and Emmerich (1990). The osmotic solution with 0 MPa was water with no PEG added. Seeds required no pre-treatment or stratification prior to testing (ISTA 2003; Miller 1984). Germination counts were continued for 50 d (radiata pine) and 30 d (buddleia). Germinated seeds (with radicle protruding more than 2 mm from the seed coat) were counted and discarded. HTT model (Equation 1) parameter values(θ_{HT} and T_b) were first estimated from sub-optimal germination time data. $\Psi_b(G)_{supra}$ was then determined from supra-optimal germination time data by rearranging Equation 1 to give Equation 4:

$$\Psi_b(G)_{supra} = \Psi - \{\theta_{HT}/[(T - T_b)t(G)]\} \qquad (4)$$

$\Delta\Psi_b(G)$ for all germinated seeds at supra-optimal temperatures were determined from Equation 3, using $\Psi_b(G)_{supra}$ from Equation 4 and Ψ_b(G) from the sub-optimal HTT model. Values of $\Delta\Psi_b$(G) were then plotted against temperature and time to germination in order to test conformity of supra-optimal data with the RFS model.

Table 1 Factorial (temperature × water potential) germination treatments for radiata pine and buddleia experiments.

Treatment	Radiata pine	Buddleia
Sub-optimal temperatures (°C)*	12.5 to 20	10 to 25
Supra-optimal temperatures (°C)*	22.5 to 32.5	26 to 32
Water potential (MPa)	0 to –1.2	0 to –0.6

*For convenience data for $T \leq T_o$ will be hereafter referred to as 'sub-optimal', and data for $T > T_o$ will be referred to as 'supra-optimal'.

Results

Radiata pine germination

Figure 1a shows that as predicted by the RFS model, $\Delta\Psi_b$(G) values increase in magnitude with temperatures above T_d = 20°C, but there was considerable variation within each temperature level. Figure 1b shows that other factors accounted for part of the variation in the values for $\Delta\Psi_b$(G), with 1) $\Delta\Psi_b$(G) also increasing as an asymptotic function of germination time (Figure 1b); and 2) the rate of this increase scaling positively with supra-optimal thermal time index, defined as $(T - T_d)t(G)$, and water potential (Figure 1c). Therefore $\Delta\Psi_b$(G) was also plotted against a 'supra-optimal hydrothermal time index' *SOHTI* = $[\Psi - (-1.5)][T - T_d]\ t(G)$ (Bloomberg *et al.* 2009). *SOHTI* differs from the population hydrothermal time constant θ_{HT}, because it is a variable calculated using a base temperature T_d = 20°C rather than T_b (9.0°C) and the base water potential (–1.5 MPa) is an approximation for $\Psi_b(50)$ rather than the base water potential of a particular seed percentile (Ψ_b(G)).

The relationship between $\Delta\Psi_b$(G) and *SOHTI* is consistent for all data, and appears to have an asymptotic exponential form with an asymptote of 1.5 MPa (Figure 1d). This relationship between $\Delta\Psi_b$(G) and *SOHTI* was modelled using the asymptotic exponential equation (Equation 5):

$$\Delta\Psi_b(G) = a - [b \exp(-c\ SOHTI)] \quad (5)$$

Estimated parameter values were a = 1.45, b = 1.56 and c = 0.00596. The model accounted for 83% of the variance in $\Delta\Psi_b$(G).

Germination of buddleia

Base water potential values of buddleia seeds at supra-optimal temperatures ($T > T_d$, where T_d = 25°C) showed similar responses to radiata pine seeds. Temperature exhibited a weak positive relationship with $\Delta\Psi_b$(G) in the supra-optimal temperature range (Figure 2a). There was a stronger relationship between $\Delta\Psi_b$(G) and time, with $\Delta\Psi_b$(G) increasing exponentially with time to an asymptote (Figure 2b). As the magnitude of this asymptote and the rate of change scaled positively with temperature, $\Delta\Psi_b$(G) was plotted against a supra-optimal thermal time index, defined as $[(T - T_d)\ (t(G) - t_s)]$, where t_s defines the start time of germination, which was empirically fitted as 74.5 h. For the relationship between $\Delta\Psi_b$(G) and supra-optimal thermal time, water potential

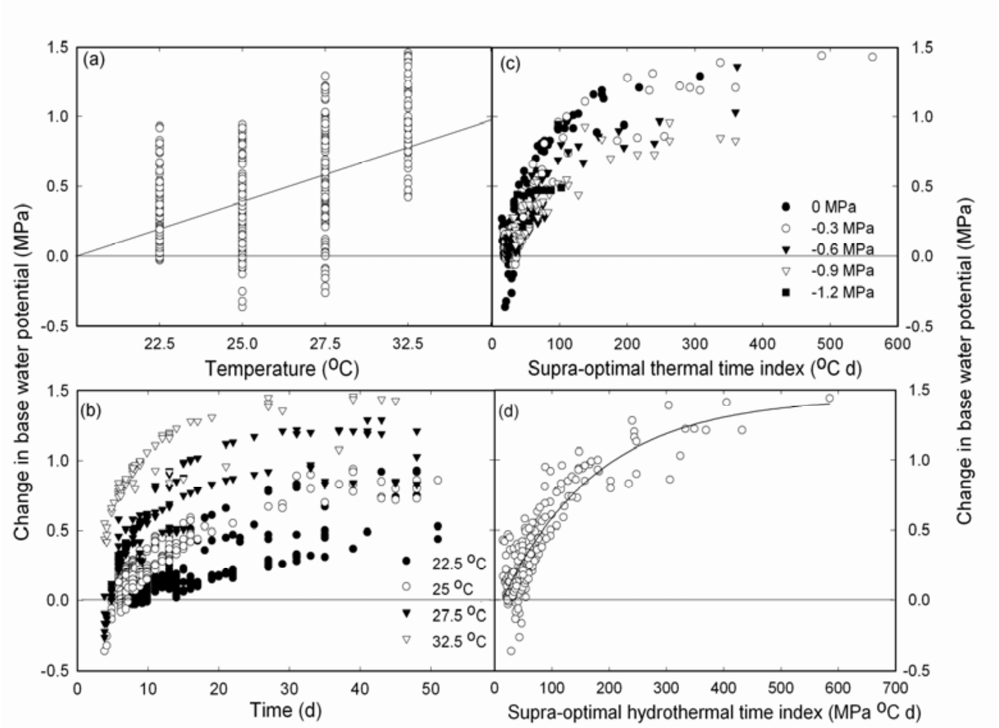

Figure 1 Relationship between change in base water potential ($\Delta\Psi_b$) and (a) temperature, where the solid line is $\Delta\Psi_b = 0.0729(T - T_d)$ (b) time to germination for each temperature (c) supra-optimal thermal time index $(T - T_d)\,t(G)$, for each water potential and (d) supra-optimal hydrothermal time index (*SOHTI*) where the solid line is $\Delta\Psi_b = 1.45 - [1.56 \exp(-0.00596\ SOHTI)]$.

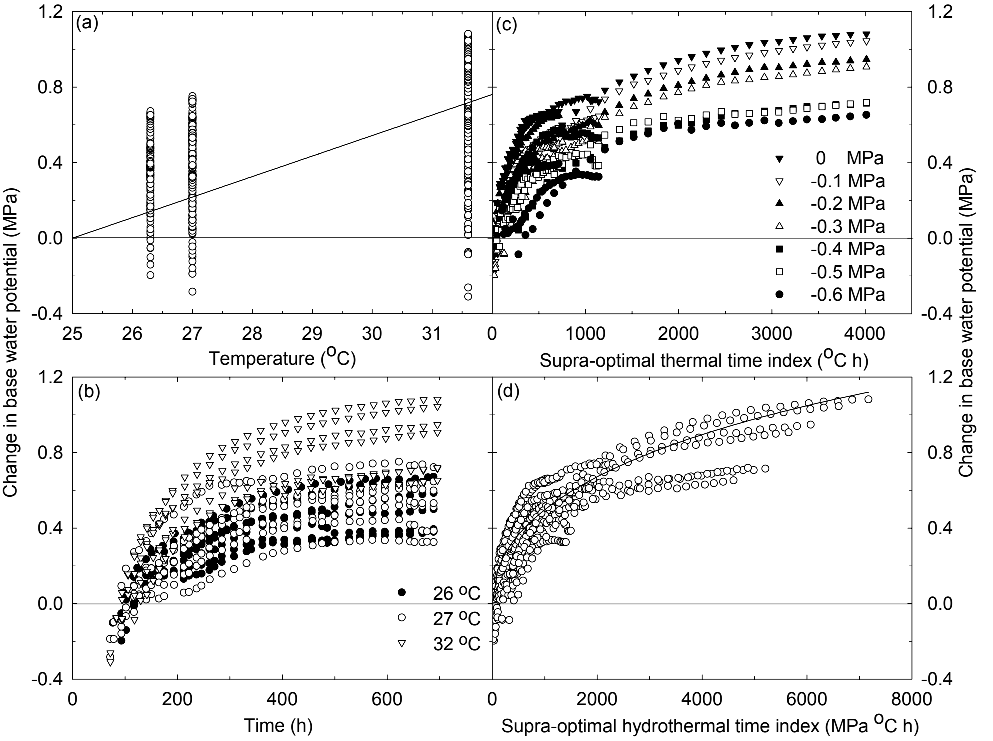

Figure 2. Relationship between $\Delta\Psi b$ and (a) temperature where the solid line is $\Delta\Psi b = 0.1105(T - T_d)$ (b) time to germination for each temperature (c) supra-optimal thermal time index $[(T - T_d)\,(t(G) - t_s)]$, for each water potential and (d) supra-optimal hydrothermal time index (*SOHTI*) where the solid line is $\Delta\Psi_b(G) = 1.81[1 - \exp(-0.0000591\ SOHTI)]^{0.452}$.

treatments showed a consistent pattern, with $\Delta\Psi_b(G)$ increasing as water potential increased towards zero (Figure 2c). To account for this variation *SOHTI*, was modified to $SOHTI = (\Psi - \Psi_b(0))(T - T_o)(t(G) - t_s)$. Figure 2d shows there was a strong exponential asymptotic relationship between $\Delta\Psi_b(G)$ and *SOHTI* which was modelled using the von-Bertalanffy sigmoidal equation as:

$$\Delta\Psi_b(G) = d[1 - \exp(-e\ SOHTI)]^f \qquad (6)$$

where d is the asymptote and e and f are empirical parameters, with values of 1.81, 5.91×10^{-5}, and 0.452. Equation 6 accounted for 79% of the variance in $\Delta\Psi_b(G)$.

Discussion

Bloomberg *et al.* (2009) found that the RFS model (Equation 2) provided only a partial description of the upwards shift in seed base water potential ($\Delta\Psi_b(G)$) at supra-optimal temperatures. This was also observed with the buddleia data. $\Delta\Psi_b(G)$ was found to be dependent not only on temperature above T_d, but also on time to germination and on the water potential of the seed's environment.

$\Delta\Psi_b(G)$ was found to increase most rapidly at warm temperatures under moist conditions. Paradoxically, this means that seeds most strongly inhibited their germination when conditions for germination of seed and growth of seedlings were highly favourable. For example, germination of radiata pine seed was inhibited at temperatures above 20-22°C, yet young radiata pine seedlings can grow vigorously at daytime temperatures ≈ 30°C if acclimated to warm growing temperatures (Hellmers and Rook, 1975).

This paradoxical behaviour does make sense as a survival adaptation to avoid mass germination following summer rainfall. The risk of mass germination under these conditions is that evapotranspiration rates will be high, and that the seed-bed, although temporarily moist, will rapidly dry out causing death of newly germinated seedlings. The seed population therefore 'hedges its bets' by allowing a few seeds to rapidly germinate in response to favourable temperature and moisture; in the unlikely event that the seed-bed does stay moist, it is important that at least some seeds have germinated early. This is because to wait for safer germination conditions runs the risk that the site will already be fully occupied by established plants of other competing species, which are not so conservative in their germination behaviour. Alternatively, if the seed-bed rapidly dries out in an ensuing dry spell, the upwards adjustment of the seed base water potential towards zero means that the rest of the seed population will remain safely ungerminated.

To date, the use of 'supra-optimal hydrothermal time index' to predict germination decline has been tested for two species, radiata pine and buddleia. There seems to be considerable scope for research to investigate the value of the model to explain seed behaviour in other species above optimum germination temperature.

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