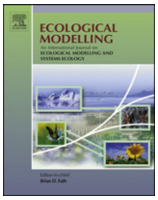
Ecological Modelling 221 (2010) 1267–1272

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Development of a hydrothermal time seed germination model which uses the Weibull distribution to describe base water potential

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ARTICLE INFO

Article history:
Received 9 October 2009
Received in revised form 12 January 2010
Accepted 31 January 2010
Available online 1 March 2010

Keywords:
Base water potential
Buddleia davidii
Butterfly bush
Hydrothermal time
Radiata pine
Weibull distribution

ABSTRACT

Seed germination has been modelled extensively using hydrothermal time (HTT) models, that predict time to germination as a function of the extent to which seedbed temperature, T, and water potential, Ψ, exceed the base temperature, T_b, and base water potential, Ψ_b, of each seed percentile, g. Within a seed population the variation in time to germination arises from variation in $\Psi_b(g)$ modelled by a normal distribution. We tested the assumption of normality in the distribution of $\Psi_b(g)$ by germinating seed of two unrelated species with non-dormant seed (*Buddleja davidii* (Franch.) and *Pinus radiata* D. Don) across a range of constant Ψ at sub-optimal T. When incorporated into a HTT model the Weibull distribution more accurately described both the right skewed distribution of $\Psi_b(g)$ and germination time course over sub-optimal T than the HTT based on the normal distribution, for both species. Given the flexibility of the Weibull distribution this model not only provides a useful method for predicting germination but also a means of determining the distribution of $\Psi_b(g)$.

1. Introduction

Seed germination is a complex physiological process largely determined in non-dormant seeds by temperature and water potential of the seedbed. These two factors have been successfully combined in hydrothermal time (HTT) models to describe the time course of germination for a wide range of plant species. The HTT model is a threshold model that simultaneously accounts for germination percentages and germination rates of a seed population (Gummerson, 1986; Bradford, 1995, 2002; Finch-Savage, 2004). At temperatures (T) between the base threshold temperature (T_b) and the optimum temperature (T_o), germination time is described as a function of the amount by which seedbed water potential (Ψ) and T exceed thresholds or base values (Ψ_b, T_b) below which germination will not occur. The distribution of germination time can be expressed mathematically as,

$$t_g = \frac{\theta_{HT}}{[(\Psi - \Psi_b(g))(T - T_b)]} \quad (1)$$

In this model, t_g is the time to germination for the gth percentile of the germination time distribution, and hydrothermal time (θ_{HT}), and the base temperature (T_b) are assumed constant for all seeds in the population. It is assumed that only the base water potential (Ψ_b) varies with g, so that the distribution of germination times within the population is determined by the distribution of $\Psi_b(g)$. Most previous research has assumed that the base water potential within the seed population follows a normal distribution, which can be modelled using the following equation,

$$\Psi_b(g) = \Psi_b(50) + \text{probit}(g)\sigma_{\Psi_b} \quad (2)$$

where $\Psi_b(50)$ is the 50th percentile of the base water potential distribution, probit (g) is the probit function that calculates the standard normal deviate (z) for a specified cumulative probability (= g) in a normally distributed population, and σ_{Ψ_b} is the standard deviation of Ψ_b values in the population. The HTT model is usually fitted to germination data by substituting the right hand side of Eq. (2) for $\Psi_b(g)$ in Eq. (1) and rearranging the resultant equation in terms of probit as,

$$\text{probit}(g) = \frac{\Psi - \{\theta_{HT}/[(T - T_b)t_g]\} - \Psi_b(50)}{\sigma_{\Psi_b}} \quad (3)$$

Despite the wide use of HTT models to simulate germination, little research has critically examined the assumption that $\Psi_b(g)$ within these models is normally distributed. An alternative to the normal distribution that can fit a range of distribution types is the Weibull distribution (Weibull, 1951). Since its development, the Weibull distribution has been widely used as a function in many diverse applications. It has commonly been used to describe wind speed variation (Deaves and Lines, 1997; Roney, 2007), and is important in extreme value theory and weather forecasting.

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doi:10.1016/j.ecolmodel.2010.01.017

However, the most common use of the distribution is in life data analysis, an application that involves modelling the time to failure of components in mechanical (Dodson, 2006) and biological systems (Watt et al., 2007).

Using the Weibull distribution, $\Psi_b(g)$ in the sub-optimal temperature range can be modelled by the percent point function (or inverse of the cumulative distribution function), given as,

$$\Psi_b(g) = \mu + \alpha(-\ln(1-g))^{1/\gamma} \tag{4}$$

where the parameter μ describes the location of the lowest value of $\Psi_b(g)$ (i.e. $\Psi_b(0)$), γ is the shape parameter, and α is the scale parameter. Substitution of this equation for $\Psi_b(g)$ into the sub-optimal HTT model, rearranged in terms of germination percentile yields,

$$g = 1 - \left\{ exp\left[-\left\{ \frac{[(\Psi - \{\theta_{\mathrm{HT}}/[(T - T_b)t_g]\} - \mu)]}{\alpha} \right\}^{\gamma} \right] \right\} \tag{5}$$

Using germination data collected from two unrelated species over a range of constant Ψ and sub-optimal T we compare the utility of the normal and Weibull distribution at estimating $\Psi_b(g)$. The accuracy of their respective HTT models in predicting germination percentage across the sub-optimal temperature range is also examined.

2. Materials and methods

2.1. Species used

In this study *Buddleja davidii* Franch. and *Pinus radiata* D. Don. seeds were used as they do not exhibit dormancy and previous germination of these seeds at 0 MPa has been shown to display clear sub- and supra-optimal ranges of *T* (Miller, 1984; Bloomberg et al., 2009). *P. radiata* is a fast growing tree, originating from Monterey, California, that has been widely planted as a plantation species throughout the Southern Hemisphere. *B. davidii* is a shrub originating from subtropical regions of China, that has become highly invasive in many countries over the last century (Tallent-Halsell and Watt, 2009).

2.2. Seed germination

Germination data for *P. radiata* was obtained from the experiment fully described in Bloomberg et al. (2009). Briefly seed from a commercial seedlot was germinated in incubators across a factorial combination of four sub-optimal (Bloomberg et al., 2009) temperatures (12.5, 15, 17.5, 20 °C) and five water potentials (0, −0.3, −0.6, −0.9, −1.2 MPa). For each combination of water potential and temperature there were four replicates of 25 seeds.

Seed germination of *B. davidii* was recorded over a factorial combination of three constant sub-optimal temperatures (10, 17, 25 °C) and seven constant water potentials (0, −0.1, −0.2, −0.3, −0.4, −0.5, −0.6 MPa). For each combination of water potential and temperature there were three replicates, of 50 seeds each. Seeds were germinated on a 85 mm Petri dish with a single filter paper. The filter paper was suspended 3–4 mm off the base of the dish by wire mesh. Following Hardegree and Emmerich (1990) the filter paper was immersed in a solution of known osmotic potential, at a solution to filter paper weight ratio exceeding 15, for at least 48 h prior to use. Five millilitres of freshly prepared osmotic solution was poured into each dish. Although the centre of the filter paper on which the seeds were placed did not contact this solution, the solution contact with the downwards-turned outside edge of the filter paper ensured diffusion of solution to the seeds. As this reservoir of osmotic solution was regularly exchanged it was used to maintain the filter paper at a constant water potential over the course of the experiment. Dishes were sealed using adhesive tape to reduce evaporation and the minimal solution losses that occurred were replaced with fresh solution on a daily basis. Dishes were placed into constant temperature chambers. Temperatures within the chamber were monitored, and actual mean recorded temperatures are used for the analysis in this paper.

Water potentials were established using appropriate strength of polyethylene glycol 6000 (PEG 6000) solutions made up according to Hardegree and Emmerich (1990). The water potentials of solutions in all dishes with water potential less than zero were measured twice every week using a vapour pressure osmometer (Model 5500; Wescor Inc., Logan, UT, USA). Immediately after these measurements, reservoir solutions were exchanged with fresh solutions, to mitigate the decline in water potential that occurred with time. Average recorded measurements of water potential for each temperature and water potential combination were used in all reported models. Seeds were considered to be germinated when the radicle protruded more than 2 mm from the seed coat. Germination was recorded at least once per day and seeds that had germinated were removed.

2.3. Data analysis

All analyses were undertaken using SAS (SAS-Institute-Inc., 2000). The HTT models, based on the normal (Eq. (3)) and Weibull distributions (Eq. (5)), were fitted to data from all combinations of Ψ and T using a non-linear model (PROC NLIN). The base temperatures, T_b, for both species were estimated prior to this fitting. Values for T_b were determined as the *x*-axis intercept obtained by fitting a linear regression of $1/t(50)$ against sub-optimal temperatures for seeds germinated at 0 MPa (for further details of method see Finch-Savage et al., 1998). All other parameters, described in Eqs. (3) and (5) were estimated by fitting the model to the data. Parameter values used for both models are shown in Table 1.

Using parameter values derived from these fitted models, a "virtual" base water potential was determined, from the time to germination, by rearranging Eq. (1), in terms of $\Psi_b(g)$ as;

$$\Psi_b(g) = \Psi - \left\{ \frac{\theta_{\mathrm{HT}}}{[(T - T_b)t_g]} \right\} \tag{6}$$

Table 1

Parameters for the hydrothermal time models, based on normal and Weibull distributions. Also shown are model statistics describing the coefficient of determination (R^2) and root-mean square error (RMSE).

	Model parameters							Model statistics	
	T_b (°C)	$\Psi_b(50)$ (MPa)	σ_{Ψ_b} (MPa)	θ_{HT} (MPa °C d)	μ (MPa)	γ	α	R^2	RMSE
Pinus radiata									
Normal	9.0	−1.42	0.45	164.9	–	–	–	0.964	0.052
Weibull	9.0	–	–	162.9	−2.23	1.79	0.94	0.977	0.042
Buddleja davidii									
Normal	6.1	−1.12	0.33	104.5	–	–	–	0.891	0.096
Weibull	6.1	–	–	101.6	−1.64	1.85	0.61	0.903	0.091