Weed Science, 50:248–260. 2002

Applications of hydrothermal time to quantifying and modeling seed germination and dormancy

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Knowledge and prediction of seasonal weed seedling emergence patterns is useful in weed management programs. Seed dormancy is a major factor influencing the timing of seedling emergence, and once dormancy is broken, environmental conditions determine the rate of germination and seedling emergence. Seed dormancy is a population-based phenomenon, because individual seeds are independently sensing their environment and responding physiologically to the signals they perceive. Mathematical models based on characterizing the variation that occurs in germination times among individual seeds in a population can describe and quantify environmental and after-ripening effects on seed dormancy. In particular, the hydrothermal time model can describe and quantify the effects of temperature and water potential on seed germination. This model states that the time to germination of a given seed fraction is inversely proportional to the amount by which a given germination factor (e.g., temperature or water potential) exceeds a threshold level for that factor. The hydrothermal time model provides a robust method for understanding how environmental factors interact to result in the germination phenotype (i.e., germination pattern over time) of a seed population. In addition, other factors that influence seed dormancy and germination act by causing the water potential thresholds of the seed population to shift to higher or lower values. This relatively simple model can describe and quantify the germination behavior of seeds across a wide array of environmental conditions and dormancy states, and can be used as an input to more general models of seed germination and seedling emergence in the field.

Key words: Seedling emergence, population-based model, temperature, threshold, water potential.

Seed dormancy has been defined as "an internal condition of the seed that impedes its germination under otherwise adequate hydric, thermal and gaseous conditions" (Benech-Arnold et al. 2000). This ability of seeds to remain viable but quiescent allows them to persist in soil for months or even years until the environmental conditions, interacting with the seeds' physiological sensory mechanisms, trigger germination. The timing of germination is critical, as the likelihood of seedling survival is dependent upon the subsequent availability of adequate water, temperature, light and nutrients to support plant growth. Seed dormancy is a characteristic feature of many weed species, allowing them to persist as soil seed banks from which a fraction of seeds are available to germinate in response to changes in environmental conditions or cultivation (Fenner 2000). Weed management strategies often focus on seeds and seedlings, as this is when weeds are most easily controlled (Ghersa et al. 2000). However, modeling the composition of soil seed banks and their relative dormancy status and using this information to predict seedling emergence patterns for weed control decisions remains a difficult task (Benech-Arnold and Sánchez 1995; Forcella et al. 2000; Vleeshouwers and Bouwmeester 2001). Many factors contribute to the timing and success of weed emergence, but seed dormancy "is the most important of a series of components and processes that affect seedling emergence" (Forcella et al. 2000).

Seed dormancy is a very large topic and many excellent and comprehensive reviews are available (e.g., Baskin and Baskin 1998; Benech-Arnold et al. 2000; Hilhorst and Toorop 1997). This paper will not attempt to review this vast literature, but will instead focus only on some specific components of the phenomenon of seed dormancy. How do seeds integrate the signals from their environment to determine when to initiate germination and commit to seedling development? What physiological mechanisms underlie the changes in dormancy that occur seasonally and in response to specific environmental cues? How can variation in germination behavior among seeds and seed populations be quantified using physiologically and ecologically meaningful parameters? How can an understanding of these processes contribute to the development of predictive models for weed seed germination and seedling emergence? The hydrothermal time concept (Bradford 1995; Gummerson 1986) will be advocated as a unifying model to describe the patterns of potential germinability that occur as seed populations enter and leave environmentally induced dormant or inhibited states. The hydrothermal time model proposes that seed germination rates are proportional to the amount by which temperature (T) and water potential (ψ) exceed base or threshold values for these environmental factors. Hydrothermal time models have considerable potential for characterizing and quantifying the effects of the thermal and hydric environment on seed dormancy and subsequent germination and seedling emergence. The conceptual and mathematical basis of the hydrothermal time model will be described, some applications in characterizing seed dormancy and germination behavior will be examined, and directions for future development will be discussed.

In addition to the definition of dormancy given above, some further definitions are needed for clarity. Germination

will be defined in the physiological sense as the initiation of embryo growth and is completed by penetration of the embryo through any covering tissues. Thus, the time to germination is the time from a starting point (imbibition of the seed or the end of a dormancy-breaking treatment) until visible emergence of embryonic tissues from the seed. This is generally the "point of no return" where the seedling is committed to continue growing. Following recent authors (e.g., Benech-Arnold et al. 2000; Hilhorst and Toorop 1997), the condition or state of dormancy will be distinguished from whether germination is completed. Seeds buried in soil can undergo long-term cycles of dormancy release and imposition without completing germination (Karssen 1982). In many cases, a final trigger is required to stimulate germination of non-dormant seeds, such as exposure to light, fluctuating temperatures, or nitrate, while dormant seeds will not respond or will only respond partially to those same factors. However, it is often difficult to distinguish dormancy per se from lack of a required germination inducer or a non-permissive temperature. Thus, the term dormancy may sometimes be used here in a broader sense to indicate that constraints to germination are present, without specifying their underlying mechanisms.

Temperature, Dormancy and Germination

Temperature is the primary environmental signal regulating both dormancy and germination (Roberts 1988). Two distinct effects of temperature have been identified, the first acting on dormancy per se, and the second determining the rate of progress toward germination in non-dormant seeds. With respect to dormancy, seasonal changes in temperature are a major determinant of the loss of primary dormancy and of the cycling of secondary dormancy (Hilhorst 1998). Chilling of imbibed seeds breaks dormancy in many species, and the dry after-ripening periods required to break primary dormancy in many species are also temperature-dependent (Baskin and Baskin 1998). Once the chilling or after-ripening requirements are met, the seed is considered to be non-dormant and either begins to progress toward germination or is in a suspended state pending exposure to a remaining trigger (e.g., light, nitrate). A second role for temperature is to determine the rate of progress toward completion of germination once a non-dormant seed is stimulated to germinate. This can also be complex, as the temperature range permissive for germination widens as dormancy is released and narrows as dormancy is induced (e.g., Benech-Arnold et al. 2000; Karssen 1982; Vegis 1964).

Three "cardinal temperatures" generally characterize germination responses to temperature: the minimum, optimum and maximum. The minimum (or base, T_b) and maximum (or ceiling, T_c) are the temperatures below or above which germination will not occur, while the optimum (T_o) is the temperature at which germination is most rapid. If the time to germination of a specific fraction or percentage (g) of the seed population (t_g) is plotted as a function of temperature, broad U-shaped "germination characteristic" curves generally show a wide optimum range and sharp increases in time to germination near the minimum and maximum temperatures (see, e.g., Hilhorst 1998). However, if the germination rate (GR_g), or the inverse of time to germination for a given percentage of the seed population ($1/t_g$), is plotted versus

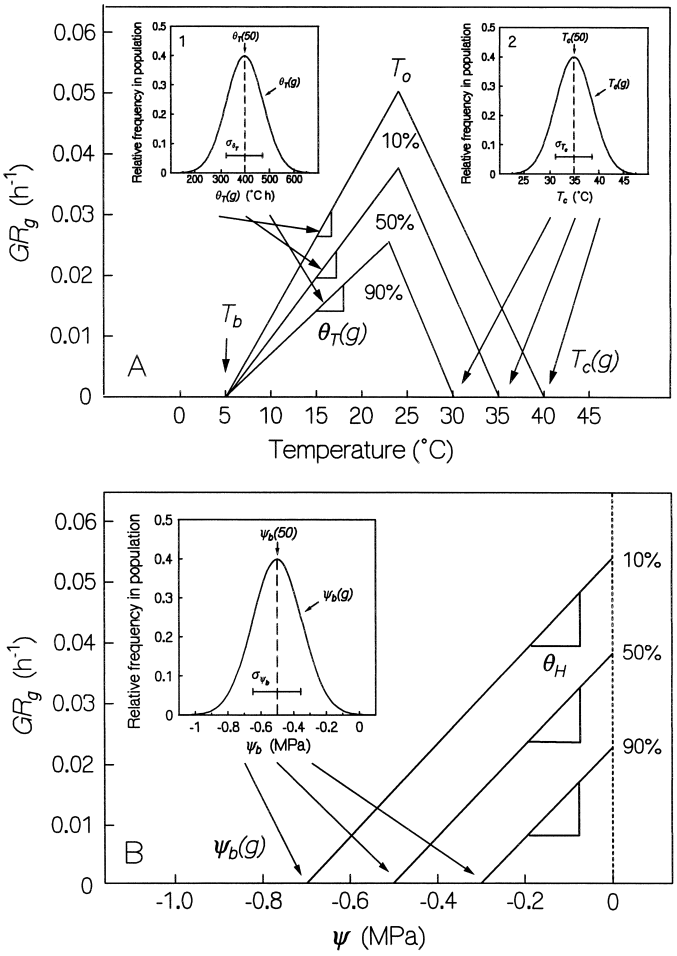

FIGURE 1. **A.** Relationship between germination rates and temperature. At sub-optimal temperatures, germination rates ($GR_g = 1/t_g$) for different fractions (percentages) of the seed population increase linearly with temperature above a common base temperature (T_b). The slopes of the lines are equal to the inverses of the thermal times to germination ($1/\theta_T(g)$), which vary among individual seeds in a normal distribution (inset 1; in some cases, $\theta_T(g)$ is normally distributed on a logarithmic time scale, not shown.) The maximum GR_g occurs at the optimum temperature (T_o), and above this temperature GR_g decreases linearly. The ceiling temperatures for germination ($T_c(g)$) vary among seed fractions in a normal distribution (inset 2). **B.** Relationship between germination rates and water potential (ψ). As ψ decreases, germination rates for different percentages decrease linearly with a common slope of $1/\theta_H$, intercepting the x-axis at different threshold or base water potential values ($\psi_b(g)$), which are normally distributed among seeds in the population (inset).

temperature, an inverted V-shaped curve is often observed (Figure 1A). That is, the germination rate for a given seed fraction (GR_g) is often a linear function of temperature between T_b and T_o (Bierhuizen and Wagenvoort 1974; Labouriau 1970). This can be formulated in a thermal time or "heat sums" model as:

$$\theta_T(g) = (T - T_b)t_g, \quad (1)$$

where $\theta_T(g)$ is the thermal time to germination of fraction or percentage g, T is the germination temperature and T_b is the base temperature. This equation states that for a given seed fraction g, the time to completion of germination is a constant at all sub-optimal temperatures when expressed on a thermal time basis, i.e., as the degrees in excess of T_b multiplied by the actual time to germination (e.g., hours or days). This is a threshold type of model, since T_b sets a

threshold temperature below which germination will not occur, and the rate of germination increases linearly above T_b with a slope of $1/\theta_T(g)$, as seen by rearranging Equation 1:

$$GR_g = 1/t_g = (T - T_b)/\theta_T(g). \quad (2)$$

In many cases, T_b is similar for all seeds in a given population, so the GR_g versus T plots for different fractions of the population have a common intercept on the T axis (Figure 1A; Covell et al. 1986; Kebreab and Murdoch 1999b). However, there are exceptions to this generalization (Fyfield and Gregory 1989; Labouriau and Osborn 1984), and more complex models may be needed to account for seed germination behavior near T_b in those cases (Kebreab and Murdoch 2000; Phelps and Finch-Savage 1997). The thermal time model can account for alternating or variable temperatures by summing the thermal times accumulated at each T (Ellis and Barrett 1994). Overall, the thermal time approach to modeling germination rates at sub-optimal temperatures has been quite successful (e.g., Covell et al. 1986; Dahal and Bradford 1994; Dahal et al. 1990; Garcia-Huidobro et al. 1982), and most models predicting seedling emergence in the field use a thermal time scale (degree-days) to normalize for temperature variation over time (e.g., Forcella 1998; Vleeshouwers and Kropff 2000).

The thermal time to germination must be defined for a specific germination fraction ($\theta_T(g)$), as the thermal time requirements vary among seeds in the population. Graphing the data as GR_g versus T plots (as in Figure 1A) is a clear way of presenting the data, and can be used to estimate T_b by regression of germination rate data for specific values of g (e.g., Steinmaus et al. 2000). However, that approach requires estimating times to specific germination percentages (e.g., 50%) by curve fitting or interpolation of the original time course data and then regressing those values versus T and extrapolating to $GR_g = 0$ to obtain T_b values, which is statistically less desirable due to the need to both estimate t_g values and extrapolate beyond the experimental data (Phelps and Finch-Savage 1997). Population-based methods (probit analysis) have been used to analyze germination time courses at different sub-optimal temperatures to estimate T_b and $\theta_T(g)$ values (Battaglia 1997; Covell et al. 1986; Dahal et al. 1990; Dahal and Bradford 1994; Ellis et al. 1986, 1987; Kebreab and Murdoch 1999b; Steinmaus et al. 2000). The probit analysis methods combine complete original germination time course data in a single regression to determine T_b and also provide estimates for the variation in $\theta_T(g)$ among seeds. The variation in $\theta_T(g)$ values among seeds in a population is often either normally (Ellis et al. 1987) or log-normally distributed (Covell et al. 1986; Dahal et al. 1990; Ellis and Butcher 1988), and can be characterized by the mean and standard deviation on the appropriate scale (Figure 1A, inset 1).

The model of Equation 2 predicts that GR_g would continue to increase (t_g would decrease) with increasing temperature, but this is not the case. Above T_o, germination rates decrease approximately linearly until T_c is reached and germination is prevented (Figure 1A). In some cases, there is a plateau in GR_g around T_o, rather that a sharp change in rate at T_o (Laboriau and Osburn 1984; Orozco-Segovia et al. 1996). In addition, it is often observed that different seed fractions have different T_c values; i.e., individual seeds in a population vary in their ceiling temperatures (Figure 1A; Covell et al. 1986; Ellis et al. 1987; Ellis and Butcher 1988), although exceptions to this have been reported (Garcia Huidobro et al. 1982; Orozco-Segovia et al. 1996). Germination time courses in the supra-optimal temperature range can be analyzed in a manner similar to Equations 1 and 2, but in this case the thermal time is held constant (θ_{Tc}) and the ceiling temperature varies among different seed fractions ($T_c(g)$) (Ellis et al. 1986, 1987; Ellis and Butcher 1988):

$$\theta_{T_c} = (T_c(g) - T)t_g \quad \text{or} \quad [3]$$

$$GR_g = 1/t_g = (T_c(g) - T)/\theta_{T_c} \quad [4]$$

In the supra-optimal range of T, these equations predict that GR_g will decrease as T increases, that the slope of this decrease ($1/\theta_{Tc}$) will be the same for all fractions in the population, and that these lines will intercept the temperature axis at different T_c values (Figure 1A). When applied to seed germination time courses at supra-optimal temperatures using probit analysis, this method allows the seed population to be characterized in terms of the distribution of $T_c(g)$ values (i.e., the mean and standard deviation) in the supra-optimal range (Figure 1A, inset 2).

While the increase in GR with T at sub-optimal temperatures can be understood as a consequence of thermodynamics, the reasons for the decrease in GR and inhibition of germination at supra-optimal T are less obvious. Thermal denaturation of proteins and effects on membranes have been proposed as candidate mechanisms, and certainly an absolute temperature ceiling is eventually reached where seed viability is affected. However, T_o values are often quite low, 20°C or less in some cases, and small increases in T above T_o would be unlikely to cause thermal denaturation of proteins. Changes in membrane composition could affect lipid transition temperatures or molecular mobility of membrane components, possibly accounting for changes in T_c that can occur during release or imposition of dormancy (Hilhorst 1998). After introducing the hydrotime concept, another explanation for seed germination behavior at supra-optimal temperatures will be proposed.

The Hydrotime Concept

Water is essential for seed germination, and its availability is a key factor affecting seed dormancy and germination timing. To account for the effects of reduced water potential on progress toward germination, Gummerson (1986) proposed the hydrotime concept. In analogy with thermal time or degree-days, the time to germination was related to the magnitude of the difference between the seed water potential (ψ) and a physiological base or threshold water potential for radicle emergence (ψ_b). ψ_b can be thought of as the lowest (most negative) ψ at which a given seed can complete germination, or as the highest (least negative) ψ that just prevents germination. The concept of a threshold or base ψ is obvious, as it is evident that as a seed is dried from the fully hydrated state, there must be some point at which it will no longer be able to initiate embryo growth and complete germination. In fact, Gummerson (1986) showed that if GR_g values were plotted as a function of ψ, the resulting curves were essentially linear and parallel, having a common slope and intercepting the ψ axis at different ψ_b values (Figure 1B). Since the slopes were the same, the total hydrotime

(MPa-hours or MPa-days) to radicle emergence was the same for all seeds in the population, but individual seeds varied in their threshold $\psi_b(g)$ at which radicle emergence would be prevented. In analogy to the thermal time model (Equation 1), the hydrotime model (Gummerson 1986; Bradford 1990) can be defined as:

$$\theta_H = (\psi - \psi_b(g))t_g \quad \text{or} \qquad [5]$$

$$GR_g = 1/t_g = (\psi - \psi_b(g))/\theta_H \qquad [6]$$

where θ_H is the hydrotime constant, ψ is the seed water potential, and $\psi_b(g)$ is the base or threshold water potential for a specific germination fraction g. [The term g here refers to a specific fraction or percentage of the total seed population; recalculating the fraction or percentage on the basis of only the number of germinated seeds under a given condition (e.g., Grundy et al. 2000) is inappropriate for this model.] If θ_H is a constant, then t_g must increase proportionately as ψ is reduced; that is, t_g is inversely related to the difference between the ψ of the seed and the ψ_b value of that seed (see Bradford 1997 for an illustration). A plot of GR_g versus ψ for different values of g gives straight lines with slopes of $1/\theta_H$ and intercepts on the ψ axis equal to the ψ_b for different fractions ($\psi_b(g)$) (Figure 1B). Experimentally, it has been found that in most cases the $\psi_b(g)$ values vary among seeds in the population in a normal or Gaussian distribution (e.g., Bradford 1990; Dahal and Bradford 1990; Gummerson 1986). The relative frequencies of $\psi_b(g)$ values among seeds in the population result in a normal bell curve, which can be defined by its mean ($\psi_b(50)$) and standard deviation (σ_{ψ_b}) (Figure 1B, inset). As for temperature, probit analysis methods for estimating the hydrotime parameters from original germination time course data at different water potentials have been developed (Bradford 1990, 1995; Dahal and Bradford 1990).

If θ_H is a constant, and ψ is determined by the seed's environment, then it is evident from Equations 5 and 6 that the primary physiological determinant of t_g is the distribution of $\psi_b(g)$ values within the seed population. The more ψ exceeds the ψ_b value of a given seed, the more rapid is its progress toward germination (t_g is small). If the difference between ψ and $\psi_b(g)$ for a particular seed is small, then t_g will be large and germination will be slow. The variation in $\psi_b(g)$ values in the population therefore results in the spread in germination times (Bradford 1997). The total hydrotime required for germination (θ_H), on the other hand, is the same for all seeds in the population.

Although this is straightforward mathematically, the population aspects of the hydrotime model are sometimes difficult to grasp. To clarify conceptually how the hydrotime model works, a hydraulic analogy is presented in Figure 2. Consider the height of water in a tank to represent the total water potential (ψ), and assume that an inlet pipe is connected to a mechanism (not shown) that regulates the flow to maintain this constant height of water in the tank. Outlet pipes placed into the wall of the tank at different heights represent the different threshold values ($\psi_b(g)$) for different seed fractions in the population (i.e., $\psi_b(10)$, $\psi_b(50)$, and $\psi_b(90)$ for the 10th, 50th and 90th germination percentiles in the population, respectively). The height of the water above a given outlet (i.e., $\psi - \psi_b(g)$) determines the rate at which water flows from the outlet; those outlets with the greatest height of water above them will have the most rapid

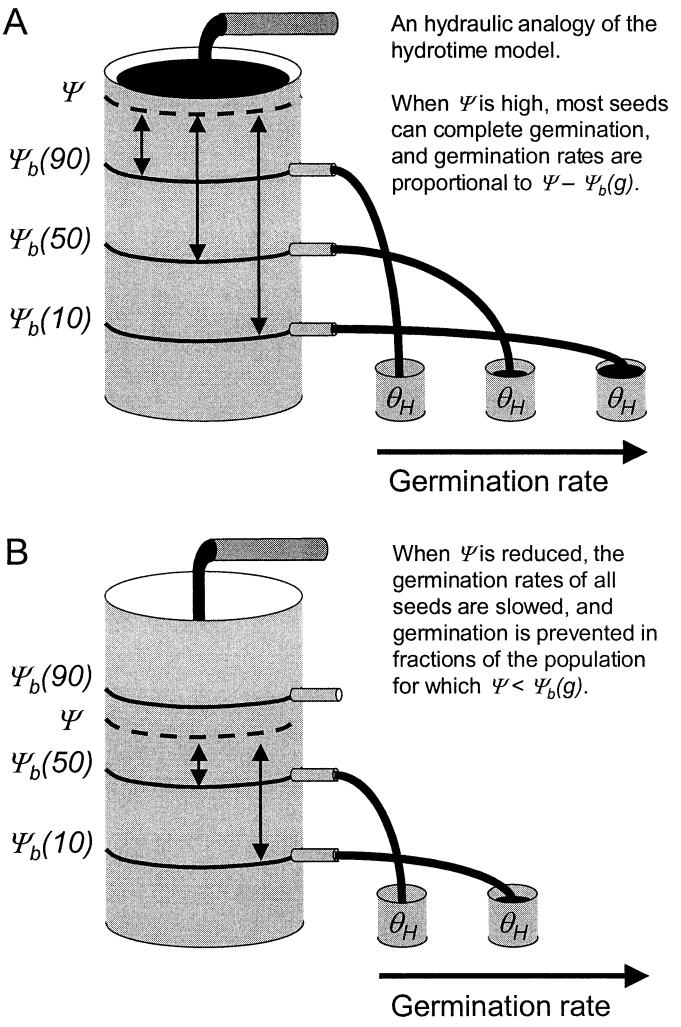

FIGURE 2. An hydraulic analogy of the hydrotime model of seed germination. **A.** The total ψ is represented by the height of water in the tank, while outlets at different heights on the tank indicate values for germination thresholds ($\psi_b(g)$). The water level in the tank is maintained by the flow from the inlet pipe, which is adjusted by a mechanism (not shown) to exactly match the flow from the outlets, so ψ is constant. The hydrotime required for germination is represented by cups of the same size that are filled by the flow from different outlets. The greater the height of water above an outlet, the faster the flow and the quicker the θ_H cup is filled (germination occurs). **B.** When the water in the tank is lowered to a new constant level (ψ is reduced), some outlets stop flowing when the water level is below the outlet (i.e., germination does not occur for that fraction). The rate of flow from other outlets is reduced in proportion to the lower water height, taking a longer time to fill the θ_H cup (complete germination). Note that the same effect on outflows shown in panel B would be attained if the outlets in panel A were raised by the same amount that the water level is lowered in panel B.

rates of flow. The hydrotime constant (θ_H) can be considered as a cup that is filled with the flow from each outlet (Figure 2A). Because these cups are all the same size, those fed by the outlets having the fastest flow will fill most rapidly (i.e., germinate first), while those fed by outlets with slower flow rates will take longer to fill (i.e., germinate later). Thus, while the hydrotime requirement for different seeds is the same (θ_H), the actual times to germination vary in relation to the distribution of $\psi_b(g)$ values (i.e., placement of the outlet pipes) relative to the height of water in the tank (ψ).

What is the effect of a reduction in ψ on seed germina-

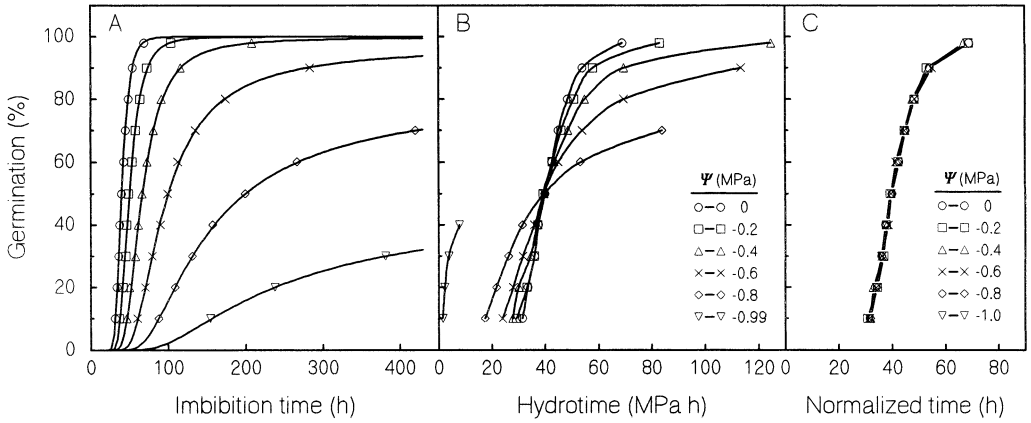

FIGURE 3. Simulation of germination time courses at different water potentials. **A.** A series of germination time courses are shown based upon the parameters θ_H = 40 MPa h, $\psi_b(50)$ = −1.0 MPa, σ_{ψ_b} = 0.2 MPa and imbibition at 0 (○), −0.2 (□), −0.4 (△), −0.6 (×), −0.8 (◇) and −1.0 (▽) MPa. **B.** To illustrate that a single hydrotime scale is not appropriate for plotting time courses at different ψ, the indicated data points from panel A were plotted on a hydrotime scale generated using the value of $\psi_b(50)$ = −1.0 MPa in the equation $\theta_H = (\psi - \psi_b(50))t_g$. All of the curves coincide at 50%, as this was the value used for $\psi_b(g)$, and at that percentage, the θ_H values will be the same at all ψ. At high ψ, the curves tend to coincide, but for fractions below and above 50%, the curves increasingly deviate as ψ decreases. This is evident particularly for −1.0 (–0.99 was used in the simulation, since at ψ = −1.0 MPa, no hydrotime would accumulate). Times to germination for fractions <50% are underestimated, while times for fractions above 50% are overestimated. **C.** The same points are plotted on a normalized time axis, i.e., normalized to the predicted time course in water based upon $t_g(0) = [1–(\psi/\psi_b(g))]\, t_g(\psi)$ (Equation 7). Since this is a simulation, all points coincide exactly, as this normalization equation is derived mathematically from the defining equation for the model (Equation 5).

tion? In the hydraulic analogy, this would be equivalent to lowering the height of the water in the tank. If the water level is lowered to below the 90% outlet, then obviously no water will flow from that outlet (Figure 2B); similarly, seeds having thresholds above the current ψ will never germinate. At the same time, the height of the water above all remaining outlets is reduced, slowing their flow rates and extending the time required to fill their respective hydrotime cups. Thus, there is an immediate and proportional response of all seed fractions to a change in ψ, depending upon their respective $\psi_b(g)$ values. In addition, the spread in germination times is determined by the width (or standard deviation, σ_{ψ_b}) of the $\psi_b(g)$ distribution (i.e., by the spread of outlet locations in the tank wall). Together, these features of the model automatically adjust both the timing and the final extent of germination of the seed population as ψ decreases (see Figure 3A for typical germination time courses).

Another important implication of Equations 5 and 6 is that as far as the timing of germination is concerned, it does not matter whether ψ is reduced or $\psi_b(g)$ is increased, since t_g is determined only by the difference between these two parameters. Thus, the germination time course of a seed population will be identical regardless of whether ψ is reduced by a specific amount, or all $\psi_b(g)$ values are increased by the same amount. In the hydraulic analogy (Figure 2), this means that lowering the height of water in the tank or raising the level of all of the outlets by the same amount will have the same effect. As will be discussed later, this is a key insight for understanding how dormancy is regulated in seed populations.

This hydraulic analogy is only a conceptual aid to understanding and should not be taken too far. However, it illustrates how the hydrotime model can simultaneously account for both the timing and the extent of germination of a given seed population in relation to its ψ environment. In addition, the hydrotime model provides parameters that are useful in characterizing the properties of seed populations. The θ_H value quantifies the inherent speed of germination, which can vary among species and physiological states. The median $\psi_b(g)$ value, or $\psi_b(50)$, is an indication of the average stress tolerance of the population. That is, a population with a high (less negative) $\psi_b(50)$ value will be slower to germinate and will be inhibited at higher ψ (less stress) than will a population with a lower $\psi_b(50)$ value. Finally, the standard deviation of $\psi_b(g)$ values, or σ_{ψ_b}, is a quantitative estimate of the uniformity or synchrony in germination timing among seeds in the population. These three parameters alone, θ_H, $\psi_b(50)$ and σ_{ψ_b}, are sufficient to predict complete germination time courses at any ψ at a constant T, including both rate and extent of germination in the seed population (Bradford 1995).

An additional feature of the hydrotime model is that germination time courses at different ψ can be normalized on a common time scale, just as biological processes at a range of sub-optimal temperatures can be normalized on a common thermal time scale using degree-days. However, the way that this is done for hydrotime is different from the application of thermal time scales. In the latter case, T_b is assumed to be essentially constant for all seed fractions and the accumulated thermal time varies among fractions (Equation 1), so thermal time is an appropriate time scale for normalizing germination time courses. The hydrotime to germination, however, is a constant (θ_H) (Equation 5) for all seed fractions, and it is the threshold values ($\psi_b(g)$) that vary among seeds. Thus, if germination percentages were plotted as a function of accumulated hydrotime, using the $\psi_b(g)$ value appropriate for each fraction as in Equation 5, this would simply result in a vertical row of points above the θ_H value. Nonetheless, some studies have plotted germination percentages as a function of accumulated hydrotime and found that germination time courses at different ψ coincided on this time scale in cumulative normal or skewed cumulative (e.g., Weibull) distributions (Finch-Savage et al. 1998; Grundy et al. 2000; Roman et al. 1999; Shrestha et al. 1999). In these studies, the $\psi_b(50)$ value was used in Equation 5 to calculate the accumulated hydrotime

for the 50th percentile, and then germination time courses at different ψ were plotted on this scale. This approach is inappropriate for the hydrotime model, as illustrated by the simulation in Figure 3. A set of germination time courses was generated for a seed population having values of θ_H = 40 MPa h, $\psi_b(50)$ = −1.0 MPa, and σ_{ψ_b} = 0.2 MPa and imbibed at 0, −0.2, −0.4, −0.6, −0.8, and −1.0 MPa (Figure 3A). These represent a characteristic family of germination time courses that result from the effect of decreasing ψ on both germination timing and extent (Bradford 1995; 1997). A hydrotime scale was calculated using the value of $\psi_b(50)$ = −1.0 MPa in Equation 5, and the data points for each decile of germination percentages from Figure 3A were plotted on this time scale (Figure 3B). Consistent with Equation 5, each of the resulting curves coincides identically at 50% germination. At high ψ, the curves also appear to coincide relatively well at other percentages. However, as ψ is decreased, the curves deviate increasingly. This is due to the fact that seeds representing fractions other than the 50th percentile have ψ_b values lower or higher than that of the 50th percentile, and therefore accumulate hydrotime more or less rapidly. Thus, times to germination plotted on a hydrotime scale calculated using only $\psi_b(50)$ will be systematically underestimated for fractions less than 50% and will be systematically overestimated for fractions greater than 50% (Figure 3B). This is purely a mathematical consequence of the model itself that invalidates the approach of plotting germination time course data on a hydrotime scale based upon a single $\psi_b(g)$ value (e.g., Finch-Savage et al. 1998; Roman et al. 1999; Shrestha et al. 1999). An accumulated hydrotime scale can be used in modeling seedling emergence under variable conditions, but it must either be with reference only to a specific germination fraction or the variation in $\psi_b(g)$ must be explicitly incorporated into the model (Battaglia 1997; Bauer et al. 1998).

There is a way to achieve the objective of normalizing germination time courses for the effects of reduced ψ. Using the parameters from the hydrotime model, germination time courses at any ψ can be normalized to the time course that would occur in water for that seed population. This method in effect normalizes for the influence of $\psi < 0$ MPa on the time courses, and if the time courses all coincide, it is evident that the model accurately accounts for the germination patterns observed. The relationship between the time to germination in water ($t_g(0)$) and the time to germination at any other ψ ($t_g(\psi)$) was derived as (Bradford 1990):

$$t_g(0) = [1 - (\psi/\psi_b(g))]t_g(\psi) \quad \text{or} \qquad [7]$$

$$t_g(\psi) = t_g(0)/[1 - (\psi/\psi_b(g))] \qquad [8]$$

When ψ = 0 MPa, then $\psi/\psi_b(g) = 0$ and $t_g(0) = t_g(\psi)$, as expected. When $\psi = \psi_b(g)$, then $\psi/\psi_b(g) = 1$, or $t_g(\psi)$ essentially becomes infinite (i.e., germination does not occur or takes infinitely long). At any ψ between 0 MPa and $\psi_b(g)$, the time to germination at that ψ is lengthened relative to that in water by the factor $1/[1-(\psi/\psi_b(g))]$. Thus, once $\psi_b(g)$ has been characterized for a seed lot (i.e., its mean and standard deviation are known), the germination time course at any ψ can be normalized to the germination time course for that seed population in water by multiplying the actual time to germination by $1-(\psi/\psi_b(g))$ (Equation 7). This is illustrated in Figure 3C, where each of the time points in Figure 3A has been multiplied by the appropriate factor, based upon the $\psi_b(g)$ value for that percentage, to normalize it back to the predicted time to germination in water. (Because this is a simulation, the points all coincide identically, illustrating that this normalization function is a mathematical consequence of the model itself). Alternatively, the time to germination at any $\psi < 0$ MPa can be predicted using Equation 8. This has been a useful and robust approach for comparing germination time courses across different ψ in a number of experimental applications (Alvarado 2000; Bradford 1990; Bradford and Somasco 1994; Cheng and Bradford 1999; Dahal and Bradford 1990, 1994). In particular, it can reveal situations where the model does not fit adequately, indicating that some change has occurred in the experimental conditions or in the physiology of the seeds, such as when $\psi_b(g)$ distributions shift during prolonged incubation at low ψ (Dahal and Bradford 1994) or in response to high temperature or plant hormones (Bradford and Somasco 1994; Ni and Bradford 1993).

Temperature and the Hydrotime Model

The effect of sub-optimal temperatures can easily be included in the hydrotime model by using thermal time instead of actual time in the model. Combining Equations 1 and 5, a hydrothermal time constant (θ_{HT}) for sub-optimal T can be defined as (Gummerson 1986; Bradford 1995):

$$\theta_{HT} = (\psi - \psi_b(g))(T - T_b)\ t_g \qquad (9)$$

This hydrothermal model has worked well to describe germination time courses at constant sub-optimal temperatures in the relatively high ψ range (e.g., Alvarado 2000; Dahal and Bradford 1994; Gummerson 1986). Assumptions of this equation are that $\psi_b(g)$ is constant and independent of temperature, and that T_b is independent of ψ, which are not always the case (Dahal and Bradford 1994; Bradford and Somasco 1994; Kebreab and Murdoch 1999b). However, under conditions where T_b and $\psi_b(g)$ are constant, the hydrothermal time model (Equation 9) provides a simple method to integrate the effects of both T and ψ on progress toward germination at sub-optimal temperatures.

As shown in Figure 1A, GR is reduced at supra-optimal temperatures, which is not predicted in Equation 9. A well-studied case of inhibition of germination by supra-optimal temperatures is that of thermoinhibition of lettuce (*Lactuca sativa* L.) seed germination, and similar behavior is exhibited by many species that normally germinate in the fall or winter (Baskin and Baskin, 1998). Bradford and Somasco (1994) showed that as T approached the upper limit for germination of lettuce seeds, the $\psi_b(g)$ distribution shifted to higher values. As noted above, this has the same effect as reducing ψ, so GR decreases as T increases above T_o. As T approaches T_c, part of the $\psi_b(g)$ distribution will extend above 0 MPa, which means that the ψ_b threshold for that fraction of the population is higher than 0 MPa, making them incapable of germinating in water (see Bradford 1996). This mechanism can account for the progressive decrease in GR and for the distribution of T_c values among seeds in the population (Figure 4A). That is, as $\psi_b(g)$ values become less negative with increasing temperature, the ψ_b values of different fractions of the seed population reach the point where $\psi_b \geq 0$ MPa at different temperatures, accounting for the normal distribution of $T_c(g)$ values. Other studies have also found that $\psi_b(g)$ values are at a minimum around the op-

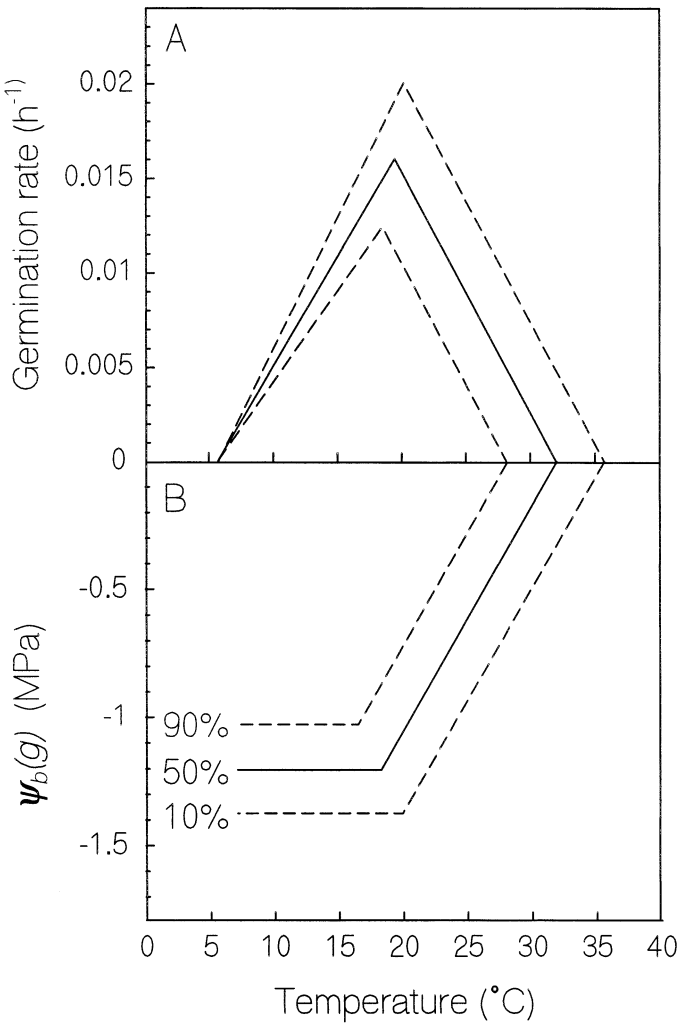

FIGURE 4. Germination rates across temperatures are determined by both thermal and hydrotime components. **A.** Diagram of germination rates for the 10th, 50th and 90th percentiles at different temperatures based upon experiments with true (botanical) potato seeds. **B.** Base water potentials for the 10th, 50th and 90th germination percentiles at different temperatures. At temperatures below T_o, $\psi_b(g)$ is relatively constant. Above T_o, $\psi_b(g)$ increases linearly until it intercepts 0 MPa, or the point where germination for that fraction is inhibited. The increase in $\psi_b(g)$ with temperature accounts for the distribution of ceiling temperatures among seeds in the population. (Adapted from Alvarado 2000).

timum T and become higher at supra-optimal T (Christensen et al. 1996; Kebreab and Murdoch 1999b; Meyer et al. 2000).

Recently, this mechanism of thermal inhibition of germination in relation to dormancy was studied using true (botanical) potato (*Solanum tuberosum* L.) seeds (Alvarado 2000; V. Alvarado and K.J. Bradford, in preparation). Fresh true potato seeds exhibit conditional dormancy in which they are capable of germination at low T (<17 C), but are increasingly inhibited at higher T (Pallais 1995). When $T < T_o$, $\psi_b(g)$ was relatively constant and Equation 9 accounted well for germination timing. The variation in $\psi_b(g)$ values is the basis of the different thermal time ($\theta_T(g)$) requirements among seeds in this temperature range (Figure 4). Above T_o, $\psi_b(g)$ increased linearly with T, accounting for the parallel decreases in GR_g. For different seed fractions, the extrapolation of the $\psi_b(g)$ lines intercepted the $\psi = 0$ MPa axis at the T_c for that fraction, as would be expected. Thus, for the supra-optimal range of T, Equation 9 can be modified as follows (Alvarado 2000):

$$\theta_{HT} = \{\psi - [\psi_b(g)_o + [k_T(T - T_o)]\}(T_o - T_b)t_g \quad (10)$$

where k_T is a constant (the slope of the $\psi_b(g)$ versus T line when $T > T_o$) and $\psi_b(g)_o$ represents the values of the $\psi_b(g)$ distribution at T_o. This equation adjusts $\psi_b(g)_o$ to higher values as T increases above T_o. Because the standard deviation of the $\psi_b(g)$ distribution was not affected, the ψ_b values of all of the seeds were adjusted upward by the same amount for each increment in T above T_o. Equation 10 also stops the accumulation of thermal time at the value equivalent to that accumulated at T_o. Thus, temperatures above T_o do not contribute additional thermal time in the supra-optimal range (degree-day models also generally put an upper temperature limit on thermal time accumulation); instead, effects on germination are accounted for by the change in $\psi_b(g)$. By applying the hydrothermal time model in sub-optimal (Equation 9) and supra-optimal T (Equation 10) components, Alvarado (2000) showed that germination timing and percentages across all T from T_b to T_c and $\psi > -0.5$ MPa could be fit very well according to:

$$\theta_{HT} = \{\psi - \psi_b(g) - [k_T(T - T_o)]\}(T - T_b)t_g \quad (11)$$

where $[k_T(T - T_o)]$ applies only when $T > T_o$, and in this supra-optimal range of T the value of $\psi_b(g)$ is set equal to $\psi_b(g)_o$ and $T - T_b$ is set equal to $T_o - T_b$. This model can be fit to germination time course data by repeated probit regressions to optimize the values of k_T, T_b, T_o, and θ_{HT} according to:

$$\text{probit}(g) = \{[(\psi - k_T(T - T_o)) - \theta_{HT}/((T - T_b)t_g)] - \psi_b(50)\}/\sigma_{\psi_b} \quad [12]$$

where again $[k_T(T - T_o)]$ applies only when $T > T_o$ and in this supra-optimal range $T - T_b$ is equal to $T_o - T_b$. In fitting this equation by repeated probit regressions, the values of k_T and T_o were varied for germination time courses at $T > T_o$ until a good fit was obtained that resulted in θ_{HT}, $\psi_b(50)$ and σ_{ψ_b} values close to those obtained at or below T_o. Presumably, a similar modification of Equations 11 and 12 might also account for cases where $\psi_b(g)$ values are also affected by temperatures near T_b (Kebreab and Murdoch 1999b, 2000).

Dormancy and the Hydrothermal Time Model

The ability of $\psi_b(g)$ values to shift in response to environmental conditions provides a coherent explanation for many phenomena associated with dormancy. As demonstrated above, an increase in $\psi_b(g)$ can readily explain the inhibition of germination at supra-optimal temperatures. In true potato seeds, when dormancy was broken by chilling or after-ripening, $\psi_b(g)$ values decreased correspondingly (Alvarado 2000). Excellent examples of ecological applications of this concept are found in studies of downy brome (*Bromus tectorum* L.) (Bauer et al. 1998; Christensen et al. 1996) and squirreltail [*Elymus elymoides* (Rafin.) Swezey] (Meyer et al. 2000). The loss of dormancy in seeds of both species could be attributed to a decrease in median ψ_b values of the seed population during after-ripening. Initially after shedding, $\psi_b(50)$ values were at or above 0 MPa, and the seeds were dormant. During after-ripening, $\psi_b(50)$ decreased lin-

early with time until minimum values were attained, with a corresponding increase in germination rates and percentages (Christensen et al. 1996; Meyer et al. 2000). These observations were expanded into a simulation model to predict germination in the field based upon the rate of change in $\psi_b(50)$ with after-ripening time and the soil T and ψ (Bauer et al. 1998). An interesting result was that after-ripening itself could be modeled as a thermal time phenomenon; i.e., the rate of loss of primary dormancy increased linearly as T increased above a threshold (Kebreab and Murdoch 1999a; Meyer et al. 2000). Similarly, Pritchard et al. (1996) developed a thermal time model for dormancy loss due to moist chilling (stratification) in horse chestnut (*Aesculus hippocastanum* L.) seeds, and Battaglia (1997) used the population-based threshold concept in a somewhat different approach to model the response of *Eucalyptus delagatensis* R.T. Baker seeds to moist chilling. Other examples in the literature where the hydrotime concept can explain dormancy release due to various factors have been noted previously (Bradford 1995, 1996, 1997). The hydrothermal time model can therefore link environmental temperature during dormancy loss to shifts in $\psi_b(g)$ values of the seed population, which in turn determine the potential for germination when T and ψ are suitable.

An expanded hydrothermal time model accounts for many of the characteristic features of seed dormancy and provides a quantitative way to characterize the potential for a seed population to germinate under a given set of environmental conditions. It describes seed germination in response to environmental conditions and gives quantitative indices of the sensitivity of a seed population to environmental signals. Battaglia (1997) formulated this into a dose-response model that can incorporate multiple factors while retaining the advantages of the population-based threshold approach. Thus, the potential for germination (i.e., dormancy state) can be integrated on a seasonal time scale by gradual changes in $\psi_b(g)$ values in response to dormancy-inducing or dormancy-breaking conditions, while sensitivity of germination to current conditions, particularly T and ψ, is simultaneously predicted using a minimal set of parameters. The following are brief descriptions of how the hydrothermal time concept can explain some of the characteristic features of seed dormancy.

Primary Dormancy

Studies have clearly shown that the loss of dormancy during after-ripening is the result of a gradual shift in $\psi_b(g)$ to more negative values (Alvarado 2000; Bauer et al. 1998; Christensen et al. 1996; Meyer et al. 2000). As a consequence of this, germination rates and percentages increase, germination becomes more synchronous in time, and seeds are able to progress toward germination at lower ψ (i.e., become more tolerant of stress). As abscisic acid (ABA) is essential for the induction of primary dormancy (Hilhorst 1995), it is not surprising that ABA can increase $\psi_b(g)$ values and interact with ψ to control germination (Corbineau and Côme 2000; Ni and Bradford 1992, 1993; Schopfer and Plachy 1985; Toorop et al. 2000). ABA is also involved in the enforcement of dormancy in imbibed seeds (Alvarado et al. 2000; Grappin et al. 2000; Toorop et al. 2000; Yoshioka et al. 1998), possibly by countering the action of gibberellin (GA) (Gómez-Cadenas et al. 2001).

Temperature Limits for Germination

A decrease in $\psi_b(g)$ is related to the widening of the temperature "window" for germination that occurs during dormancy release. For example, as $\psi_b(g)$ decreased during after-ripening of true potato seeds, the range of temperatures at which germination could occur increased (Alvarado 2000). Kebreab and Murdoch (1999b) found that $\psi_b(g)$ values of *Orobanche aegyptiaca* Pers. seeds increased at temperatures both above and below the optimum range. The latter may contribute to the apparent increase in T_b they observed in seeds imbibed at low ψ. High values of $\psi_b(g)$ can increase the apparent T_b, even if the thermodynamic T_b is not affected by dormancy. For example, germination rates decrease (germination times increase) markedly as T approaches T_b. If $\psi_b(g)$ is also high, further decreasing germination rates, many seeds in a population will not complete germination within a reasonable time at low T and low ψ even if both T and ψ are above their respective physiological thresholds. Meyer and Monsen (1991) have noted that in a fluctuating environment, slow progress toward germination is as good as dormancy, as either condition will prevent emergence when conditions are unfavorable for seedling growth and allow the seed to wait for a better opportunity to complete germination.

Dormancy Cycling

Cycling of secondary dormancy on a seasonal basis is a common phenomenon in weed seed banks (Hilhorst and Toorop 1997), and is likely to be associated with corresponding cycling of $\psi_b(g)$ values. By definition, if a seed does not germinate in water it is dormant, but this also implies that its ψ_b threshold for germination must be equal to or greater than 0 MPa. Lowering of $\psi_b(g)$ values as the population cycles out of dormancy due to environmental cues would automatically increase the fraction of germinable seeds in the population, increase germination rates, increase synchrony of germination, and widen temperature limits, while rising $\psi_b(g)$ values would have the opposite effects during the imposition of dormancy. Alvarado (2000) showed that this was the case for secondary dormancy in true potato seeds, and the results of Kebreab and Murdoch (1999a) for induction of secondary dormancy in *Orobanche* spp. are consistent with this model. The fact that the hydrotime model can simultaneously and automatically account for and adjust all of these related features of dormancy cycling simply by adjusting $\psi_b(g)$ to higher or lower values is strongly in its favor in comparison with other models that must empirically account for each of these components separately.

Germination-initiating Factors

Seeds that are considered to be non-dormant may still require light, nitrate or other factors for the initiation of germination even when T and ψ are permissive (i.e., exceed their respective thresholds). Seasonal signals may allow $\psi_b(g)$ to decrease only to a certain point, increasing the potential for germination, but additional triggers may be required to overcome remaining barriers to germination. For example, GA is required for germination of many seeds and has been shown to lower $\psi_b(g)$ values (Ni and Bradford 1993). Phy-

tochrome is undoubtedly involved in many seeds (Benech-Arnold et al. 2000), possibly through induction of GA-synthesizing enzymes (Kamiya and Garcia-Martinez 1999), and sensitivity of seeds to light is itself dependent upon the seed water status (Botto et al. 2000). It is possible that sensitivity to these permissive factors in seed germination is actually what changes seasonally (Derkx and Karssen 1993, 1994), with $\psi_b(g)$ thresholds being dependent upon their action. Fennimore and Foley (1998) used the GA-time model, an extension of the population-based threshold approach (Ni and Bradford 1993), to quantify and characterize increases in sensitivity of wild oat (*Avena fatua* L.) seeds to GA during dormancy release. Because GA induces a number of hydrolase and expansin genes associated with the early stages of seed germination (e.g., Bradford et al. 2000; Nonogaki et al. 2000; Chen and Bradford 2000), the products of these genes may be involved in determining ψ_b thresholds.

"Residual" Dormancy

If dormancy is defined operationally as the failure of a viable seed to germinate, it is a quantal character; i.e., an individual seed is either dormant or not. In this case, greater or less dormancy on a population basis relates to the percentage of seeds that either do or do not complete germination. However, it is a common observation that as dormancy is broken, germination rates as well as germination percentages increase. Thus, among seeds that will eventually complete germination, the presence of "residual" dormancy or "resistance to germination" (Gordon 1973) is shown by slower germination rates. Similarly, we can expect that among seeds that fail to germinate, some may be more dormant than others (i.e., will require stronger or longer dormancy-breaking treatments before they will germinate). In some cases, seeds can be forced to germinate, but this is not always identical to breaking dormancy (Myers et al. 1997). Thus, there is a continuum of dormancy states among both germinable and non-germinable fractions of the seed population.

The population-based hydrothermal time model readily accounts for residual dormancy by allowing $\psi_b(g)$ to vary among individuals while the rate of progress toward germination is proportional to the extent by which ψ exceeds the $\psi_b(g)$ threshold. If all $\psi_b(g)$ values are lower than 0 MPa, all seeds will eventually germinate in water. However, shifting this distribution even lower by further exposure to dormancy-breaking stimuli will increase the germination rates of all seed fractions. Moving the $\psi_b(g)$ distribution to higher or lower values automatically generates the expected effects on both germination percentage and rate. This can be illustrated by Figure 3A. If, instead of each curve representing imbibition at a different ψ, all the seeds were imbibed in water and the median $\psi_b(g)$ of the population were progressively shifted from −1.0 to −0.8 to −0.6 MPa, etc., the identical family of curves would result. Thus, a continuous array of dormancy states can be generated simply by changing the mean or distribution of $\psi_b(g)$ values, even in the range where most or all seeds are capable of germination.

Priming and the Hydrothermal Time Model

While having many useful features, the hydrothermal time models described above still do not account for all aspects of seed dormancy and germination. Equations 5 and 9 predict that no progress toward germination is made by seeds when $\psi < \psi_b(g)$. However, this is not the case, as illustrated by the phenomenon known as seed priming (Taylor et al. 1998). During priming, seeds are imbibed at a ψ that prevents completion of germination, can then be dehydrated, and will subsequently germinate more rapidly when imbibed again at $\psi > \psi_b(g)$. Thus, seeds are able to progress toward germination at $\psi < \psi_b(g)$ and can retain this advancement during drying and rehydration (i.e., GR_g will be increased after priming). Some physiological and biochemical activities associated with progress toward germination show a threshold-type behavior at low ψ (e.g., Chen and Bradford 2000; de Miguel and Sánchez 1992; Spyropoulos and Reid 1988; Toorop et al. 1998).

To account for this phenomenon in hydrothermal terms, the concept of a minimum water potential (ψ_{min}) was introduced as the lowest ψ at which physiological advancement can occur (Bradford and Haigh 1994; Tarquis and Bradford 1992). It was proposed that when $\psi_b(g) > \psi > \psi_{min}$, then the accumulated hydrothermal priming time (θ_{HTP}) is:

$$\theta_{HTP} = (\psi - \psi_{min}(g))(T - T_{min})\ t_p, \qquad (13)$$

where T_{min} is the minimum temperature at which priming advancement can occur and t_p is the duration of priming. This increase in GR will be in addition to the GR without priming, so that the following equation can be derived (Bradford 1995):

$$GR_g(\text{primed}) = \{[(\psi - \psi_b(g))(T - T_b)]/\theta_{HT}\} + k'\{[(\psi - \psi_{min}(g))(T - T_{min})t_p]\} \qquad [14]$$

where k' is a "hydrothermal priming time constant" and is the slope of a plot of GR versus accumulated hydrothermal priming time. The first term is derived from Equation 9, and gives GR_g when $\psi > \psi_b(g)$ [note that there is an error in this equation in Bradford (1995)]. The second term in Equation 14 then adds an additional increment to GR_g as a result of accumulated hydrothermal priming time at $\psi_b(g) > \psi > \psi_{min}$. This equation predicts that germination rates will increase linearly in proportion to the accumulated hydrothermal time during priming (to a point; there is obviously a limit to this relationship with extended priming durations or at supra-optimal T). This relationship was confirmed for a number of tomato (*Lycopersicon esculentum* Mill.) seed lots (Bradford and Haigh 1994; Cheng and Bradford 1999). In effect, priming primarily reduced θ_{HT}, shortening the time to germination proportionately for all seeds, rather than speeding germination by lowering $\psi_b(g)$ (Dahal and Bradford 1990). The relationship was tested only for the median percentile of the seed populations (GR_{50}), but it can be expected that the minimum ψ might vary among seeds ($\psi_{min}(g)$), allowing some seeds to progress further than others during priming. In fact, σ_{ψ_b} has been found to increase in some cases after priming, although germination uniformity in actual time is generally improved as a result of faster germination rates (Dahal and Bradford 1990).

While Equation 14 works conceptually and empirically (Bradford and Haigh 1994; Cheng and Bradford 1999), it is not particularly convenient to apply, and it should be noted that θ_{HT} and θ_{HTP} are not numerically comparable.

Accumulated hydrothermal priming time cannot simply be calculated from the priming conditions and subtracted from θ_{HT} to estimate germination timing, and k', the proportionality constant that relates the accumulation of hydrothermal priming time to the subsequent effect on GR, will vary among species and seed lots (Cheng and Bradford 1999). Meyer et al. (2000) have extended this concept and developed a method to estimate the contribution of accumulated hydrothermal priming time to the θ_{HT} requirement for germination. Rowse et al. (1999) have also proposed a variant of the hydrotime concept based on "virtual" osmotic accumulation that can be used to model advancement during hydration prior to germination. Other factors may also be involved, as natural priming by burial in the field was more effective in enhancing germination than was laboratory priming under constant conditions (González-Zertuche et al. 2001). Additional work is needed to understand how best to account for natural priming in the field and to incorporate it into emergence models.

The hydrothermal priming time concept also addresses the fact that seeds may experience multiple cycles of hydration and drying prior to emergence. Seeds can progress toward germination during intermittent hydration-dehydration cycles, and advancement toward germination can be attributed to the summation of the hydrated periods (Allen et al. 1993; Adams 1999). Finch-Savage and Phelps (1993) used this approach to predict onion (*Allium cepa* L.) seedling emergence under variable water supply. They applied the hydrothermal time concept, but simply stopped the accumulation of thermal time during periods when soil $\psi < \psi_b(50)$. The accumulation of thermal time only during the periods when $\psi > \psi_b(50)$ matched well with seedling emergence (when corrected for the time required for seedling growth to the surface). They argued that when soils dry rapidly, the seeds would spend relatively little time in the intermediate ψ range where hydropriming time would have been significant. Similar results were also found with carrot (*Daucus carota* L.) (Finch-Savage et al. 1998). In a subsequent study, including hydropriming time in the model improved prediction of field emergence somewhat, but the best model was still that described above (Finch-Savage et al. 2000). Roman et al. (1999, 2000) also used this threshold approach for hydrothermal time accumulation to successfully model germination and emergence in the field of seeds of common lambsquarters (*Chenopodium album* L.). This may be a useful simplification of the hydrothermal time model that has sufficient accuracy for field studies under rapidly fluctuating conditions. Battaglia (1997) included stratification time in an emergence model, and concluded that part of the advancement in germination rates after stratification was due to accumulated hydrothermal time after dormancy was broken. Bauer et al. (1998) also discussed this issue, as their data suggested that some seeds having shorter after-ripening requirements would be released from dormancy and would begin to progress toward germination while other seeds in the population were still dormant. This is undoubtedly the case with mixed populations of seeds in soil seed banks derived from different genotypes and years, and it complicates simple approaches to modeling both the release from dormancy and subsequent seedling emergence. However, an extension of the approach of Battaglia (1997) may allow multiple factors to be included directly in a population-based model, or multiple-component models may need to explicitly incorporate this population behavior into the relevant subroutines (Vleeshouwers and Bouwmeester 2001; Vleeshouwers and Kropff 2000).

Applications of Hydrothermal Time Models to Predicting Seedling Emergence

It is beyond the scope of this article to review all models of dormancy and seedling emergence, and excellent recent reviews are available by experts in this field (Allen and Meyer 1998; Benech-Arnold and Sánchez 1995; Forcella et al. 2000; Vleeshouwers and Kropff 2000). Thus, only some general observations and suggestions for future development will be offered. Within the literature on modeling of germination and seedling emergence, two philosophies or approaches can be identified. One approach is pragmatic and seeks to predict seedling emergence patterns primarily from inputs of environmental data such as temperature, moisture, cultivation, etc. (e.g., Forcella 1998; Kebreab and Murdoch 1999a; Vleeshouwers and Bouwmeester 2001). Although physiological information may be incorporated as subroutines in these models, they primarily seek to develop empirical equations that will predict the timing and extent of emergence from a seed bank in response to environmental or seasonal inputs. This can be considered as more of an "engineering" approach, where continuous functions across the range of inputs are preferred, numerous parameters or variables may be required to fit different components of the model, and in some cases the biological meaning of the parameters may become obscure or even be irrelevant. These approaches may be the best for obtaining broadly applicable predictive forecasts from the type of meteorological and soil seed bank data that are readily available.

The alternative (or complementary) approach is to attempt to understand how seeds respond to environmental conditions and model germination and emergence on a physiological basis. The hydrothermal time model is being applied in this effort by basing simulations on the hydrothermal sensitivity or potential of seed populations to germinate and predicting emergence on the basis of how seeds in a given physiological or dormancy state will respond to current environmental conditions (e.g., Battaglia 1997; Bauer et al. 1998; Meyer et al. 2000). Some groups have taken what might be considered to be an intermediate approach, using hydrothermal and population concepts, but then applying empirical equations when the simple hydrothermal time model is deemed inadequate (e.g., Grundy et al. 2000; Kebreab and Murdoch 2000; Murdoch et al. 2000; Roman et al. 1999, 2000). In a number of cases, the inadequacy of the hydrothermal time model is due to the assumption that a fixed set of values must be used across all dormancy states or environmental conditions. It has been argued here that the hydrothermal time model should be viewed instead as providing values that characterize the changing status of seed dormancy or thermal responses. As Meyer et al. (2000) concluded, "The simple relationships between hydrothermal time parameters and temperature response, dormancy loss, and priming. . . strongly suggest that the hydrothermal time theory has an underlying physiological basis and is not just another way of empirically fitting germination time course data."

Where should research be focused in the future with respect to these approaches? Two recent reviews of weed seed emergence models came to strikingly similar conclusions. Forcella et al. (2000) concluded, "In brief, the most critical need for improving models of seedling emergence in the future is mechanistic integration of microclimate and management variables with the rates of dormancy alleviation/induction, germination and seedling elongation. Equally important is the integration of these latter three components of emergence." After carefully examining the component processes in a sophisticated emergence model, Vleeshouwers and Kropff (2000) concluded, "Research to improve the prediction of weed seedling emergence in the field should. . . focus on improving the simulation of seasonal changes in dormancy of buried seeds." These are exactly the areas where the hydrothermal time model has its greatest advantages. The accumulation of thermal and hydrotime above specific thresholds is an intuitively simple concept that also provides specific parameters useful in characterizing seed populations, such as T_b, $\psi_b(50)$, σ_{ψ_b}, θ_H, θ_{HT}, ψ_{min}, and θ_{HTP}. This common set of parameters can be used to characterize the ecological relationships of different species' germination sensitivities to their environments (Allen et al. 2000; Flores and Briones 2001). It is relatively simple to adjust $\psi_b(g)$ distributions in response to environmental conditions (e.g., Eqn. 11), after-ripening (Meyer et al. 2000) or seasonal changes in dormancy cycling, and changing only this parameter automatically adjusts the fraction of germinable seeds, the rate of germination, and the effect of current T and ψ of the environment on these. The model provides a mechanistic link between physiological and biochemical processes and their consequences for germination (Still and Bradford 1997; 1998) and longevity (Bradford et al. 1993).

A scheme is presented in Figure 5 illustrating how the hydrothermal time model could be applied to integrate the environmental inputs to seeds over both the short and the long term and to adjust the descriptive parameters to predict the germination rate and percentage of the seed population. This information about seed dormancy and potential germination status can then be used as an input into more comprehensive seedling emergence models. Perhaps the most important but least appreciated feature of the hydrothermal time model is the explicit incorporation of population distributions in the model. Individual seeds vary widely in their physiological and dormancy status, particularly among seeds in a soil seed bank. If they did not, there would be no persistent seed bank from which successive flushes of emergence could occur. A significant advantage of the hydrothermal time model is that it explicitly incorporates this variation and can predict how any specific fraction of the seed population will respond to an environmental perturbation, given its physiological state. Further research focusing on population-based threshold models would seem to be a fruitful avenue for achieving the goals identified above.

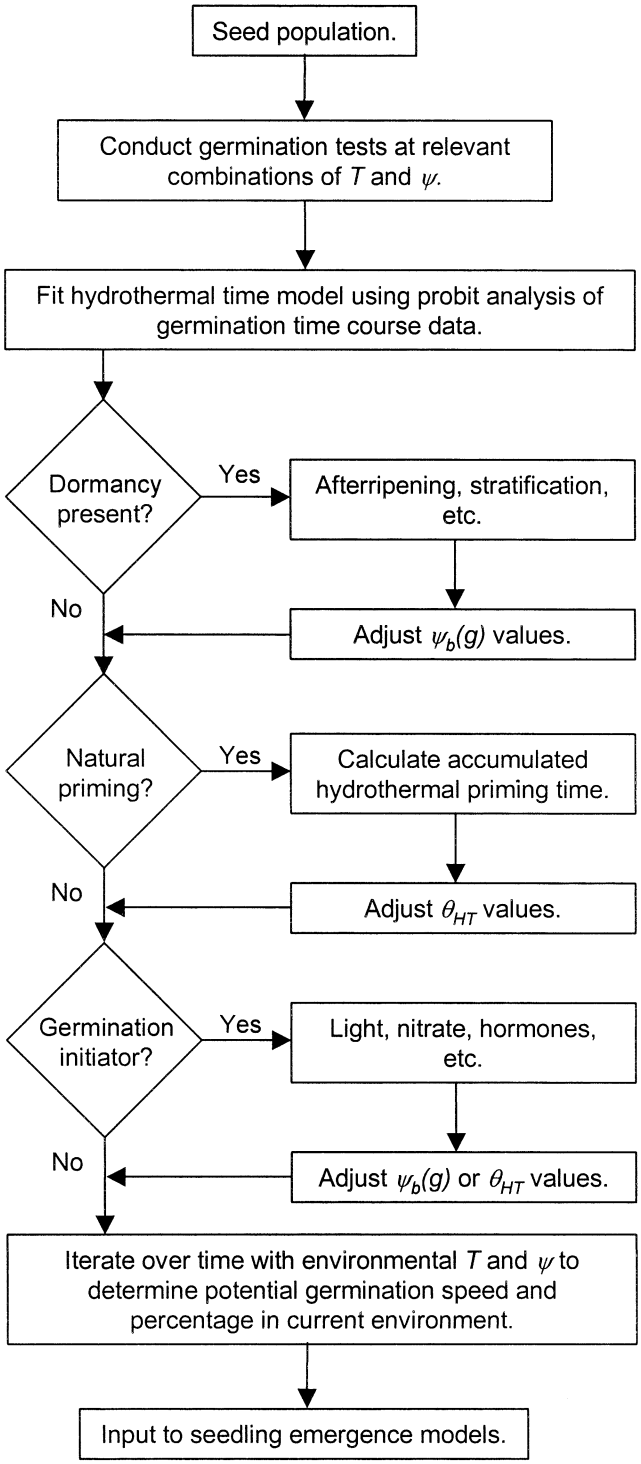

FIGURE 5. Flow chart illustrating how information from the hydrothermal time model can be developed and utilized to predict seed germination behavior. The current physiological status of a seed population can be characterized by germination tests at a matrix of T and ψ combinations and fitting the time course data to the hydrothermal time model (Equation 12). Adjusting the parameters of the hydrothermal time model can also incorporate the influences of dormancy and its releasing factors, natural priming, and any requirements for germination-initiating factors. The germination behavior of this seed population under field conditions could then be predicted by iterating over time, adjusting the parameters as needed and utilizing the current environmental conditions (i.e., T and ψ) to predict the percentage of potentially germinable seeds at a given time. This information could then be used as an input to models that incorporate other factors (e.g., seedling growth, soil conditions, etc.) to predict final seedling emergence.

Acknowledgments

Original work from the Bradford laboratory has been supported by grants from the National Science Foundation, the U.S. Department of Agriculture, Regional Research Project W-168 and the Western Regional Seed Physiology Research Group.

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Received July 10, 2001, and approved November 18, 2001.