Mathematical Thermal Time Model to Explain Seed Germination

Atif Hassan Naim

Faculty of Agricultural and Environmental Sciences, University of Gadarif, Sudan

Introduction

Seed germination is an intricate physiological process which commences as the seed coat imbibes water and culminates in emergence of the radicle or hypocotyl. The rate of water uptake depends largely on the gradient of water potential between the non-dormant seed and the growth medium. A reduction in water potential of the surrounding growth medium will reduce the rate of water uptake by the seed because the gradient between them is less (Finch-Savage, 2004).

Germination is a critical stage in plant development and establishment, and is affected by many environmental and genetic factors. In classical methods of germination data analysis, statistics such as total, mean, variance of time to germination, quartiles, and percentiles are used to represent the process and assimilate final germination (Tucker and Wright, 1965; Nicholls and Hewdecker, 1968; Orchard,1977; Shafii and Price, 2001). Shafii and Price (2001) summarized the shortcomings of such germination indices into: (1) lack of information about the onset, speed and extent of germination, (2) ambiguity and inconclusiveness, (3) limiting distributional assumptions and therefore unable to describe rather than just represent the germination process. On the contrary to traditional methods of germination data analysis which include single-value indices, the growth models (i.e., empirical and mechanistic models offer an ideal description of germination, which is complete, concise, unambiguous, and amenable to statistical analysis (Brown and Mayer, 1988). The key advantage of growth models is that their equations apply to the entire seed population and lead to simultaneously prediction of germination rate and percentage (Allen, 2003). Moreover, physiologically relevant models rather than strictly empirical models will undoubtedly prove critical in related processes such as dormancy loss and seedling emergence(Benech-Arnold et al., 2000, Forcella et al., 2000)

A number of attempts have been made to apply empirical based models to describe germination attributes according to the effects of temperature or/and water potential (Brown and Mayer, 1988, Forcella,1988, Bradford *et al*., 1993, Ghorbani et al., 1999, Kebreab and Murdoch,1999 , Vleeshouwers and Bouwmeester,2001, Odabaş and Mut,2007, Watt et al.,2010). It is useful to construct an empirical model which has a physiological interpretation. But many of fitted curves do not have biological meaning, because the aim of building the empirical models is primarily to find a convenient means of describing events rather than explaining them (Brown and Mayer, 1988). Alternatively, mechanistic or methodology based models offer a better description of germination events and allow germination responses to environmental factors to be summarized in terms of quantitative parameters. These parameters can then be used to predict germination rate and final germination percentages at any levels of environmental regulators such as temperature and water potential. The thermal time and hydrothermal time models represent such mechanistic or physiological approaches (Meyer and Allen, 2009).

Temperature plays a critical role through affecting the ‘biological clock’ of many physiological processes, speeds up and slows down according to the sum of all biochemical reactions involved. Hence, ‘the concept of ‘thermal time’ is considered as an acceptable proxy for the more complex (biological timing) ’ (Allen, 2003). At suboptimal temperatures, germination rate, the reciprocal time to germination, often increases linearly with germination temperature (Bierhuizen and Wagenvoort, 1974), although the relationship may be nonlinear in certain cases (Marshall and Squire, 1996). Basic thermal time model aren’t applicable at temperature above the optimum temperature, therefore many research has been undertaken either considering an empirical model () or make some amendments to accommodate the variation in thermal time for super optimal temperatures (Rowsw and Finch-Savage, Alvarado and Bradford,2002). In case of a linear relationship, germination response to suboptimal temperature can often be described by a thermal time model, which assumes that to germinate, a seed requires accumulation of a certain thermal time or heat sum, [θ_T], above a minimum base temperature, [T_b], under which the germination rate is theoretically zero (Bierhuizen and Wagenvoort, 1974: Garcia-Huidobro et al., 1982; Bradford, 1995, Kebreab and Murdoch,1999 ,Yeh and Atherton, 2000, Alvarado and Bradford, 2002). Mathamtically the thermal time can be expressed according to the Equation:

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

Where $\theta_{T(g)}$ is the thermal time for a certain germination percentile, Tb is the base temperature and tg is the time to germination to reach the germination percentile(g).

As germination rate is defined as the reciprocal of germination time (tg) equation (1) can be rearranged as follows:

$$GR= 1/tg= (T-Tb)/\ \theta_{T(g)} \quad (2)$$

The assumptions of thermal time are: (1) base temperature is considered to be constant and is a seed lot and probably species characteristics (Ellis and Butcher, 1988, Kebreab and Murdoch,1999) while thermal time varies within the seed lot and differ between germination percentile (Garcia-Huidobro et al., 1982; Washitani and Takenaka, 1984, Dahal et al., 1990). Many researchers found that the thermal time is normally or log-normally distributed (Covell et al., 1986; Ellis et al., 1986, Alvarado and Bradford, 2002). Accordingly, the germination time (tg) can be normalized in terms of thermal time by using probit analysis and by multiplying the germination time (tg) by (T-Tb) and the probit equation will be as follows:

$\text{probit}(g) = K_T + (\theta_{T(g)} / \sigma_{\theta T})$ (3)

where Kt is constant and $\sigma_{\theta T}$ is the standard deviation of the frequency of distribution of thermal time in the population. According to the probit concept, probit (50%) is zero when expressed in normal deviates, therefore by substituiting probit (50%) with zero in equation (2) it follows that $K_T = -(\theta_{T(50)} / \sigma_{\theta T})$ where $\theta_{T(50)}$ is called the median thermal time to germination, that is the 50th percentile. By substituting $\theta_{T(g)}$ from equation

$\text{probit}(g) = [(T-T_b)t_g - \theta_{T(50)})] / \sigma_{\theta T}$ (4)

These equation represent the cumulative normal distribution function and analogues to the equation

$Z = X-U/\sigma$ (5)

Using the thermal model equation (4), one may describe the cumulative germination over time at different temperatures and predict the germination percentage by knowing three parameters, Tb, $\theta_{T(50)}$ and $\sigma_{\theta T}$.

Despite the wide use of the thermal time and hydrothermal time models to simulate germination of many species, little research has critically examined their assumptions. Many researchers found that the basic hydrothermal model aren't applicable at certain cases . Kebreab and Murdoch (1990) clearly stated that two crucial assumption of the hydrothermal time appear to be incorrect in *Orobanche aegyptiaca, firstly base temperature is not constant and interact with water potential.* Some researchers found the same trend in different plant species (Fyfield and Gregory, 1989, El-Sharkawi and Springuel, 1977, Gummerson, 1986, Akeson et al., Williams and Shaykewich, 1971) . Secondly , although base water potential values found to be normally distributed, the median water potential varied systematically with temperature and declared that seeds are capable to germinate at higher level of water stress at optimal temperatures. Allen (2003) reviewed that basic hydrothermal models aren't applicable at temperatures above the optimum where germination is progressively inhibited as addressed by Rowse and Finch-Savage (). Alvarado and Bradford (2002) and Rowse and Finch-Savage showed that seeds incubated at the supra-optimal also showed an upward shift in base water potentials. Shifts in base water potential might be explained by sensitivity to decresing water potential between species (Allen et al., 2000a), control of germination via abscisic acid (ABA) (Toorop et al.,2000) and weaking of tissues that form a barrier to radicle emergence (Welbaum eta al., 1998).

References

Bradford, K.J., Dahal, P., Ni, B-R. (1993). Quantitative models describing germination responses to temperature, water potential, and growth regulators, pp. 239-248 in Côme, D; Corbineau,F.(Eds). *Basic and aplied aspects of seed biology Proceedings,Fourth International Workshops on Seeds*. Paris: Association pour la Formation Professionelle de l'Interprofession Semences.

Brown R.F. and Mayer, D.G. (1988). Representing cumulative germination.2.the use of the Weibull Function and other empirically derived curves. *Annals of Botany* **61**, 127-138.

Forcella,F., Benech-Arnold, R.L., Sanchez, R.A. and Ghersa, C.M. (2000). Seed dormancy in red rice .X11.population –based analysis of dry –afterripening with a hydrotime model. *Seed Science Research* **17**, 253-271.

Vleeshouwers, L.M. and Bouwmeester, H. J. (2000) A simulation model for seasonal change in dormancy and germination of seeds. *Seed Science Research* **11**, 135-148.

Odabaş, M.S. and Mut, Z. (2007). Modeling the effect of temperature on percentage and duration of seed germination in grain legumes and cereals. American Journal of plant physiology **2(5)**, 303-310.

Meyer, S. E. and Allen, P.S. (2009). Predicting seed dormancy loss and germination timing for Bromus tectorum in a semi-arid environment using hydrothermal time models. *Seed Science Research* **19**, 225-239.

Watt, M.S., Xu V., Bloomberg M. (2010). Development of a hydrothermal time seed germination model which uses the weibull distribution to describe base water potential*. Ecological Modelling* **221**, 1267-1272.

Finch-Savage, W.E.(2004). The use of population-based threshold models to describe and predict the effects of seedbed environment on germination and seedling emergence of crops,pp.52-95 in Benech-Arnold, R.L. and Sànchez,A.(Eds) *Handbook of seed physiology, application to agriculture*. Binghamton, New York, Food Products Press and the Haworth reference press.

Ghorbani, R., Seel,W., Leifert, C. (1999). Effects of environmental factors on germination and emergence of *Amaranthus retroflexus*. *Weed Science* **47**,505-510.

Shafii, B. and Price, W.J. (2001). Estimation of cardinal temperatures in germination data analysis. Journal of Agricultural, biological and environmental statistics **6**, 356-366.

Garcia-Huidobro , J., Monteith J.L. and Squire,G.R. (1982). Time, temperature and germination rate of pearl millet (*Pennisetum typhoides* S. &H.). 1. Constanat temperature. *Journal of experimental botany* **33**,288-296.

Washitani, I. and Takenaka, A. (1984). Germination responses of a non-dormant seed population of *Amaranthus patulus* Bertol. to constant temperatures in the sub-optimal range. Plant cell environment **7**,353-358