The Rate of Biological Development and Thermal Time

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May 3, 2022

Biological development is the orderly progression through defined growth stages made by an organism. For example, an annual plant proceeds from germination to emergence, continues on to flowering, and eventually reaches senescence and maturity. A butterfly hatches from an egg as a caterpillar, makes a chrysalis, emerges with wings, reaches its full development, and eventually dies. Different stages of development are also called phenological stages, and the timing of the occurrence of these stages are often called an organism's phenology.

If $r(t)$ is the rate of biological development at time t, defined as the fraction of development completed per time between two phenological stages, then $f(t)$, the total fraction of development completed at time t, is

$$f(t) = \int_0^t r(t')\, dt'. \tag{1}$$

If t_c is the time needed to complete the development between two phenological stages, then

$$f(t_c) = 1. \tag{2}$$

The rate of development will depend on organism temperature, $T(t)$. For endotherms like humans, an organism's temperature is approximately constant. Hence $f(t) = r\, t$ which results in $t_c = 1/r$ according to (2). Consequently, if we say that a human reaches adulthood at $t_c = 18$ years, and assume for simplicity that they develop at a constant rate, then $r = 1/18 = 0.056$ year^{-1} between the ages of 0 and 18.

Thermal Time

For ectotherms (like plants) whose body temperature depends on their environment, the rate of development can be written $r\,[T(t)]$. If the rate is a linear function of temperature, then

$$r\,[T(t)] = m\,[T(t) - T_b] \tag{3}$$

where m is the change in rate per change in temperature and T_b is a "base temperature" below which no development occurs: $r\,[T(t) \leq T_b] = 0$. When $T(t) > T_b$, (1) can be written

$$f(t) = \int_0^t r\,[T(t')]\; dt' = m \int_0^t [T(t') - T_b]\; dt' = m\,\tau(t) \tag{4}$$

where $\tau(t)$ can be called a "thermal time" defined as

$$\tau(t) = \int_0^t [T(t') - T_b] \; dt'. \tag{5}$$

Practically, $\tau(t)$ is calculated by discretizing the integral in (5) such that

$$\tau(t) = \int_0^t [T(t') - T_b] \; dt' \approx \sum_{j=1}^{n} (T_j - T_b) \; \Delta t \tag{6}$$

where $n = t/\Delta t$ and Δt is a time period over which it is reasonable to consider $T(t) = T$ (a constant temperature). If $\Delta t = 1$ day, then we are assuming that T is either constant over the course of a day, or more likely that it represents the average temperature of a day. In this case the units of τ would be °C · day. But τ could also have units °C · hour if Δt is an hour, or °C · s for that matter if $\Delta t = 1$ s.

If S is the total thermal time needed for development from one stage to another, then

$$\tau(t_c) = S \tag{7}$$

and $f(t_c) = 1 = m\,S$ according to (2) and (4). Therefore,

$$m = \frac{1}{S} \tag{8}$$

which means that if we were to plot r versus T, the slope of the line (m) would be inversely proportional to S. When S is small, the slope m would be steep, and not much thermal time is needed because the rate of development increases quickly with temperature. When S is large, the slope m would be nearly flat.

Growing Degree Days

Note that if $\Delta t = 1$ day in (6), average daily temperature can be roughly calculated as

$$T_j = \frac{T_{max,j} - T_{min,j}}{2} \tag{9}$$

where $T_{max,j}$ and $T_{min,j}$ are the high and low temperatures, respectively, on the j^{th} day. Then according to (6) and (7) we simply need daily T_{max} and T_{min} to calculate the thermal time that elapses for a specific organism each day, and then accumulate the daily values until we reach the total amount of thermal time needed for a certain type of development to occur. For example, $S = 60$ °C·day for maize emergence (the VE stage), or 120 °C·day for the first bloom of a Norway maple tree to appear, or 870 °C · day for fall webworm to hatch. Here we are assuming that $t = 0$ occurs at some point before $T(t) > T_b$, which can be thought of as the start of the "growing season" for a particular organism, or that $t = 0$ when a crop is planted. This fits the model for development that is described in *Campbell and Norman* (1998) and referred to as "growing degree days" or GDD in various crop growth publications.

Heat Units?

Although GDD are often referred to as "heat units" or "heating units," this is not an accurate representation of what is actually happening.

It is true that at some point heat (energy) from the environment must flow into an ectotherm to "warm it up." However, an organism accumulates thermal time simply according to its temperature, regardless of whether heat is flowing into (or out of) the organism. At a basic level, an organism's body temperature determines the rates of the biochemical reactions which are going on within the cells that make up the organism. At lower temperatures close to T_b these biochemical reactions will be "slow" and little if any development will occur. As the temperature of the organism increases, so do the rates of these biochemical reactions, and there is development.

Recall that temperature determines the direction of energy flux and its magnitude. Heat flows from hotter to colder objects, and this flux increases as the temperature difference increases. If H is sensible heat flux (sensible means "due to a temperature difference"), then $H = g\ \Delta T$ where g is a conductance for heat and ΔT is the temperature gradient. Consider an organism in thermal equilibrium with its environment (like an ectotherm). If this organism is above its T_b development will occur. But no heat will flow into (or out of) the organism from (or to) its environment because $\Delta T = 0$! Endotherms, on the other hand, are almost always warmer than their environment. In this case, $\Delta T \neq 0$, but regardless of the magnitude (and direction) of H, their rate of development will not change.

Development also does not depend on how much heat is contained within an organism. Larger organisms will contain more thermal energy simply because they are more massive, since the amount of energy is determined by the organism's specific heat capacity (which has units of $\mathrm{J \cdot kg^{-1} \cdot K^{-1}}$), its temperature, and its mass. Again, as long as the temperature of the organism is above its T_b, development will occur. Of course, energy is required to "power" development. However, essentially all of this potential energy is stored in carbohydrates that have either been consumed by the organism (eaten) or generated by the organism itself (photosynthesis in plants).

Assumptions Made When Using Thermal Time

We make four key assumptions when we use thermal time as defined by (6) to predict the timing of the development of an organism.

1. The rate of development r can be approximated by a linear function of temperature.

2. No development occurs for $T(t) \leq T_b$. (And perhaps no development occurs for $T(t) > T_c$, where T_c is a "ceiling" or upper threshold, above which it is too hot for development. Ceiling temperatures have been identified for some organisms.)

3. The time-varying temperature $T(t)$ over each time interval Δt can be adequately represented by either a single temperature T, or reconstructed from a limited number of temperature observations such as T_{max} and T_{min}.

4. The temperatures used to calculate thermal time are the temperatures actually experienced by the organism.

These assumptions are *never* completely valid. For example, *Stewart et al.* (1998) critically examined the phenology of maize and found that it could be best described as a nonlinear function of temperature, which violates Assumption 1. Assuming that the rate is a linear function of temperature can lead to an overestimation of the true T_b, effectively violating Assumption 2. Different methods have been developed to better estimate a representative T over Δt (see *Zalom et al.* (1983) for methods when $\Delta t = 1$ day) but no method is exact (because the variation in temperature over each Δt is unique) and thus Assumption 3 is never strictly satisfied. Finally, Assumption 4 is likely the most important. Temperatures used to calculate thermal time are often obtained from readily-available sources like weather stations located at airports or in urban areas, which are rarely coincident with the organism of interest.

In spite of all of this, thermal time has been shown to be a useful model in many situations! For example, it has been used successfully to predict the dates on which maize reaches certain phenological stages such as emergence (VE), tassel (VT), milk (R3), etc. The key, then, is that as with any model, one must be careful to use it appropriately and not "stretch" the model too far. While the rate of development is likely never linear, Assumption 1 can normally be made over long periods of time at warmer temperatures. And while a linear rate may lead to a violation of Assumption 2, relatively little development occurs at temperatures near T_b.

The predictions of (6) will never be "exact." How accurate can the predictions be? Certainly not better than Δt, but as j increases, the accuracy will improve simply due to the form of (6). An integration or summation of values will tend to perform better over time even if its integrand is not truly representative of the real process because these functions act as "smoothers" that reduce the error in calculations. Using terminology from the field of signal processing, an integration is a low-pass filter which removes high-frequency noise (variation in τ from t to $t + \Delta t$) that occurs because all of the assumptions are never strictly satisfied. However, given enough time (large j) the errors associated with each Δt tend to cancel each other out if the method in Assumption 3 employed to reconstruct $T(t)$ over each Δt is not biased high or low.

The more important question is "How accurate do the predictions *need* to be?" Resolving the timing of a specific phenological event to less than $\Delta t = 1$ day is probably not necessary. To best assess the usefulness of the model for a particular application, we must think critically about Assumptions 3 and 4.

References

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