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Estimation of thermal time model parameters for seed germination in 15 species: the importance of distribution function

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Abstract

Thermal time models have been widely applied to predict temperature requirements for seed germination. Generally, a log-normal distribution for thermal time [$\theta_{T(g)}$] is used in such models at suboptimal temperatures to examine the variation in time to germination arising from variation in $\theta_{T(g)}$ within a seed population. Recently, additional distribution functions have been used in thermal time models to predict seed germination dynamics. However, the most suitable kind of the distribution function to use in thermal time models, especially at suboptimal temperatures, has not been determined. Five distributions (log-normal, Gumbel, logistic, Weibull and log-logistic) were used in thermal time models over a range of temperatures to fit the germination data for 15 species. The results showed that a more flexible model with the log-logistic distribution, rather than the log-normal distribution, provided the best explanation of $\theta_{T(g)}$ variation in 13 species at suboptimal temperatures. Thus, at least at suboptimal temperatures, the log-logistic distribution is an appropriate candidate among the five distributions used in this study. Therefore, the distribution of parameters [$\theta_{T(g)}$] should be considered when using thermal time models to prevent large deviations; furthermore, an appropriate equation should be selected before using such a model to make predictions.

Introduction

Seed germination is a pivotal stage in the life cycle of plants (Walck et al., 2011; Baskin and Baskin, 2014). Temperature is a critical environmental factor regulating seed dormancy break, germination and subsequent seedling establishment (Bradford, 2002; Baskin and Baskin, 2014). Three 'cardinal temperatures', the minimum, optimum and maximum temperatures, are used to characterize seed germination responses to temperature. The minimum (or base, T_b) and maximum (or ceiling, T_c) temperatures are below and above those at which germination will occur, respectively, while germination is most rapid at the optimum temperature (T_o) (Alvarado and Bradford, 2002; Bradford, 2002; Bewley et al., 2013; Dürr et al., 2015). Thus, the knowledge of seed germination responses to temperature is required not only for understanding the ecological adaptation of species but also for formulating effective strategies for restoration (Fenner et al., 2005; Baskin and Baskin, 2014).

Many studies have found that the germination rate (GR_g, the reciprocal of time to a given germination fraction, $1/t_g$) is linearly related to temperature (Gummerson, 1986; Bradford, 2002; Hardegree, 2006; Hu et al., 2015; Felipe Daibes and Cardoso, 2018; Carhuancho León et al., 2020; Zhang et al., 2020). Thus, the thermal time model has been developed to evaluate the effect of temperature on progress towards germination (Covell et al., 1986; Ellis et al., 1986; Gummerson, 1986; Allen et al., 2000; Bradford, 2002). In this model, several parameters were fitted and used to quantify temperature requirements for seed germination, such as the cardinal temperatures (T_b, T_o and T_c) and thermal time (θ_T, the thermal time required to reach the germination requirement of individual seeds in the population) (Bradford, 2002; Hu et al., 2015; Saberali and Shirmohamadi-Aliakbarkhani, 2020; Zhang et al., 2020). Although thermal time models are empirical, rather than mechanistic, they provide biologically meaningful parameters. The intrinsic germination rate, reaction to temperature and uniformity of germination correspond to $\theta_{T(g)}$, T_b and $\sigma_{\theta T}$, respectively, at suboptimal temperatures (Bradford, 2002).

Generally, implicit in thermal time models are the assumptions that the minimum temperature, T_b, is constant for all fractions of the seed population and that thermal time, $\theta_{T(g)}$, follows a log-normal distribution with a mean [$\ln(\theta_{T(50)})$] and standard deviation [$\sigma_{\ln(\theta T)}$] at suboptimal temperatures (Covell et al., 1986; Cheng and Bradford, 1999; Hu et al., 2013, 2015; Rong et al., 2015; Daibes and Cardoso, 2018; Ostadian Bidgoly et al., 2018; Zhang et al., 2020). The log-normal (or normal) distribution was originally selected for thermal time modelling on the basis of its adequate fit to data from original studies and its mathematical convenience, rather than for any theoretical reasons (Mesgaran et al., 2013). However, $\theta_{T(g)}$ is defined explicitly as an extreme value, at or below which no germination occurs. Thus, thermal time may be expected to follow skewed frequency patterns, and some generalized extreme-value models, such as the Gumbel and Weibull distributions, may be satisfied in describing the pattern of $\theta_{T(g)}$ variation (Bradford, 2002; Watt et al., 2010). Sakanoue (2010) showed that the exponential distribution with a lag phase provided concise and practical estimates of germination rates in the determination of the base temperature and thermal time required for seed germination of nine herb species. Rosbakh et al. (2015) reported that the Weibull distribution provided a consistently close fit to the data when used in thermal time models to calculate the cardinal temperatures of 49 species. In addition, Peng et al. (2018) combined the logistic function and a thermal time model to estimate the base temperature and the thermal time for germination of two desert species in the Junggar Basin of China. Moreover, using the inverse normal distribution function (Cave et al., 2011) in thermal time models also has led to more accurate and non-biased estimates of cardinal temperatures and thermal time for seed germination.

Although many distribution functions have been used in thermal time models to describe the thermal requirements for seed germination (Covell et al., 1986; Sakanoue, 2010; Cave et al., 2011; Hu et al., 2015; Rosbakh et al., 2015; Peng et al., 2018; Zhang et al., 2020), a conclusion regarding the most suitable distribution function for fitting germination data in thermal time models based on a comparison of multiple distributions has not yet been reached, which may lead to biased parameter estimates. However, with the exception of a study on hydrothermal time models (Mesgaran et al., 2013) in which the log-logistic distribution consistently provided the best explanation of $\Psi_{b(g)}$ variation among eight distributions for three weed species, little is known about which kind of the distribution is most suitable when used in thermal time models, especially at suboptimal temperatures. In addition, it is also not clear whether the best distribution function differs among species, since the inconsistencies among previous studies may have been due to differences among species. Therefore, a systematic evaluation of the best distribution function to use in thermal time models is needed for estimating temperature or thermal time requirements for seed germination and predicting seed germination dynamics.

In our study, five distribution functions, including log-normal, Gumbel, logistic, Weibull and log-logistic, were explored to describe the variation in $\theta_{T(g)}$ at suboptimal temperatures for 15 common species, and the following questions were addressed: (1) Does distribution function selection lead to a biased estimation for parameters of the thermal time model? (2) If it is, which function provides the best estimation? (3) Does the best distribution function differ among species?

Materials and methods

Seed collection

Seeds of *Elymus dahuricus*, *Elymus nutans*, *Elymus sibiricus*, *Ephedra intermedia*, *Festuca sinensis*, *Hedysarum multijugum*, *Lepidium apetalum*, *Lolium multiflorum*, *Lolium perenne*, *Medicago sativa*, *Onobrychis viciifolia*, *Poa crymophila*, *Sorghum bicolor*, *Trifolium pratense* and *Trifolium repens* were used in this study, and they were provided by the Official Herbage and Turfgrass Seed Testing Centre, Lanzhou, Ministry of Agriculture and Rural Affairs, China. Seeds were stored dry in paper bags at 4°C until used in experiments in March 2017. On the one hand, these species are common herbages and weeds in China, and thus the conclusion based on these species is universal. On the other hand, species with a germination percentage of more than 80% were selected and used in the present study, which is helpful to estimate the thermal time model correctly and effectively and get a more accurate conclusion.

The initial seed germination percentage and the thousand-seed weight (TSW) of all tested species and water-impermeable seeds of *H. multijugum*, *M. sativa*, *O. viciifolia*, *T. pratense* and *T. repens* were determined before the experiments commenced (supplementary Table A1). The seed germination percentage and the TSW were determined according to the International Seed Testing Rules (the seed germination percentages of *E. dahuricus*, *E. nutans*, *E. sibiricus*, *F. sinensis*, *H. multijugum*, *L. apetalum* and *P. crymophila* were based on those for corresponding genera, while the seeds of *E. intermedia* were examined at 20°C according to the habitat conditions of the species, as this genus is not included in the International Seed Testing Rules) (ISTA, 2014). The percentage of water-impermeable seeds was determined by incubating seeds at 20°C for 14 d, after which the number of seeds remaining water-impermeable was determined (Hu et al., 2015). The initial seed germination percentage of all species was greater than 80%, and the water-impermeable percentage of the five species was less than 5%.

Effect of temperature on germination

Germination responses to temperature were tested for seeds of all species by incubation at six constant temperatures from 10 to 35°C, depending on the species, at 5°C intervals. Seeds were exposed to a 12/12 h daily photoperiod (white fluorescent tubes, photo irradiance: 60 μmol m^{-2} s^{-1}, 400–700 nm). For each treatment, three replicates of 50 seeds were placed in 10-cm-diameter Petri dishes on two sheets of filter paper (Shuangquan, Hangzhou, China) moistened with 7 ml of distilled water. Seeds were monitored for germination every 8, 16 and 24 h, depending on the germination rate, for at least 28 d until no further germination occurred for three consecutive days; seedlings were removed at each counting. Seeds were counted as germinated when the radicle was visible (≥2 mm). All chambers used for temperature experiments were set to have the same light and humidity conditions. The temperature, light and humidity in each chamber were monitored carefully, and the position of Petri dishes inside each chamber was randomized every day. Thus, we assumed that temperature was the only environmental factor that varied between the chambers.

Distributions

In this study, five distribution functions, namely, the log-normal, Gumbel, logistic, Weibull and log-logistic functions, were used to fit the data and describe the variation in $\theta_{T(g)}$ at suboptimal temperatures [see Mesgaran et al. (2013) for more details on these distributions].

Log-normal distribution

At suboptimal temperatures, the log-normal distribution of the thermal time model is as follows:

$$\theta_{T(g)} = e^{\sigma \cdot \mathrm{probit}(g) + \mu} \quad (1)$$

$$\mathrm{probit}(g) = \frac{\ln\left((T - T_b) \cdot t_g\right) - \mu}{\sigma} \quad (2)$$

where $\theta_{T(g)}$ is the thermal time required to reach the germination requirements among individual seeds in the population at the suboptimal temperatures (with units of °C per day or hour); probit(g) is the probit transformation of cumulative germination percentage g, which linearizes the sigmoidal time course on a log time scale (Finney, 1971); $\mu(\ln(\theta_{T(50)}))$ and $\sigma(\sigma_{\ln\theta T})$ are the median thermal time and standard deviation of $\ln(\theta_T)$ requirements among individual seeds in the population, respectively; T is the germination temperature; T_b is the minimum temperature and t_g is the actual time to germination of fraction g. If $\theta_{T(g)}$ follows a log-normal distribution, then at $\ln(\theta_{T(g)}) = \mu$, the fraction of germinated seeds is 0.5.

Gumbel distribution

The inverse cumulative distribution for predicting θ_T and the cumulative distribution function for predicting the germination percentage (g) with the Gumbel distribution can be formulated into a thermal time model at suboptimal temperatures as follows:

$$\theta_{T(g)} = \mu - \sigma \cdot \left[\ln\left(\ln\left(\frac{1}{g}\right)\right)\right] \quad (3)$$

$$g = \exp\left[-\exp\left(-\left(\frac{((T - T_b) \cdot t_g - \mu)}{\sigma}\right)\right)\right] \quad (4)$$

where μ and σ are location and scale parameters, respectively. If $\theta_{T(g)}$ follows a Gumbel distribution, then at $\theta_{T(g)} = \mu$, the fraction of germinated seeds is ≈0.366 (with a log-normal distribution, the value is 0.5).

Logistic distribution

An applicability of the logistic distribution in thermal time models at suboptimal temperatures was evaluated as follows:

$$\theta_{T(g)} = \mu + \sigma \cdot \ln\left(\frac{g}{1 - g}\right) \quad (5)$$

$$g = \frac{1}{1 + \exp\left(-\left(\frac{((T - T_b) \cdot t_g - \mu)}{\sigma}\right)\right)} \quad (6)$$

Weibull distribution

The Weibull distribution can be incorporated into a thermal time model at suboptimal temperatures as follows:

$$\theta_{T(g)} = \mu + \sigma \cdot [-\ln(1 - g)]^{1/\lambda} \quad (7)$$

$$g = 1 - \left[\exp\left(-\left(\frac{((T - T_b) \cdot t_g - \mu)}{\sigma}\right)^{\lambda}\right)\right] \quad (8)$$

where λ is the shape parameter that determines the skewness and kurtosis of the distribution. Regardless of the shape value, if $\theta_{T(g)} - \mu = \sigma$, then the proportion of germinated seeds is ≈0.632.

Log-logistic distribution

For this distribution, the thermal time model at suboptimal temperatures becomes the following:

$$\theta_{T(g)} = \mu + \sigma \cdot \left(\frac{g}{1 - g}\right)^{1/\lambda} \quad (9)$$

$$g = \frac{1}{1 + \left(\frac{((T - T_b) \cdot t_g - \mu)}{\sigma}\right)^{-\lambda}} \quad (10)$$

Data analysis

All distributions, having been formulated into a thermal time model, were fitted to data using non-linear regression in SPSS 25.0 (SPSS Inc., Chicago, IL). The value of $\theta_{T(50)}$ can be obtained from regression (equations 1, 3, 5, 7 and 9) when $g = 50\%$ in all models (in a log-normal distribution, the value is e^{μ}). The model parameters, μ, σ, λ and T_b, were estimated by an iterative method until the residual sum of squares (RSS) (equation 11) of the regression (equations 2, 4, 6, 8 and 10) was minimized (Ellis et al., 1986). To identify the best model for estimating T_b and $\theta_{T(50)}$ at suboptimal temperatures, the adjusted coefficient of determination (Ra^2) (equation 12) and the corrected Akaike information criterion (AICc) (equation 13) were used (Sugiura, 1978; Hu et al., 2015; Parmoon et al., 2015).

$$\mathrm{RSS} = \sum (y_{obs} - y_{pre})^2 \quad (11)$$

$$Ra^2 = 1 - \frac{\sum (y_{obs} - y_{pre})^2/(n - k - 1)}{\sum (y_{obs} - \bar{y}_{obs})^2/(n - 1)} \quad (12)$$

$$\mathrm{AICc} = n \cdot \ln\left(\frac{\mathrm{RSS}}{n}\right) + 2k + \left(\frac{2k \cdot (k + 1)}{n - k - 1}\right) \quad (13)$$

$$\Delta_i = \mathrm{AICc} - \mathrm{AICc}_{min} \quad (14)$$

where y_{obs} refers to the observed values, y_{pre} refers to the predicted values, $\bar{y}_{obs}$ is the mean of the observed values, n is the number of observations, k is the number of model parameters, and AICc_{min} is the minimum calculated AICc among all distribution models.

The most accurate estimation model is the one with the lowest RSS value, highest Ra^2 value and lowest AICc value, when the AICc value is estimated according to Parmoon et al. (2015). If

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Table 1. Estimated parameters for five statistical distributions used in thermal time models for seed germination of 15 species at suboptimal temperatures

Species	Distributions	μ (°C h)	σ	λ	$\theta_{T(50)}$ (°C h)	T_b (°C)	RSS	Ra^2	AICc	Δ_i
E. dahuricus	Log-normal	1,408.687	0.614	–	1,408.687	8.114	0.276	0.784	−78.162	1.819
	Gumbel	995.482	711.770	–	1,256.355	9.412	0.271	0.787	−78.527	1.454
	Logistic	694.945	358.427	–	694.945	17.350	0.252	0.802	−79.981	0.000
	Weibull	599.466	1,084.159	0.846	1,302.447	7.952	0.236	0.803	−78.126	1.855
	Log-logistic	553.848	713.022	1.298	1,266.870	7.964	0.226	0.811	−78.992	0.989
E. nutans	Log-normal	1,016.691	0.505	–	1,016.691	7.010	0.283	0.811	−116.026	0.482
	Gumbel	892.579	464.797	–	1,062.933	6.763	0.278	0.814	−116.508	0.000
	Logistic	1,103.549	318.014	–	1,103.549	6.648	0.302	0.798	−114.272	2.236
	Weibull	406.911	833.409	1.221	1,024.208	6.931	0.269	0.815	−114.622	1.886
	Log-logistic	212.717	816.618	2.376	1,029.335	6.847	0.275	0.808	−114.026	2.482
E. sibiricus	Log-normal	1,046.545	0.479	–	1,046.545	6.193	0.371	0.672	−103.400	4.783
	Gumbel	878.775	428.111	–	1,035.683	6.130	0.380	0.664	−102.777	5.406
	Logistic	1,053.754	333.758	–	1,053.754	6.118	0.430	0.620	−99.563	8.620
	Weibull	723.790	413.149	0.416	894.979	6.501	0.289	0.733	−107.080	1.103
	Log-logistic	641.683	290.490	1.017	932.173	6.468	0.277	0.744	−108.183	0.000
E. intermedia	Log-normal	1,701.016	0.848	–	1,690.996	8.205	0.170	0.777	−123.690	1.683
	Gumbel	1,459.247	1,217.747	–	1,905.567	7.242	0.198	0.740	−119.726	5.647
	Logistic	2,004.248	845.755	–	2,004.248	7.026	0.237	0.689	−115.052	10.321
	Weibull	890.252	2,436.009	0.378	1,814.061	7.347	0.179	0.754	−119.535	5.838
	Log-logistic	747.529	1,017.044	0.665	1,764.573	7.643	0.143	0.803	−125.373	0.000
F. sinensis	Log-normal	2,218.925	0.704	–	2,218.925	7.037	0.308	0.880	−229.749	0.000
	Gumbel	1,727.772	1,219.584	–	2,174.765	7.319	0.329	0.872	−226.649	3.100
	Logistic	2,172.606	841.546	–	2,172.606	7.698	0.392	0.847	−218.414	11.335
	Weibull	560.881	2,177.001	1.187	2,159.557	7.186	0.313	0.875	−226.598	3.151
	Log-logistic	214.070	1,917.733	2.108	2,131.803	7.149	0.297	0.881	−229.064	0.685
H. multijugum	Log-normal	774.941	0.439	–	812.420	8.336	0.069	0.930	−72.544	2.930
	Gumbel	645.145	275.489	–	746.115	8.439	0.067	0.932	−72.985	2.489
	Logistic	707.119	201.023	–	707.119	8.888	0.090	0.909	−68.558	6.916
	Weibull	488.555	406.026	0.998	769.784	8.090	0.058	0.935	−71.330	4.144
	Log-logistic	476.653	278.487	1.557	755.140	8.076	0.044	0.951	−75.474	0.000
L. apetalum	Log-normal	368.153	0.666	–	368.153	11.412	0.164	0.893	−136.923	2.094
	Gumbel	335.723	183.892	–	403.122	11.129	0.214	0.860	−129.472	9.545
	Logistic	424.930	156.215	–	424.930	10.858	0.235	0.847	−126.850	12.167
	Weibull	214.001	253.193	0.983	388.392	11.178	0.149	0.899	−136.869	2.148
	Log-logistic	127.273	262.121	2.242	389.394	11.195	0.138	0.906	−139.017	0.000
L. multiflorum	Log-normal	724.519	0.637	–	724.519	3.672	0.233	0.916	−211.533	7.012
	Gumbel	566.398	333.002	–	688.448	4.112	0.233	0.916	−211.533	7.012
	Logistic	704.200	243.220	–	704.200	4.131	0.290	0.896	−202.341	16.204
	Weibull	279.868	539.697	1.102	666.866	4.105	0.219	0.919	−211.686	6.859
	Log-logistic	157.484	500.745	2.236	658.229	4.185	0.186	0.931	−218.545	0.000
L. perenne	Log-normal	2,246.793	0.745	–	2,246.793	7.083	0.301	0.908	−298.699	2.929
	Gumbel	1,743.622	1,363.858	–	2,243.494	7.226	0.364	0.889	−287.676	13.952
	Logistic	2,298.378	994.028	–	2,298.378	7.389	0.471	0.856	−272.729	28.899

(*Continued*)

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Table 1. (*Continued.*)

Species	Distributions	μ (°C h)	σ	λ	$\theta_{T(50)}$ (°C h)	T_b (°C)	RSS	Ra^2	AICc	Δ_i
	Weibull	652.114	2,152.797	1.005	2,147.043	7.237	0.302	0.906	−296.196	5.432
	Log-logistic	463.836	1,646.252	1.663	2,110.088	7.184	0.275	0.915	−301.628	0.000
M. sativa	Log-normal	632.074	0.529	–	632.074	−2.394	0.161	0.875	−118.988	3.854
	Gumbel	491.270	210.437	–	568.398	−0.065	0.138	0.893	−122.842	0.000
	Logistic	590.836	165.564	–	590.836	−0.425	0.149	0.884	−120.924	1.918
	Weibull	299.163	347.684	1.219	556.562	0.008	0.141	0.885	−119.447	3.395
	Log-logistic	86.337	464.022	3.453	550.359	0.330	0.129	0.895	−121.670	1.172
O. viciifolia	Log-normal	1,988.441	1.158	–	1,988.441	4.906	0.072	0.895	−159.972	24.313
	Gumbel	1,519.829	2,307.756	–	2,365.651	3.922	0.146	0.784	−140.178	44.107
	Logistic	2,594.499	1,863.565	–	2,594.499	3.433	0.180	0.738	−134.316	49.969
	Weibull	806.203	2,227.710	0.430	1,756.119	5.017	0.028	0.957	−183.678	0.607
	Log-logistic	612.447	1,166.889	0.799	1,779.336	5.052	0.027	0.959	−184.285	0.000
P. crymophila	Log-normal	2,355.432	0.655	–	2,355.432	6.851	0.280	0.875	−179.895	3.990
	Gumbel	1,784.435	1,256.246	–	2,244.865	7.261	0.315	0.859	−175.419	8.466
	Logistic	2,141.150	879.663	–	2,141.150	8.170	0.387	0.827	−167.597	16.288
	Weibull	902.543	2,006.594	0.920	2,249.779	6.753	0.253	0.883	−181.242	2.643
	Log-logistic	749.418	1,452.522	1.492	2,201.940	6.753	0.236	0.891	−183.885	0.000
S. bicolor	Log-normal	536.942	0.543	–	536.942	7.402	0.153	0.935	−126.430	0.864
	Gumbel	443.343	230.621	–	527.869	7.511	0.148	0.937	−127.294	0.000
	Logistic	536.664	163.260	–	536.664	7.671	0.167	0.929	−124.153	3.141
	Weibull	196.962	430.359	1.347	524.801	7.425	0.151	0.932	−123.958	3.336
	Log-logistic	−6.881	528.298	3.326	521.417	7.463	0.140	0.937	−125.925	1.369
T. pratense	Log-normal	558.393	0.528	–	599.684	6.317	0.292	0.873	−172.424	60.616
	Gumbel	458.524	163.003	–	585.525	6.642	0.173	0.925	−191.792	41.248
	Logistic	522.050	124.246	–	595.175	6.682	0.245	0.894	−178.917	54.123
	Weibull	435.812	118.693	0.487	547.016	6.533	0.114	0.949	−204.702	28.338
	Log-logistic	348.740	150.467	1.467	540.392	6.576	0.053	0.976	−233.040	0.000
T. repens	Log-normal	533.624	0.617	–	533.624	6.736	0.252	0.821	−131.623	0.000
	Gumbel	429.522	296.725	–	538.276	6.753	0.274	0.805	−128.236	3.387
	Logistic	543.848	221.692	–	543.848	6.808	0.310	0.779	−124.656	6.967
	Weibull	245.124	418.169	0.926	526.610	6.657	0.256	0.810	−127.500	4.123
	Log-logistic	146.894	380.107	1.861	527.001	6.664	0.261	0.807	−126.939	4.684

$\Delta_i < 10$, there is no significant difference between models, and the model with a higher AICc value is also suitable. If $\Delta_i > 10$, the model with a higher AICc value is not suitable and does not fit well. Therefore, to select the best model, appropriate AICc values were first determined according to the Δ_i value, and then, the values of RSS and Ra^2 were assessed.

Thermal time models include residuals, which were estimated from the difference between the virtual $\theta_{T(g)}$ and predicted $\theta_{T(g)}$ at suboptimal temperatures, and denoted RT. The residuals were plotted against fitted values to evaluate each distribution function visually for any systematic bias, and a quadratic polynomial was used to fit the residuals for better visualization of trends (Mesgaran et al., 2013).

Results

The parameter estimates of the 15 species obtained with the five distributions at suboptimal temperatures are summarized in Table 1. The log-logistic distribution provided the best fit to the $\theta_{T(g)}$ [or $\ln(\theta_{T(g)})$] data for 13 of the 15 species in this study (*E. dahuricus*, *E. sibiricus*, *E. intermedia*, *F. sinensis*, *H. multijugum*, *L. apetalum*, *L. multiflorum*, *L. perenne*, *M. sativa*, *O. viciifolia*, *P. crymophila*, *S. bicolor* and *T. pratense*). The log-normal and Weibull distributions provided the best fit for seeds of *T. repens* and *E. nutans*, respectively. On the contrary, the logistic and log-normal distributions provided the worst fit for 12 and 3 species, respectively (Table 1).

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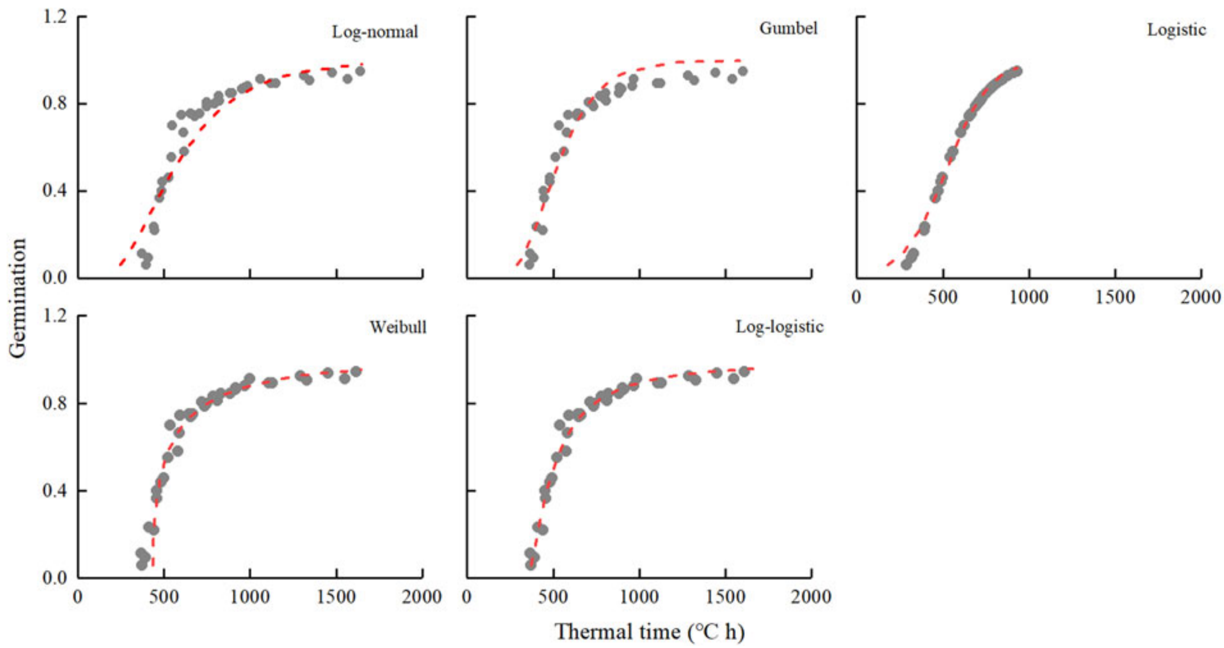

Fig. 1. Thermal time of *T. pratense* seeds predicted by thermal time models based on five distributions at suboptimal temperatures. Circles show the observed mean thermal times. The red dashed lines show the predicted thermal time, which was fitted by the thermal time model based on the five distributions.

Using *T. pratense* as an example, the log-logistic distribution resulted in the best fit, with the lowest RSS and AICc values and the highest Ra^2 value among the five distributions (0.053, −233.040 and 0.976, respectively) (Table 1). The log-normal distribution gave the poorest fit (the RSS, AICc and Ra^2 values were 0.292, −172.424 and 0.873, respectively), and the other three distributions (Gumbel, logistic and Weibull) performed only slightly better. The fits between seed germination and thermal time at suboptimal temperatures for the five distributions are shown in Fig. 1, which shows the best agreement between the predicted and observed values for the log-logistic distribution. All these results were further evaluated by inspecting residual plots (Fig. 2), which showed that using the log-normal, Gumbel or logistic distribution led to highly biased predictions of $\theta_{T(g)}$ residuals (RT) compared with those obtained with the log-logistic and Weibull distributions. Similarly, the log-logistic distribution gave the best fit for 12 species (Table 1; supplementary Appendixes B and C).

The Weibull and log-normal distributions were the most suitable distributions for *E. nutans* and *T. repens*, respectively, and the RSS, AICc and Ra^2 values were 0.269, −114.622 and 0.815 for *E. nutans*, respectively, and 0.252, −131.623 and 0.821 for *T. repens*, respectively (Table 1; supplementary Appendixes B and C). The logistic distribution provided the worst fit for these two species, with an apparent predicted thermal time–RT relationship; in other words, the outputs obtained with the logistic distribution were highly biased (supplementary Appendix C). Similarly, the logistic distribution provided the worst data fit for *E. sibiricus*, *E. intermedia*, *F. sinensis*, *H. multijugum*, *L. multiflorum*, *L. perenne*, *O. viciifolia*, *P. crymophila* and *S. bicolor*.

Discussion

Thermal time models, in a standard form (log-normal distribution) at suboptimal temperatures, provide several useful parameters of seed quality, which are related to the temperature tolerance (T_b), speed [$\theta_{T(50)}$] and uniformity ($\sigma_{\theta T}$) of germination (Bradford, 2002). The $\theta_{T(g)}$ [or $\ln(\theta_{T(g)})$] of the seed sample is commonly assumed to follow a log-normal (or normal) distribution (probit transformation) at suboptimal temperatures (Cheng and Bradford, 1999; Bradford, 2002). However, in the present study, the data of only one of the 15 tested species were the best fit by this distribution at suboptimal temperatures. These results are similar to those that Mesgaran et al. (2013) obtained with a hydrothermal time model, in which using the normal distribution resulted in the worst fit and led to biased predictions for three of four species. Thus, the log-normal (or normal) distribution, at least at suboptimal temperatures, is not necessarily the best distribution for thermal time [$\theta_{T(g)}$] [or ln ($\theta_{T(g)}$)] in thermal time models; indeed, it may result in biased predictions. However, the suitability of the log-normal distribution has been taken for granted in thermal time models in most studies (Cheng and Bradford, 1999; Bradford, 2002; Hu et al., 2013, 2015; Rong et al., 2015; Daibes and Cardoso, 2018; Ostadian Bidgoly et al., 2018; Zhang et al., 2020).

The log-logistic distribution (an asymmetrical model) consistently provided the best explanation of $\theta_{T(g)}$ and germination of all tested species except *E. nutans* and *T. repens*. Similar to the pattern observed for the parameter $\Psi_{b(g)}$ in hydrothermal time models (Mesgaran et al., 2013), our results indicate that $\theta_{T(g)}$ may often be right-skewed. In addition, we found that using symmetrical models (the logistic distributions) resulted in the least precise and least accurate data fits for all species, which further confirm that the distribution of $\theta_{T(g)}$ is asymmetrical. Notably, the Weibull distribution (a generalized extreme-value model) was satisfactory only for seeds of *E. nutans* in describing the pattern of $\theta_{T(g)}$ variation, which was contrary to the results from a study by Watt et al. (2010). All these results suggest that, at least at suboptimal temperatures, there will be a large deviation if the parameter distribution is not considered in the thermal time model. However, the standard form

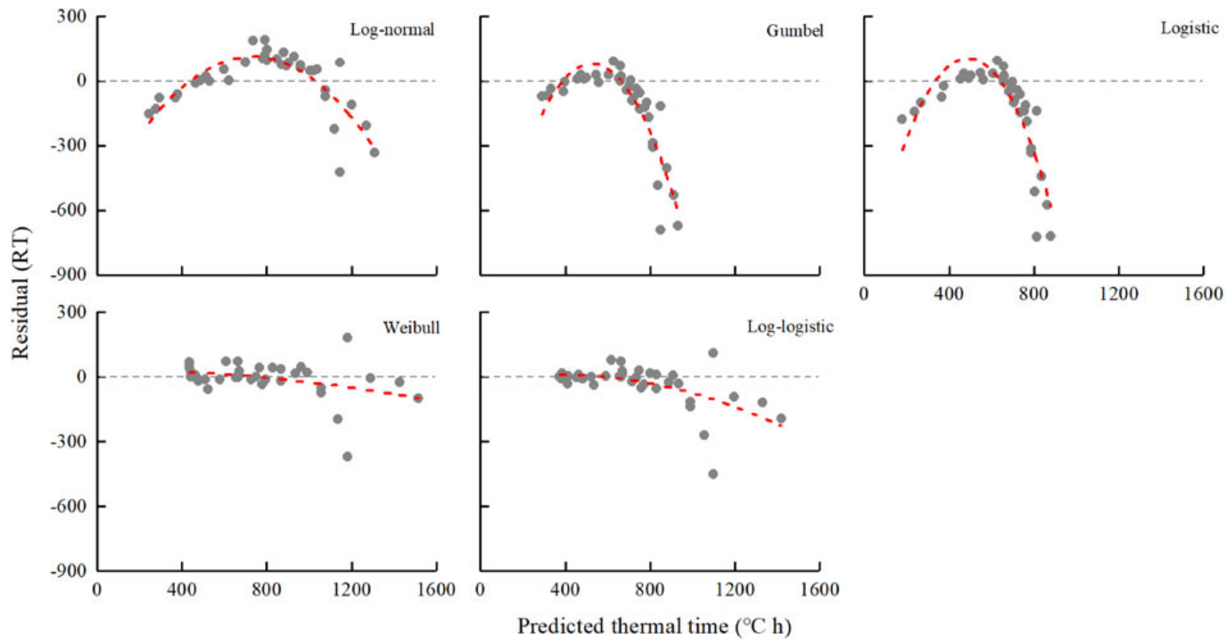

Fig. 2. Scatter plots of thermal time against residuals (RT) for five distributions used in thermal time models of *T. pratense* seeds at suboptimal temperatures. The red dashed lines are quadratic polynomials fitted to the residuals for better visualization of trends.

(the log-normal distribution) is used only for convenience. Compared with the Gumbel and logistic distributions, the log-logistic distribution is more flexible and can provide a more realistic estimate of $\theta_{T(0)}$ (Mesgaran et al., 2013). Therefore, the log-logistic distribution is an appropriate candidate among the five distributions used in this study.

It is worth noting that T_b, the minimum temperature, was more than 10°C for *L. apetalum* seeds when using all five distributions and, thus, was overestimated by all thermal time models, as seed germination was 28% for *L. apetalum* when incubated at 10°C. One possible reason for the overestimation is that the germination temperature is very close to T_b (10 *vs* 11°C), and a slight temperature fluctuation in the incubator may lead to a relatively high deviation in thermal unit, and consequently germination percentage and model fitting. Zhang et al. (2020) also found a deviation between predicted and observed T_b when the germination temperature was close to the T_b. Similarly, the logistic distribution overestimated the value of T_b for *E. dahuricus* seeds, which was two or more times greater than the values obtained with the other four distributions. This result further illustrates that the logistic distribution provided the worst fit among the five distributions used in our study. In addition, although the log-normal and Weibull distributions provided the best fit for seeds of *T. repens* and *E. nutans*, respectively, other distributions also explained the $\theta_{T(g)}$ variation of these species very well. These results imply that the appropriate distribution function used to describe the pattern of $\theta_{T(g)}$ variation in the thermal time model may not be unique for some species; similar results have been found in the study by Mesgaran et al. (2013). Moreover, whether the best distribution function differs among species remains to be further studied, since the results based on individual cases (2 species *vs* 13 species) are not sufficient. In any case, our results suggested that the distribution of parameters [$\theta_{T(g)}$] should be considered when using the thermal time model to prevent large deviations.

In conclusion, the assumption of a log-normal distribution, at least in some datasets, is clearly not appropriate and will lead to both a poor description and poor prediction of germination data when used in thermal time models. The log-logistic distribution, a more flexible distribution, can be used in thermal time models to describe the effect of temperature on seed germination. Future work should examine the reliability of our results through more empirical experiments.

Supplementary material. To view supplementary material for this article, please visit: https://doi.org/10.1017/S0960258521000040.

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Conflicts of interest. No conflicts of interest have been declared.

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