Development in Botanical Parasites

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Abstract

A widely used mathematical model of botanical parasite development – the beta model – remains poorly framed, unnecessarily clouding what should be simple analytical and statistical conclusions. We pick this proverbial low-hanging fruit by providing an alternative expression, demonstrate wide-reaching conclusions that are straightforward consequences of this framing, demonstrate proper fitting using this form, and provide computational tools for making use of the formulation.

Introduction

The response of parasite development to temperature can often be reasonably described by basic chemical kinetics. As temperature increases, the rates of advantageous and deleterious reactions increases. At first, the helpful processes outpace the harmful and overall development rate increases, but eventually they saturate and the harmful processes begin to dominate, reversing the increased development and ultimately leading to decline.

This is of course a vast oversimplification of what drives these highly interdependent processes (e.g., complex series of dependent reactions, substitution of one process for another as environmental conditions vary, competition between internal processes for resources), and worse totally ignores that these organisms are embedded in a competitive environment with other parasites and their hosts also experiencing the harms and benefits of temperature relative to development. We should hardly expect it to be suitable as a basis for detailed quantitative predictions from a "first principles" perspective even in the lab, let alone the field.

And yet, the empirical evidence indicates that as a qualitative explanation, this model is quite accurate for many plants and their parasites(not to mention many other ecological interactions). Qualitative models can be fit with more pragmatic experimentation and then be perfectly suitable for quantitative applications, especially interpolation and reference lines for detailed experiments. This is the relationship between physics and engineering in many products: basic physical principles provide a qualitative framework, engineering tests fit out those simple models, and the cost of balancing all the detailed phenomena is avoided.

cite the plethora of plant-parasite lit

e.g., malaria, white nose

This is the approach taken in many plant pathology publications, however they are typically hamstrung by overly complicated (in form, not in mechanism) models and least-squares thinking. We address particularly the *Beta model*[1]. For that model, we demonstrate:

[1] Earliest use of the model refers to it as BETE, an acronym of the German name for the model. Subsequent apparent re-discoveries prepend Beta to various synonyms of function, model, distribution, curve et cetera due to its relation to the statistical distribution of the same name. Referring to this expression hereafter, I use beta model, form, and curve interchangeably, but specifically not *beta function* or *beta distribution*. Those terms have particular definitions with a substantial history in an adjacent field that plant pathologists should be interacting with more, and confounding its terminology should be discouraged.

analysis with an alternative – but formally equivalent – expression; and parameterization against standard datasets in a way that more accurately represents the underlying data (while highlighting how incomplete that approach remains). Finally, we provide `R` and `Python` packages to apply these to other datasets.

The Beta Model

A very loose form of the model expresses development rate, D, dependent on temperature, T, on a particular interval, $[T_{\min}, T_{\max}]$, by:

$$D(T) = c(T - T_{\min})^n (T_{\max} - T)^m$$

where c sets the peak development rate, n sets the effect of approaching the minimum survivable T, and m sets the effect of approaching the maximum survivable T. The shape is fundamentally the beta distribution projected on to $[T_{\min}, T_{\max}]$ from $[0, 1]$, and with normalizing beta function replaced by a peak rate coefficient.[2]

In several publications, this form is then subjected to assorted contortions, such as fixing $T_{\min} = 0$, enforcing particular relations between n, m, and measurable features, mostly to simplify fitting or analysis. However, these manipulations ultimately resolve into convoluted expressions of long-characterized features of the alternatively normalized beta curves, though at least expressed in more phenomenological parameters.

We would be better served starting with distilled shape, and baking the desired ingredients in from that point. Fortunately, this is a straightforward exercise, as illustrated in the supplement.

Summarizing the supplement: a general form of the Beta model relating percent of peak development, $\hat{D}$, to scale-free temperature, τ, can be written in terms of two phenomenological parameters: δ, the scale-free peak development temperature, and s, the temperature specificity. A particular system model then can be written with the reference temperatures and peak development rate, $(T_{\min}, T_{\max}, D_{\max})$, to set the scale. Maximum likelihoods for these parameters can be fit with whatever additional parameters, Θ, are required by the selected distribution (e.g., σ for a Gaussian, k for Gamma).

$$\hat{D}(\tau) = \left[\left(\frac{\tau}{\delta}\right)^{\delta} \left(\frac{1-\tau}{1-\delta}\right)^{1-\delta} \right]^{s} \qquad \text{(General Form)}$$

$$D(T) = D_{\max} \hat{D}(\tau(T)) \qquad \text{(Particular Application)}$$

$$\tau(T) = \frac{T - T_{\min}}{T_{\max} - T_{\min}} \qquad \text{(Scale-Free Temp.)}$$

$$L = \prod_{(D_i, T_i)} P(D_i | T_i, (\delta, s), (T_{\max}, T_{\min}, D_{\max}), \Theta) \qquad \text{(Likelihood)}$$

We may represent these for calculation in `R` or `Python` (full details in the supplement), and then use their maximum likelihood libraries for fitting. After setting up boiler plate code, the `R` code

[2] This replacement reflects the difference in the curves' application. As a probability distribution function, the appropriate normalization constrains the integral area (i.e., the total probability of all outcomes) under the distribution to 1. As a representation of the development rate between 0 and its peak, obviously that peak is the appropriate point to constrain.

```
> # the particular form
> D <- function(temp, tmin, tmax, Dmax, delta, s) {
+   Dmax * hatD(tau(temp, tmin, tmax), delta, s)
+ }
> # binding a particular (tmin, tmax, Dmax, delta, s)
> #  to make a D(temp) function
> D.factory <- function(tmin, tmax, Dmax, delta, s) {
+   tt <- tau.factory(tmin, tmax)
+   hD <- hatD.factory(delta, s)
+   function(temp) Dmax * hD(tt(temp))
+ }
> ## transforms from optimization domain (-Inf, Inf)
> ##  to calculation domain
> xform <- function(shape, tmin, del, Dmax, delta, s) list(
+     shape = exp(shape), ## shape must be > 0
+     tmin = exp(tmin), ## tmin must be > 0
+     tmax = exp(del) + exp(tmin), ## tmax must be > tmin
+     Dmax = exp(Dmax), ## Dmax must be > 0
+     delta = plogis(delta), ## delta must be (0,1)
+     s = exp(s) ## s must be > 0
+   )
> neglogdT <- function(temp, devtimes) {
+   function(shape, tmin, del, Dmax, delta, s) with(xform(shape, tmin, del, Dmax, delta, s),{
+     DD <- D.factory(tmin, tmax, Dmax, delta, s)
+     predtimes <- 1/DD(temp) ## distribution means
+     ## have to choose distribution here
+     -sum(dgamma(devtimes, shape, scale=predtimes/shape, log=T))
+   })
+ }
> require(stats4)
> fitter <- function(temp, devtimes) {
+   ## assert: temps in Kelvin, devtimes all in same units
+   ref <- neglogdT(temp, devtimes)
+   guess.tmin <- min(temp)
+   guess.tmax <- max(temp)
+   guess.Dmax <- max(1/devtimes)
+   guess.delta <- (mean(temp[which(1/devtimes == guess.Dmax)])-guess.tmin)/(guess.tmax - guess.tmin)
+   guess.s <- 1
+   mle(ref,start=list(
+     tmin = log(guess.tmin),
+     del = log(guess.tmax-guess.tmin),
+     Dmax = log(guess.Dmax),
+     delta = qlogis(guess.delta),
+     s = log(guess.s)
+   ))
+ }
```

$$\hat{G}(\hat{\tau}) = \left[\left(\frac{\hat{\tau}}{\delta}\right)^{\delta} \left(\frac{1-\hat{\tau}}{1-\delta}\right)^{1-\delta} \right]^{s} \qquad \text{(Rev. Development Rate Coeff.)}$$

with the new parameter interpretations and relations to the original parameters:

$$\hat{\tau} = \frac{T - T_{\min}}{T_{\max} - T_{\min}} \qquad \hat{\tau} \in [0,1] \qquad \text{(Norm. Temp.)}$$

$$s = n + m \qquad s \geq 0 \qquad \text{(Temp. Specificity)}$$

$$\delta = \frac{n}{n+m} \qquad \delta \in (0,1) \qquad \text{(Peak Norm. Dev. Temp.)}$$

$$\hat{G}(\hat{\tau}) = \frac{G(T)}{(T_{\max} - T_{\min})^{s}} \qquad \hat{G} \in [0,1] \qquad \text{(\% of peak } G\text{)}$$

While there is no need to use several parameters ($T_{\min}, T_{\max}, D_{\max}$) during analysis, they are necessary for fitting exercises.

While the use of $T_{\min}$ and $T_{\max}$ could be viewed as simplifying application, they only do when comparing across systems with difference extreme limits. Even then, they can obscure comparisons: e.g., is the difference caused by the limits or the shape?

For such parasites, these rates are typically measured at several constant temperatures to establish rate curves[3]. However, the full curves are rarely used; development calculations typically use the rate at an averaged temperature. The averaging method ranges from the formal temporal expected value (*i.e.*, integrated temperature over time) to the midpoint temperature (*i.e.*, halfway between average daily extrema). This entails approximation error in follow-on calculations – such as estimates of inter-host spread, general disease burden, and economic loss – beyond any other modeling and empirical error. Given modern computational tools, these approximations are not generally necessary, and we set out to numerically describe the error associated with them.

In the following sections, we revisit the use of a particular family of non-linear development curves, the *BETE* functions[4]. First, we present an alternative (but formally equivalent) representation, taking advantage of simple normalizations and using more informative parameters. Second, we use this reformulation to provide a formal basis to inform intuitions about and numerical calculations of approximation error. Third, we apply this new framework to historical data. Finally, we provide an R library to replicate all of the above.

Development Model

We consider development in (1) the continuous regime (*i.e.*, population level aggregation), (2) with no resource constraints (free development absent capacity limits), (3) subject to temperature oscillation, and (4) in the temperature range where there is net development:

$$\dot{D} = G(T(t))D(t) \qquad \text{(Development Eqn.)}$$

This describes exponential development, which could cover populations of bacteria, or total biomass of a fungal infection, or be re-arranged to cover time-to-appearance of sporillation sites.

[3] Subject to other specific context constraints – *e.g.*, the host, presence of other competing microbes.

[4] From "Funktion zwischen biologischer Entwicklung (BE) und Temperatur (TE)" in [1]– a function relating biological development and temperature.

For the form of $G(T)$, we will focus on a reformulation of the *BETE* function discussed in previous publications:

$$G(T) = \frac{(n+m)^{(n+m)}}{n^n m^m}(T - T_{\min})^n(T_{\max} - T)^m \qquad \text{(Development Coeff.)}$$

Our reasoning about normalization and parameter selection (if not the explicit details) and numerical tools for evaluating the consequences of variability, however, may be applied to other curve families.

While [3] states that the range of G as defined above is $[0, 1]$, this is wrong; the equation's source [1], however, does not make that error. The zero lower bound is correct (as should be obvious from the temperature difference terms), but the upper bound is determined by choice of ($T_{\min}$,$T_{\max}$). We correct this error in the reformulation below.

The potential for normalization error aside, ($T_{\min}$,$T_{\max}$) also cloud mathematical discussion and physical interpretation: shifting these bounds alters results, but is that due to a fundamental change in the curve (*e.g.*, how the peak relates to the shape parameters) or is simply a change in the relative location of the region of study? By scaling T appropriately – as [1] did originally – we can see the answer is unambiguously the latter.

One last complaint before we provide the alternative formulation: the m and n parameters are opaque and entangled.

By opaque, we mean that these parameters have no intuitive connection to the real phenomena, nor do they have obvious descriptive connections to curve. If we were to plot several combinations of (m, n), useful patterns would emerge (*e.g.*, increasing m shifts the peak right, and *vv.* for n, and increasing the sum $m + n$ makes the curve sharper), but those patterns may not be immediately apparent to the casual user of the equation.

By entangled, we mean that we can say little about the curve for a particular parameter value (or changes in it) without also knowing the other. For example, we previously mentioned that increasing m shifts the curve to the right – does a particular increase mean the curve peaks to the left or right of the center of the range? Does that increase cause the curve to become sharp enough to transition from not having an inflection point to having one?

Sometimes these (anti)features are inescapable, but thankfully not in this case. One real feature, however, to the (m, n) formulation is that is quite simple, and any transformation should preserve that simplicity.

With those constraints in mind, we developed an alternative expression, normalized and defined by more meaningful parameters: The first and last definitions cover properly normalizing the equation. The middle equations introduce alternative, independent parameters with direct physical interpretation – what is the peak development temperature, and how narrow is the appreciable development window relative to the survivable range – and direct, intuitive connection to how they alter the curves – δ moves the peak left and right, s modifies how wide the peak is. This formulation also makes for very straightforward expression of curve features associated with the derivatives:

$$\hat{G}'(\delta) = 0 \qquad \text{(Peak } \hat{G} \text{ at } \delta\text{)}$$

$$\hat{\tau}_{\pm} = \delta \left[1 \pm \sqrt{\frac{1-d}{\delta(s-1)}} \right] \qquad (\hat{G} \text{ Infl. Points})$$

$$\exists \hat{\tau}_{-} \iff s > \frac{1}{\delta} \qquad \text{(Criteria for Left Infl. Point)}$$

$$\exists \hat{\tau}_{+} \iff s > \frac{1}{1-\delta} \qquad \text{(Criteria for Right Infl. Point)}$$

Finally, we can also use maximum likelihood estimation to determine these parameters.

We cover the transformation from Development Coeff. to Rev. Development Rate Coeff. in the Supplemental Information, as well as some general analysis of this curve family.

do this. Keep in mind - the actual stochastic process is (probably?) waiting times on cell division / formation. So that informs the variation / probability model of the data, as does how the data were collected (constant time, measure CFUs vs measured time to sporulation).

Using (δ, s) to Compare Pathogens

In [2], the authors present a technique to compare several pathogen strains via a linearization of the development curves. The scheme is, essentially, de-linearizing the development scale based on the aggregate of the pathogens being compared. Their technique presents a fairly compelling view, simultaneously comparing minimum, maximum, and optimum development temperatures across many pathogens.

What is slightly problematic in this plot, however, is the result of the aggregation. The non-linear rescaling based on aggregate values leads relatively large residuals for sharper development curves. The aggregation is also questionable from a physical perspective: the pathogens development curves are from multiple host species, and no doubt with other context dependencies (*e.g.*, nutrient concentration, live vs. stored host material). Fortunately, making two very simple plots – T_{min} vs $T_{\mathrm{max}} - T_{\mathrm{min}}$ and δ vs s – creates the very same comparison with no error beyond the fit for the parameters. It can also elide any context dependencies if they are not covered in the legend, but at least they are not baked into scales of the comparison.

Figure 1: Once some data is sourced, this is a pair of straightforward plots: T_{min}vs ΔT and δ vs s. The data may be a bit tricky – for some of it, there's well-determined min, max, and optimal temperatures, so the only fit component is s. For others, the temperature bounds aren't available, so they would need to be tossed into the fitting exercise. That shouldn't be a problem, since that will be part of the MLE equation, just one extra step.

The Three Regions in (δ, s) Curves & Associated Linearization Errors

When dealing with temperature oscillations, analyses often assume the development value at an intermediate temperature – between the extrema, but not always the mean temperature – is a reasonable approximation of the mean development rate over the oscillation.

If the development equation were linear, this would not only be reasonable, but exactly correct when using the mean temperature:

$$\begin{aligned} G^*(\tau) &= A\tau + B, & \tau(t) &= \langle\tau\rangle + aP(t), & \frac{\int_T \tau\, dt}{T} &= \langle\tau\rangle \rightarrow \\ \langle G^* \rangle &= & \frac{\int_T G^*(\tau)}{T} &= A\langle\tau\rangle + B & &= G^*(\langle\tau\rangle) \end{aligned}$$

Alas, our work is not so simple.

What we have instead are regions of concavity. In concave down regions, the curve bends below the tangent line on both sides, meaning that an oscillation about a particular point would see lower rates on both sides. That is, the trough in development would be lower than estimated, as would any recovery, netting a decline on both sides. Therefore, using the rate for the mean temperature will always overestimate the actual development rate.

Missing figure

Side by side: concave down vs line and concave up vs line. Highlight integration error.

Contraversely, in the concave up region the opposite is true: the curve bends above the tangent line, and both sides will be underestimating the rate. So, oscillation in a concave up region will always increase the effective rate relative to the development rate at the static mean temperature of that oscillation.

The point where these regions meet is an inflection point, and the immediate vicinity of that inflection points forms the third region. Here, a temperature oscillation will spend some time in the underestimation region and some time in the overestimation region. For given oscillation amplitude, there is an associated $\langle\tau\rangle$ where that under- and over-estimation balance (for amplitudes which do not cause the oscillation to leave the boundaries of the development region or cross another inflection point). That is

$$\exists\, \langle\tau\rangle \qquad \text{s.t.} \qquad \frac{1}{T}\int_T \hat{G}\left(\langle\tau\rangle + a\sin\frac{2\pi t}{T}\right) dt = \hat{G}(\langle\tau\rangle)$$

or any other oscillating $P(t)$, though mean would depend on the particular $P(t)$. An analytical solution for $\langle\tau\rangle$ evades us, but it's straightforward to numerically characterize these balance points as well as arbitrary limits on the error:

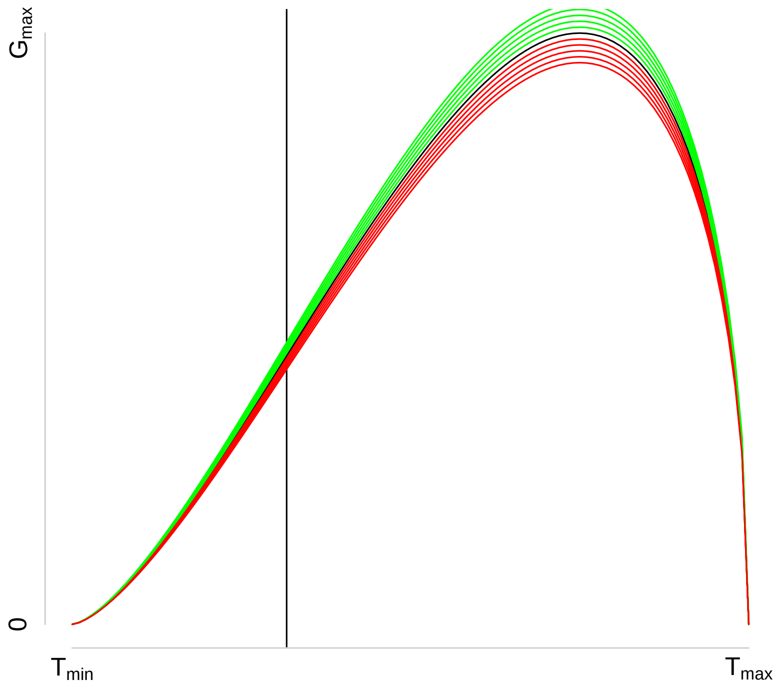

Figure 2: caption

For a particular d,s zoom on the inflection point. layout pm 1 percent error lines, 2-3-4-5 (up to useful perspective, by useful increments) lines. place points on those lines for increments of amplitude. Connect them up into contours.

$$\langle \hat{G} \rangle_T = \frac{\int_T \hat{G}(\hat{\tau}(t))\, dt}{T} \qquad \text{(Exp. Development Rate over Period)}$$

We compare this value to the simplification of only evaluating $\hat{G}$ at an aggregated temperature

$$\hat{G}\left(\langle \hat{\tau} \rangle\right) = \hat{G}\left(\frac{\int_T \hat{\tau}(t)\, dt}{T}\right) \qquad \text{(Growth Rate at } \langle \hat{\tau} \rangle\text{)}$$

and various further approximations of $\langle \hat{\tau} \rangle$, *e.g.*, $\langle \hat{\tau} \rangle \approx \frac{\hat{T_{\max}}+\hat{T_{\min}}}{2}$

We can divide the development curve by eye into three regions, Lower-Bounded (I), Linear (II), and Upper-Bounded (III)[5]. The division is deeply tied to mathematical features of the curve: extrema, concavity, and inflection points – *i.e.*, the first and second derivatives.

These features entail departure from a purely linear development response to temperature. A linear response would mean the effects of oscillation cancel.

The minima of this family of curves always fall at the boundaries, and the maximum is always uniquely at δ. There is always a concave down region around δ, and for particular (δ, s), there may be inflection point(s) on either side before the boundary and then concave up regions.

In the concave down region, any temperature oscillation will lead to overprediction by using the mean temperature. Likewise, in the concave up region, there is always underprediction. For an oscillation that crosses the inflection points, these effects can partially cancel.

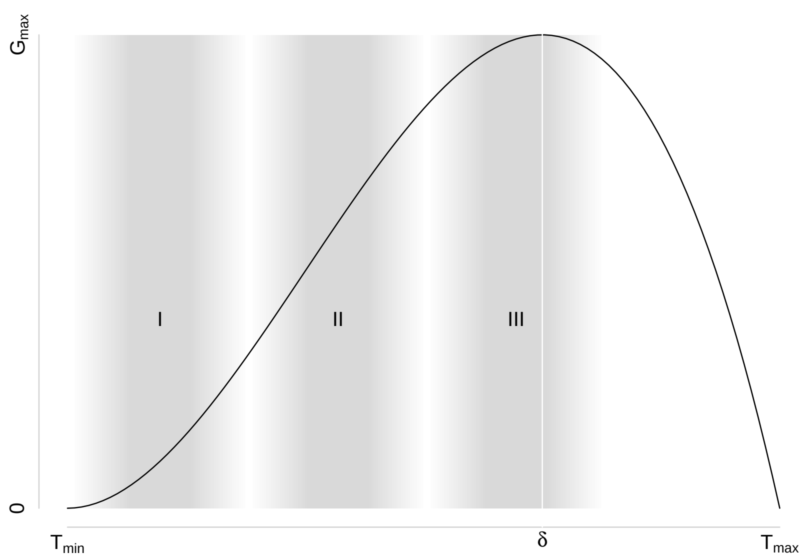

Figure 3: A rough outline of the three regions – Lower-Bounded (I), Linear (II), and Upper-Bounded (III) – for $\delta = 2/3$, $s = 3$ (the second curve considered in [3]). These regions could also fall to the right of the peak, for appropriate parameters (*e.g.*, (I) could not fall to the right in this case, but could if $\delta = 1/4$).

In [3], these regions are implied by the results of "simulation" evaluated at particular mean temperatures plus sinusoidal oscillations for a family of curves; we assume that simulation means numerical integration of some variety. We also numerically integrated the same set of curves. We obtained qualitatively similar results, but not the same points as [3];

[5]We discuss a formal characterization for these regions in the Supplemental Information. However, that formal approach is as complicated as simply proper computation of $\langle \hat{G} \rangle$. Which is to say, either own up to the crudeness of the approximation or properly calculate it.

we suspect that our numerical integration has less approximation and no other distinctions. We review the curves [3] considered in fig. 4.

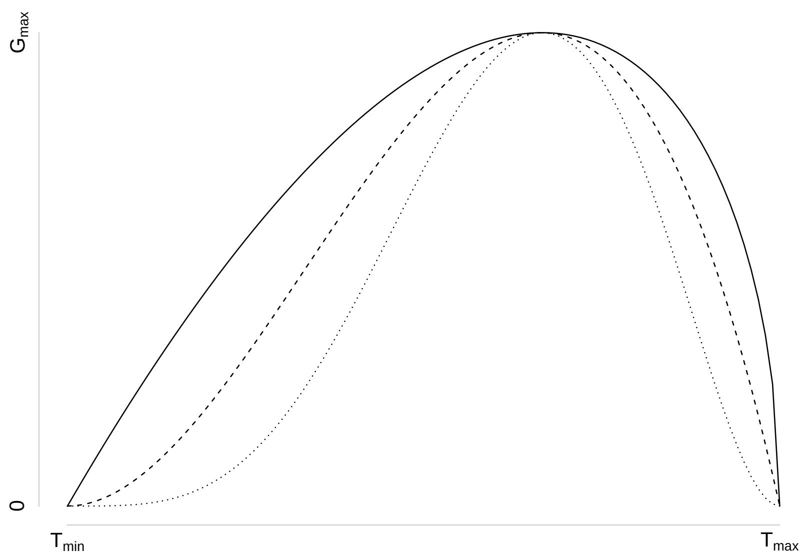

Figure 4: For $(m, n) = \{(\frac{1}{2}, 1), (1, 2), (2, 4)\}$, $(\delta, s) = \{(\frac{2}{3}, \frac{3}{2}), (\frac{2}{3}, 3), (\frac{2}{3}, 6)\}$. Note that peak coincidence is obvious from the latter parameterization, as is trend in curve width.

From these curves, we want the mean growth over an oscillation period, $\langle \hat{G}(\hat{\tau}(t)) \rangle_T$, with normalized, sinusoidal temperature oscillation around a particular mean temperature, $\hat{\tau}(t) = \langle \hat{\tau} \rangle + a_{\hat{\tau}} \sin(2\pi t)$. In [3], two oscillation amplitudes $a_{\hat{\tau}}$ were considered, 2.5C and 5C, which for their $\Delta T = 30$C correspond to $a_{\hat{\tau}} = \frac{1}{12}$& $\frac{1}{6}$, respectively.

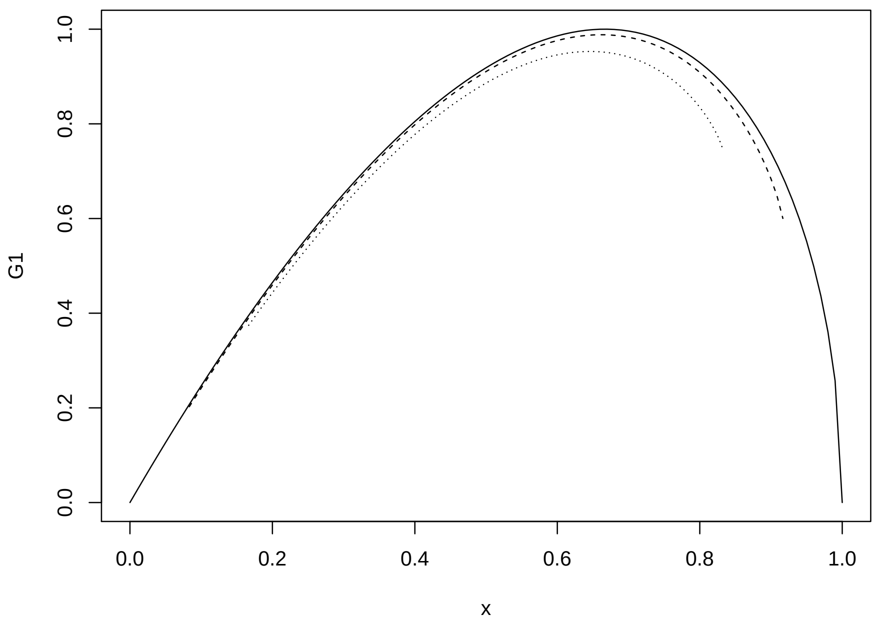

Figure 5: The $(m, n) = (\frac{1}{2}, 1)$ or $(\delta, s) = (\frac{2}{3}, \frac{3}{2})$ curves. As discussed in the supplement, these curve parameters have no inflection points, which means there can be no lower bounded region. As such, the expected development with oscillating temperature is always lower.

1 Models for $\hat{G}(\hat{\tau}, \dot{\hat{\tau}})$

2 Supplemental Information

Reparameterization of the *BETE* Function

Recall the definition of the *BETE* Function in [3]:

$$G(T) = \frac{(n+m)^{(n+m)}}{n^n m^m}(T - T_{\min})^n (T_{\max} - T)^m$$

and the chief complaints about it: (1) it is not normalized independent of $(T_{\min}, T_{\max})$, and (2) the parameters (m, n) are unintuitive (which also applies to original formulation in [1]). First, we need to deal with the error in normalization of G; to do so, we need the maximum

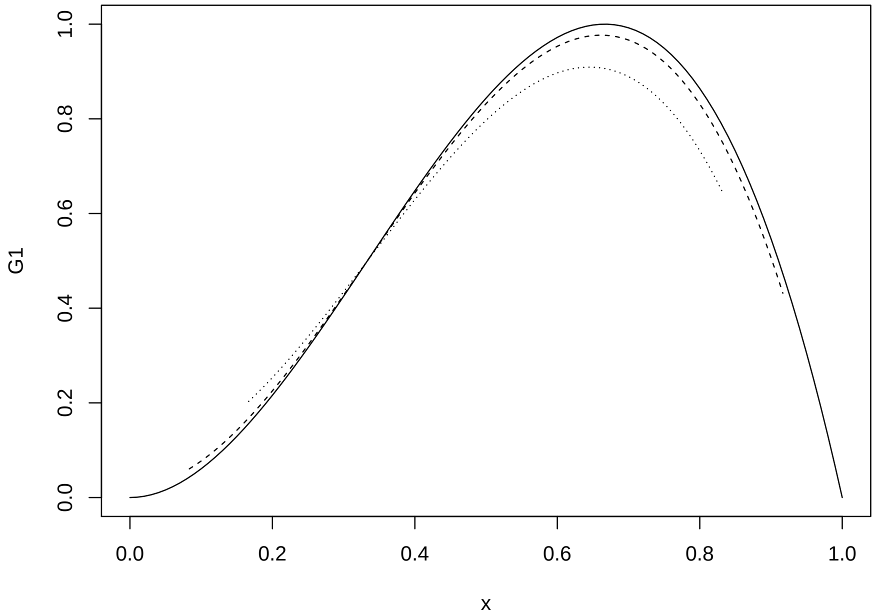

Figure 6: The $(m, n) = (1, 2)$ or $(\delta, s) = (\frac{2}{3}, 3)$ curves. Unlike the curves in fig. 5, there are inflection points, and thus some lower bounded region. When the oscillations overlap the lower bounded region, the development based on the pure temperature mean underpredicts.

value of G:

$$
\begin{aligned}
\left.\frac{dG}{dT}\right|_{T_{\text{peak}}} = 0 &= n(T_{\text{peak}} - T_{\text{min}})^{n-1}(T_{\text{max}} - T_{\text{peak}})^m - m(T_{\text{peak}} - T_{\text{min}})^n(T_{\text{max}} - T_{\text{peak}})^{m-1} \\
0 &= n(T_{\text{max}} - T_{\text{peak}}) - m(T_{\text{peak}} - T_{\text{min}}) \\
T_{\text{peak}} &= \frac{nT_{\text{max}} + mT_{\text{min}}}{n+m} \\
G(T_{\text{peak}}) &= \frac{(n+m)^{(n+m)}}{n^n m^m} \left(\frac{nT_{\text{max}} + mT_{\text{min}}}{n+m} - T_{\text{min}} \right)^n \left(T_{\text{max}} - \frac{nT_{\text{max}} + mT_{\text{min}}}{n+m} \right)^m \\
G(T_{\text{peak}}) &= \frac{(n+m)^{(n+m)}}{n^n m^m} \left(\frac{nT_{\text{max}} - nT_{\text{min}}}{n+m} \right)^n \left(\frac{mT_{\text{max}} - mT_{\text{min}}}{n+m} \right)^m \\
G(T_{\text{peak}}) &= (T_{\text{max}} - T_{\text{min}})^{n+m}
\end{aligned}
$$

so properly normalized, but still on a particular temperature scale, the development curve is

$$
\hat{G}(T) = \left(\frac{n+m}{T_{\text{max}} - T_{\text{min}}} \right)^{n+m} \frac{(T - T_{\text{min}})^n (T_{\text{max}} - T)^m}{n^n m^m}
$$

We assume the [3] plots are actually either derived from a form like this or by manual normalization by the peak. The work in [1], while mentioning that a normalization factor is required for this form, does not identify it.

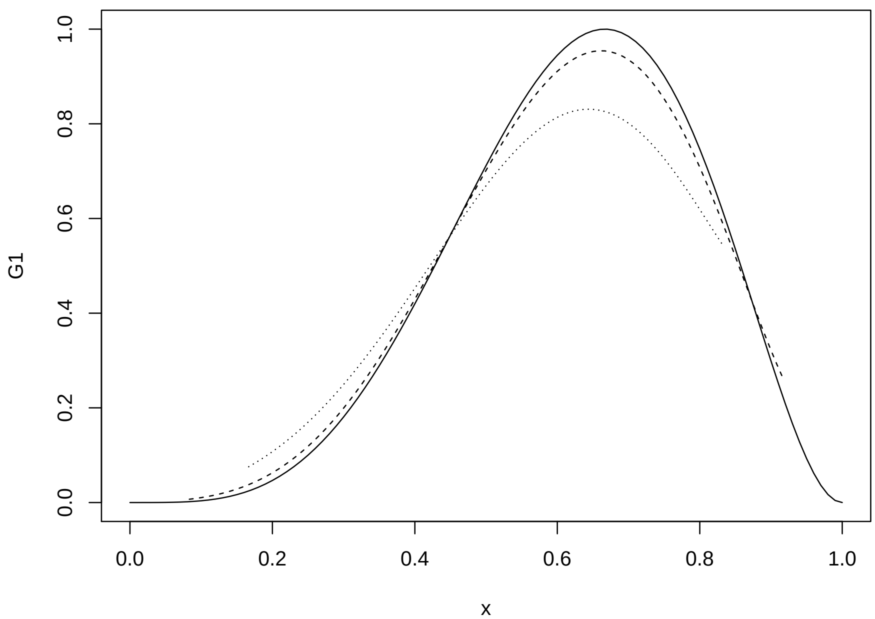

Figure 7: The $(m, n) = (2, 4)$ or $(\delta, s) = (\frac{2}{3}, 6)$ curves. With this curve, there are inflection points on both sides of the development curve that overlap with the oscillation region, thus we can observe underprediction on both sides of the curve. For many classes of pathogens, the right inflection point may not real – their death processes do not level off – so this "feature" would be a representation artifact.

Next, we would like to eliminate the specific scale associated with ($T_{\min}$, $T_{\max}$). To do so, we select a desired scale; in this case, we target $[0, 1]$, though scales that are symmetric about 0 are also often useful. We choose $[0, 1]$ because it has standard transformation that includes elements already present in $\hat{G}$, and because absolute temperature scales (*i.e.*, Kelvin and Rankin) are strictly positive; we expect [1] also used this transformation for similar reasons.

$$\begin{aligned}
\hat{\tau} &= \frac{T - T_{\min}}{T_{\max} - T_{\min}} \\
T &= (T_{\max} - T_{\min})\hat{\tau} + T_{\min} \\
\hat{G}(\hat{\tau}) &= \frac{(n+m)^{n+m}}{n^n m^m} \hat{\tau}^n (1 - \hat{\tau})^m
\end{aligned}$$

This transformed equation provides the percent of maximum development rate as a function of the percent of the temperature range, and is the same one obtained in [1].

This leaves only revisiting the shape parameters (m, n). We can start the search for better ones by trying features of the curve. That approach expects to achieve what, for example, the Gaussian does: it is parameterized by the x value where it takes on its maximum and the halfwidth between its inflection points[6].

[6]Or if you're more familiar with seeing it called the Normal Distribution, its mean and variance.

We already have one such feature in hand: the peak temperature. Transforming from the unnormalized T_{peak}, we obtain

$$\frac{\frac{nT_{\max}+mT_{\min}}{n+m} - T_{\min}}{T_{\max} - T_{\min}} = \delta = \frac{n}{m+n}$$
$$m + n = \frac{n}{\delta}$$
$$m = \frac{n}{\delta} - n$$

which can be used to rewrite $\hat{G}$ in terms of (n, δ)

$$\hat{G}(\hat{\tau}) = \frac{(\frac{n}{\delta})^{\frac{n}{\delta}}}{n^n(\frac{n}{\delta} - n)^{\frac{n}{\delta}-n}} \hat{\tau}^n (1-\hat{\tau})^{\frac{n}{\delta}-n}$$
$$\hat{G}(\hat{\tau}) = \frac{(\frac{1}{\delta} - 1)^n}{(1-\delta)^{\frac{n}{\delta}}} \hat{\tau}^n (1-\hat{\tau})^{\frac{n}{\delta}-n}$$
$$\hat{G}(\hat{\tau}) = \frac{(1-\delta)^n}{(1-\delta)^{\frac{n}{\delta}}} \left(\frac{\hat{\tau}}{\delta}\right)^n (1-\hat{\tau})^{\frac{n}{\delta}-n}$$
$$\hat{G}(\hat{\tau}) = \left(\frac{1-\hat{\tau}}{1-\delta}\right)^{\frac{n}{\delta}-n} \left(\frac{\hat{\tau}}{\delta}\right)^n$$
$$\hat{G}(\hat{\tau}) = \left[\left(\frac{\hat{\tau}}{\delta}\right)^{\delta} \left(\frac{1-\hat{\tau}}{1-\delta}\right)^{1-\delta}\right]^{\frac{n}{\delta}}$$

This re-arrangement leads to a natural second parameter, $s = \frac{n}{\delta} = m+n$, which determines how temperature-specific the development curve is. Since $\hat{G} \in [0, 1]$, increasing s causes the curve to drop off more quickly around δ. We could continue to use n as a parameter, however: while s can take on any value $\frac{n}{\delta}$ can, the effect of s can be understood independently of the value of δ. That is, s is no longer entangled with δ. This allows for a much more sensible consideration of, for example, the area under $\hat{G}$ over the parameter space, as shown in fig. 8.

Computational Form of Rev. Development Rate Coeff.

When conducting numerical analyses, the general practice is choose equivalent forms of an expression that minimizes (1) repeated calculation and (2) numerical error. For the growth equation, we can accomplish (1) by re-arranging to

$$C = \left[\frac{\left(\frac{1-\delta}{\delta}\right)^{\delta}}{1-\delta}\right]^s \qquad \text{(Rev. Development Computational Coeff.)}$$

where this value can be computed once for any given parameterization, leaving:

$$\hat{G} = C\left[\hat{\tau}^{\delta}(1-\hat{\tau})^{(1-\delta)}\right]^s$$

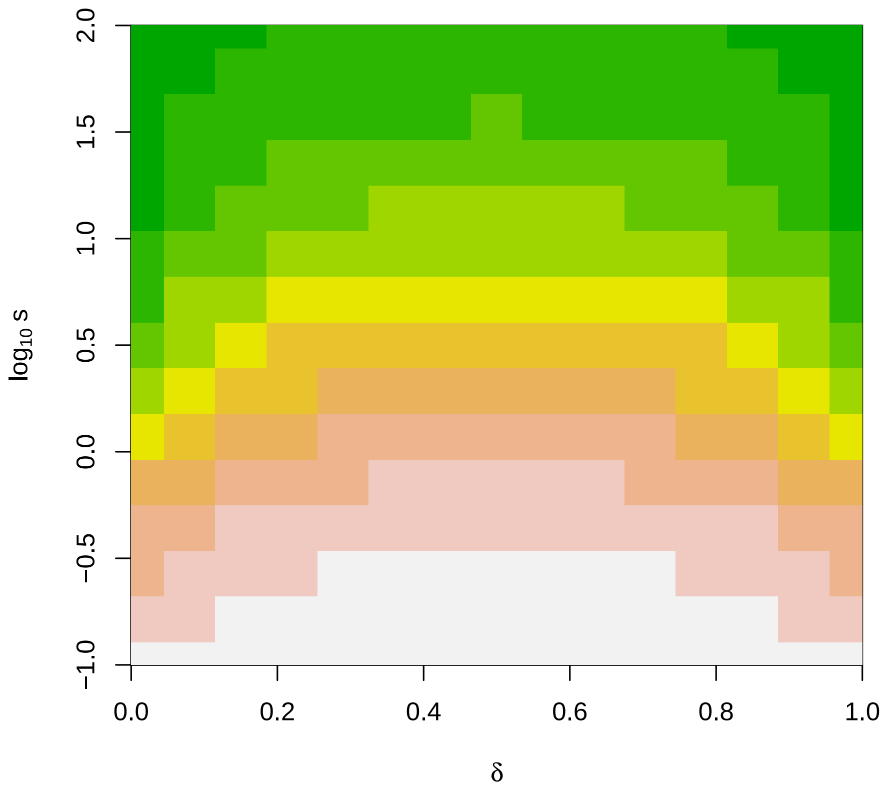

Figure 8: The area under $\hat{G}$ over a broad range of (δ,s). If we stuck with n as the shape parameter instead of s, this plot would have had a bizarre skew instead of the expected symmetry (unless of course we plotted against $\frac{n}{\delta}$, but then we are mixing axes). Given its symmetry, if we actually needed this particular result, we could save quite a bit of computation by only considering half the range, or obtain a more detailed view of the result in the same visual area without loss of information, etc.

Inflection Points of Re-Parameterized *BETE*

Recall that the inflection points determine the switches between concavity, and thus between under- and over-prediction regions. As such, their location and existence for particular parameters is an important feature.

In [1], the inflection points are identified as

$$\hat{\tau} = \frac{n}{n+m} \pm \frac{\sqrt{\frac{nm}{n+m-1}}}{n+m}$$

which we can re-arrange in terms of our parameter choice

$$\hat{\tau}_{\pm} = \delta\left[1 \pm \sqrt{\frac{1-\delta}{\delta(s-1)}}\right] \qquad (\hat{G}\text{ Inflection Points})$$

and which can then be used to determine the existence of inflection points for parameter combinations. We proceed by looking for (1) negative values in the square root (*i.e.*, imaginary or complex inflection points) and (2) inflection points that fall on or outside the domain boundaries.

We know that $\delta \in (0, 1)$ and $s \in (0, \infty)$, so negative values in the square root can only come from the $s - 1$ term. We can conclude then that inflection points do not exist for $s \leq 1$, which we state formally as

$$\exists \hat{\tau}_{\pm} \rightarrow s \in (1, \infty) \qquad \text{(Inflection Point Existence)}$$

which, as those familar with formal logic will note, does not actually tell us anything about the existence of $\hat{\tau}_{\pm}$, only that $s - 1 > 0$ when inflection point(s) exist. That fact, however, is useful for determining the left and right inflection point existence limits; it will allow us to not worry about changing the direction of inequalities over division and multiplication.

When inflection points do exist, for $\hat{\tau}_{-}$ to fall on or below the left boundary

$$\begin{aligned} 1 &> \sqrt{\frac{1-\delta}{\delta(s-1)}} \\ 1 &> \frac{1-\delta}{\delta(s-1)} \\ s\delta - \delta &> 1 - \delta \\ s\delta &> 1 \end{aligned}$$

so a left inflection point exists if and only if $s > \frac{1}{\delta}$. Before proceeding to $\hat{\tau}_{+}$, we should consider what we expect to find based on symmetry. What is $s > \frac{1}{\delta}$ telling us? The closer the peak is to the left boundary, the sharper that peak must be to still have an inflection point in that squeezed region. We would argue then the same for the right inflection point based on symmetry, which is $s > \frac{1}{1-\delta}$. Let's find out:

$$\begin{aligned} \frac{1}{\delta} - 1 &> \sqrt{\frac{1-\delta}{\delta(s-1)}} \\ \frac{1}{\delta^2}(1-\delta)^2 &> \frac{1-\delta}{\delta(s-1)} \\ \frac{1}{\delta}(1-\delta) &> \frac{1}{s-1} \\ \frac{\delta}{1-\delta} &< s - 1 \\ \frac{1}{1-\delta} &< s \end{aligned}$$

Now we can track back to the question of existence of *any* inflection points. We can start thinking with the case that is identical for $\hat{\tau}_{\pm}$: $\delta = \frac{1}{2}$. For that case, $s > 2$ is required for either inflection point. If, for example, we move the peak left to $\delta = \frac{1}{3}$, then the requirement for the left point increases to $s > 3$, but decreases to $s > \frac{3}{2}$ for the right (and *vice versa* if we mirror the move right to $\delta = \frac{2}{3}$). We can induce from this that the any inflection point criteria is

$$\exists\hat{\tau}_{\pm} \iff s \in \left(\frac{1}{\max(\delta, 1-\delta)}, \infty\right)$$
$$\exists\hat{\tau}_{-} \iff s \in \left(\frac{1}{\delta}, \infty\right)$$
$$\exists\hat{\tau}_{+} \iff s \in \left(\frac{1}{1-\delta}, \infty\right)$$

noting that for the limit that δ approaches one of the boundaries, the existence criteria (for the opposite inflection point) reduces to $s > 1$.

One final note: for some systems, $\hat{\tau}_+$ is non-physical. That is, there is no point past the peak that increasing temperture does a decreasing amount of harm to development progress. If we wish to preclude this, then, we must enforce

$$s \leq \frac{1}{1-\delta}$$

The Linear Region

In the so-called Linear Region, it is "reasonable" to approximate the development over a symmetric temperature oscillation by the development at the mean temperature of that oscillation. Formalizing the bounds of that region, however, is analytically complicated proposition for any substantive oscillation magnitude.

Thus, we will ultimately proceed numerically, but some initial analysis may prove useful. First, we know the oscillation must cross the inflection point for it to be possible for the under- and over-prediction regions to cancel. We can guess that associated mean temperature will not be far from the inflection point, since that will intractably weight one of the regions. Thus, we may get some traction considering the Taylor expansion about this value.

$$
\begin{aligned}
\hat{G}' &= Cs\left(\hat{\tau}^{\delta}(1-\hat{\tau})^{1-\delta}\right)^{s-1}\left[\delta\hat{\tau}^{\delta-1}(1-\hat{\tau})^{1-\delta} - (1-\delta)\hat{\tau}^{\delta}(1-\hat{\tau})^{-\delta}\right] \\
&= s\hat{G}\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right] \\
\hat{G}'' &= s\hat{G}'\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right] + s\hat{G}\left[-\frac{\delta}{\hat{\tau}^2} + \frac{1-\delta}{(1-\hat{\tau})^2}\right] \\
&= s\hat{G}\left[s\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right]^2 + \left[-\frac{\delta}{\hat{\tau}^2} + \frac{1-\delta}{(1-\hat{\tau})^2}\right]\right] \\
\hat{G}''' &= s\hat{G}'\left[s\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right]^2 + \left[-\frac{\delta}{\hat{\tau}^2} + \frac{1-\delta}{(1-\hat{\tau})^2}\right]\right] \\
&+ s\hat{G}\left[2s\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right]\left[\frac{\delta}{\hat{\tau}^2} - \frac{1-\delta}{(1-\hat{\tau})^2}\right] + \left[2\frac{\delta}{\hat{\tau}^3} - 2\frac{1-\delta}{(1-\hat{\tau})^3}\right]\right] \\
&= s\hat{G}\left[s^2\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right]^3 + s\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right]\left[-\frac{\delta}{\hat{\tau}^2} + \frac{1-\delta}{(1-\hat{\tau})^2}\right]\right. \\
&+ \left. 2s\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right]\left[\frac{\delta}{\hat{\tau}^2} - \frac{1-\delta}{(1-\hat{\tau})^2}\right] + \left[2\frac{\delta}{\hat{\tau}^3} - 2\frac{1-\delta}{(1-\hat{\tau})^3}\right]\right] \\
&= s\hat{G}\left[s^2\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right]^3 + s\left[\frac{\delta}{\hat{\tau}} - \frac{1-\delta}{1-\hat{\tau}}\right]\left[\frac{\delta}{\hat{\tau}^2} - \frac{1-\delta}{(1-\hat{\tau})^2}\right] + 2\left[\frac{\delta}{\hat{\tau}^3} - \frac{1-\delta}{(1-\hat{\tau})^3}\right]\right]
\end{aligned}
$$

We could obvious consider derivatives indefinitely, but we will see what sort of approximation this provides:

$$
A = \left[\frac{\delta}{\hat{\tau}_-} - \frac{1-\delta}{1-\hat{\tau}_-}\right] \tag{1}
$$

$$
\hat{G}^{(3)}\Big|_{\hat{\tau}_-} = s\hat{G}(\hat{\tau}_-)\left[\frac{1}{s} + A(\hat{\tau} - \hat{\tau}_-)\right. \tag{2}
$$

$$
\left. + \frac{(\hat{\tau}-\hat{\tau}_-)^3}{6}\left[s^2A^3 + sA\left[\frac{\delta}{\hat{\tau}^2} - \frac{1-\delta}{(1-\hat{\tau})^2}\right] + 2\left[\frac{\delta}{\hat{\tau}^3} - \frac{1-\delta}{(1-\hat{\tau})^3}\right]\right]\right] \tag{3}
$$

implies that thinking in terms of the offset from the inflection point may be a useful approach. Considering only $\hat{\tau}_-$[7], we can write $\hat{\tau} = \hat{\tau}_- + \epsilon$ where ϵ is the small difference between the oscillation mean and the inflection point (and may be positive or negative). We could then write

[7]Both because it is likely more physically meaningful, and because it should be possible to obtain $\hat{\tau}_+$ results by symmetry arguments.

$$
\begin{aligned}
\hat{G}(\epsilon) &= \left[\left(\frac{\epsilon}{\delta}+1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right)^{\delta}\left(\frac{1-\delta\left[1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]-\epsilon}{1-\delta}\right)^{1-\delta}\right]^{s} \\
&= \left[\left((1-\delta)\frac{\frac{\epsilon}{\delta}+1-\sqrt{\frac{1-\delta}{\delta(s-1)}}}{1-\delta\left[1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]-\epsilon}\right)^{\delta}\left(\frac{1-\delta\left[1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]-\epsilon}{1-\delta}\right)\right]^{s} \\
&= \left[\left(\frac{\frac{\epsilon}{\delta}+1-\sqrt{\frac{1-\delta}{\delta(s-1)}}-\epsilon-\delta\left[1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]}{1-\delta\left[1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]-\epsilon}\right)^{\delta}\left(\frac{1-\delta\left[1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]-\epsilon}{1-\delta}\right)\right]^{s} \\
&= \left[\left(1+\frac{\frac{\epsilon}{\delta}-\sqrt{\frac{1-\delta}{\delta(s-1)}}}{1-\delta\left[1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]-\epsilon}\right)^{\delta}\left(\frac{1-\delta\left[1-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]-\epsilon}{1-\delta}\right)\right]^{s} \\
&= \left[\left(1+\frac{\frac{\epsilon}{\delta}-\sqrt{\frac{1-\delta}{\delta(s-1)}}}{1-\delta\left[1+\frac{\epsilon}{\delta}-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]}\right)^{\delta}\left(\frac{1-\delta\left[1+\frac{\epsilon}{\delta}-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]}{1-\delta}\right)\right]^{s} \\
&= \left[\left(1+\frac{\frac{\epsilon}{\delta}-\sqrt{\frac{1-\delta}{\delta(s-1)}}}{1-\delta-\delta\left[\frac{\epsilon}{\delta}-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]}\right)^{\delta}\left(1-\frac{\delta\left[\frac{\epsilon}{\delta}-\sqrt{\frac{1-\delta}{\delta(s-1)}}\right]}{1-\delta}\right)\right]^{s}
\end{aligned}
$$

which is still does not provide great insight. However, it is more conducive to analysis with Taylor expansion. We can expand just the first term

Region Criteria

Any given temperature oscillation establishes the region on the growth curve. Recall that we proposed three categories for these regions – Lower Bounded (I), Linear (II), and Upper-Bounded (III) – as an indicator for whether using an average $\hat{\tau}$ with the curve will under-, accurately, or over-estimate the real growth.

These regions can be subjectively assigned. However, we recommend a simple formal assessment: approximate the curve for the covered region with two lines, one of them constant. This provides four apparent parameters for the two lines: the constant level (a), the slope for the second line (b) and it's constant offset (a_b), and the temperature to switch between them ($\hat{\tau}_0$).

However, we can reduce to two parameters, $\hat{\tau}_0$ and b. Consider a: by inspection, the mean of $\hat{G}$ in the left region minimizes the error between the curve and a constant level. Thus:

$$
a = \frac{\int_l^{\hat{\tau}_0} \hat{G}\left(\hat{\tau}\right) d\hat{\tau}}{\hat{\tau}_0 - l} = \langle \hat{G} \rangle_l
$$

Next, because the left and right region lines must join, we may eliminate a_b:

$$
a = b\hat{\tau}_0 + a_b \rightarrow a_b = \langle \hat{G} \rangle_l - b\hat{\tau}_0
$$

Now consider the least-squares error

$$F = \int_l^{\hat{\tau}_0} (\hat{G}(\hat{\tau}) - a)^2 \, d\hat{\tau} + \int_{\hat{\tau}_0}^r (\hat{G}(\hat{\tau}) - b(\hat{\tau} - \hat{\tau}_0) - a)^2 \, d\hat{\tau} \qquad \text{(Least Sq. Err.)}$$

which expands to

$$\begin{aligned}
F &= \int_l^{\hat{\tau}_0} \hat{G}(\hat{\tau})^2 - 2a\hat{G}(\hat{\tau}) + a^2 \, d\hat{\tau} \\
&\quad + \int_{\hat{\tau}_0}^r \hat{G}(\hat{\tau})^2 - 2a\hat{G}(\hat{\tau}) + a^2 - 2(\hat{G}(\hat{\tau}) - a)b(\hat{\tau} - \hat{\tau}_0) + b^2(\hat{\tau} - \hat{\tau}_0)^2 \, d\hat{\tau} \\
F &= (r - l) \left[\langle \hat{G} \rangle_l^2 + \langle \hat{G}^2 \rangle_{lr} - 2 \langle \hat{G} \rangle_l \langle \hat{G} \rangle_{lr} \right] \\
&\quad + b^2 \int_{\hat{\tau}_0}^r (\hat{\tau} - \hat{\tau}_0)^2 \, d\hat{\tau} - 2b \int_{\hat{\tau}_0}^r \hat{G}(\hat{\tau}) (\hat{\tau} - \hat{\tau}_0) \, d\hat{\tau} + 2ba \int_{\hat{\tau}_0}^r (\hat{\tau} - \hat{\tau}_0) \, d\hat{\tau} \\
F &= (r - l) \left[\langle \hat{G} \rangle_l^2 + \langle \hat{G}^2 \rangle_{lr} - 2 \langle \hat{G} \rangle_l \langle \hat{G} \rangle_{lr} \right] \\
&\quad + \frac{b^2 (r - \hat{\tau}_0)^3}{3} + b \langle \hat{G} \rangle_l (r - \hat{\tau}_0)^2 + 2b \int_r^{\hat{\tau}_0} \hat{G}(\hat{\tau}) (\hat{\tau} - \hat{\tau}_0) \, d\hat{\tau}
\end{aligned}$$

Now, consider the partial *wrt* b at the extrema:

$$\begin{aligned}
0 &= 2\frac{b(r - \hat{\tau}_0)^3}{3} + \langle \hat{G} \rangle_l (r - \hat{\tau}_0)^2 + 2 \int_r^{\hat{\tau}_0} \hat{G}(\hat{\tau}) (\hat{\tau} - \hat{\tau}_0) \, d\hat{\tau} \\
b &= 3 \frac{\langle \hat{G}(\hat{\tau}) (\hat{\tau} - \hat{\tau}_0) \rangle_r}{(r - \hat{\tau}_0)^2} - \frac{3}{2} \frac{\langle \hat{G} \rangle_l}{r - \hat{\tau}_0}
\end{aligned}$$

and the corresponding derivative extrema *wrt* $\hat{\tau}_0$:

$$\begin{aligned}
0 &= \frac{\partial \langle \hat{G} \rangle_l}{\partial \hat{\tau}_0} (r - l) \left[\langle \hat{G} \rangle_l - \langle G \rangle_{lr} \right] \\
&\quad + b(r - \hat{\tau}_0) \left[\frac{r - \hat{\tau}_0}{2} \left[\frac{\partial \langle \hat{G} \rangle_l}{\partial \hat{\tau}_0} - b \right] + \langle G \rangle_r - \langle \hat{G} \rangle_l \right]
\end{aligned}$$

noting

$$\frac{\partial \langle \hat{G} \rangle_l}{\partial \hat{\tau}_0} = \frac{G(\hat{\tau}_0) - \langle \hat{G} \rangle_l}{\hat{\tau}_0 - l}$$

we may write down an equation of $\hat{G}$ and $\hat{\tau}_0$ that is suitable (if elaborate) for numerical root finding in $\hat{\tau}_0$.

Also note, this form is independent of the exact $\hat{G}(\hat{\tau})$, though obviously the criteria only makes sense for curves "like" these. The following R code produces the $(a, b, \hat{\tau}_0)$ parameters:

```
> library(stats)
> expect <- function(G,l,u,...) {
```

```
+   ifelse(l!=u, integrate(G,l,u,...)$value / (u-l), G(l))
+ }
> dFdtauMin<-function(G,l,r) {
+   Grl <- expect(G,l,r); diff <- r - l
+   function(t0) {
+     Gl <- expect(G,l,t0)
+     ader <- (G(t0) - Gl)/(t0 - l)
+     rDiff <- r - t0
+     Gr <- expect(G,t0,r)
+     Gt <- expect(function(t) G(t)*t,t0,r)
+     b <- 3*(Gt-t0*Gr)/rDiff^2 -
+       (3/2)*(Gl/rDiff)
+     ader*diff*(Gl-Grl) +
+       b*rDiff*(rDiff*(ader-b)/2+(Gr-Gl))
+   }
+ }
> tauMin<-function(G,l,r,f=dFdtauMin(G,l,r)) {
+   optimize(f, lower=l, upper=r)
+ }
> bG<-function(G, l=NULL, u, t0, a=expect(G,l,t0) ) {
+   Gt <- Vectorize(function(t) G(t)*(t-t0))
+   (3/(u-t0)^2)*expect(Gt,t0,u)-(3/2)*a/(u-t0)
+ }
> abt<-function(interval, G, l=interval[1],r=interval[2]) {
+   t0<- tauMin(G,l,r)$minimum
+   a <- expect(G, l, t0)
+   b <- bG(G, u=r, t0=t0, a)
+   list(t0=t0,a=a,b=b)
+ }
```

3 Prep for Paramater Sweep

Since we are looking for parameter combinations that result in certain behaviors - specifically, defects in assuming a constant $\hat{G}$ when there is temporal variation in $\hat{\tau}$ - we need to partition $\hat{G}$ according to regions of behavior. We have already identified one such partition: increasing ($\hat{\tau} < \delta$) vs decreasing ($\hat{\tau} > \delta$).

Regions of concavity are probably also of interest, so we need to identify inflection points

$$\hat{G}'(\hat{\tau}) = \frac{1}{\delta^n(1-\delta)^{\frac{n}{\delta}-n}} \frac{d}{d\hat{\tau}} \left[\hat{\tau}^n(1-\hat{\tau})^{\frac{n}{\delta}-n}\right]$$

$$\hat{G}'(\hat{\tau}) = \frac{1}{\delta^n(1-\delta)^{\frac{n}{\delta}-n}} \left[n\hat{\tau}^{n-1}(1-\hat{\tau})^{\frac{n}{\delta}-n} - (\frac{n}{\delta}-n)\hat{\tau}^n(1-\hat{\tau})^{\frac{n}{\delta}-n-1}\right]$$

$$\hat{G}'(\hat{\tau}) = \frac{n\hat{\tau}^{n-1}(1-\hat{\tau})^{\frac{n}{\delta}-n-1}}{\delta^n(1-\delta)^{\frac{n}{\delta}-n}} \left[(1-\hat{\tau}) - (\frac{1}{\delta}-1)\hat{\tau}\right]$$

$$\hat{G}'(\hat{\tau}) = \frac{n}{\delta}\hat{G}\left(\hat{\tau}\right) \frac{\delta-\hat{\tau}}{\hat{\tau}(1-\hat{\tau})}$$

for manipulation sake, define $f(\hat{\tau}) = \frac{n}{\delta}\frac{\delta-\hat{\tau}}{\hat{\tau}(1-\hat{\tau})}$

$$\hat{G}''(\hat{\tau}) = f(\hat{\tau})\hat{G}(\hat{\tau})' + \hat{G}(\hat{\tau})\frac{df}{d\hat{\tau}} = f(\hat{\tau})^2\hat{G}(\hat{\tau}) + \hat{G}(\hat{\tau})\frac{df}{d\hat{\tau}}$$

so at candidate inflection points ($\hat{G}''(\hat{\tau}) = 0$), we can trivial exclude $\hat{G} = 0$ as that only occurs for $\hat{\tau} = 0, 1$ and inflection points at the boundaries are not of interest. This leaves:

$$0 = f(\hat{\tau})^2 + \frac{df}{d\hat{\tau}}$$

since

$$\frac{df}{d\hat{\tau}} = -\frac{n}{\delta}\left[\frac{\hat{\tau}(1-\hat{\tau}) + (\delta-\hat{\tau})(1-2\hat{\tau})}{\hat{\tau}^2(1-\hat{\tau})^2}\right]$$

$$\frac{df}{d\hat{\tau}} = -\frac{n}{\delta}\left[\frac{\hat{\tau}^2 - 2\hat{\tau}\delta + \delta}{\hat{\tau}^2(1-\hat{\tau})^2}\right] = -\frac{\delta}{n}f^2 - n\frac{1-\delta}{\hat{\tau}^2(1-\hat{\tau})^2} = -\frac{\delta}{n}f^2\left[1 + \delta\frac{1-\delta}{(\delta-\hat{\tau})^2}\right]$$

aside: define for later use:

$$g = \frac{\delta}{n}\left[1 + \delta\frac{1-\delta}{(\delta-\hat{\tau})^2}\right], \text{s.t. } f' = -f^2 g$$

using the results for f' we obtain

$$1 = \frac{\delta}{n}\left[1 + \delta\frac{1-\delta}{(\delta-\hat{\tau})^2}\right]$$

$$n - \delta = \delta^2\frac{1-\delta}{(\delta-\hat{\tau})^2}$$

$$(\delta-\hat{\tau})^2 = \delta^2\frac{1-\delta}{n-\delta}$$

$$\hat{\tau} = \delta\left[1 \pm \sqrt{\frac{1-\delta}{n-\delta}}\right]$$

from this result, we can draw some useful facts: if $n \leq \delta$, there are no inflection points; if $n = 1$, there is never a $\hat{\tau}_-$ inflection point and only a $\hat{\tau}_+$ inflection point for $\delta < 0.5$; finally, given a δ, n must be $> \frac{\delta}{1-\delta}$ to have a $\hat{\tau}_+$ inflection point. Also note: $g(\hat{\tau}_\pm) = 1$. Exploring g further for a moment:

$$g' = -2\frac{\delta^2}{n}\frac{1-\delta}{(\delta-\hat{\tau})^3}$$

$$g^{(m)} = (-1)^m(m+1)!\frac{\delta^2}{n}\frac{1-\delta}{(\delta-\hat{\tau})^{2+m}}$$

for inflection points

$$g^{(m)} = (-1)^m(m+1)!\frac{\delta^2}{n}\frac{1-\delta}{(\mp\delta\sqrt{\frac{1-\delta}{n-\delta}})^{2+m}}$$

$$g^{(m)} = (m+1)!\frac{1}{n}\frac{n-\delta}{(\delta\sqrt{\frac{1-\delta}{n-\delta}})^m}$$

$$g^{(m)} = (m+1)!\frac{1}{n\delta^m}\frac{(n-\delta)^{1+\frac{m}{2}}}{(\sqrt{1-\delta})^m}$$

4 Regions Of Equivalent Growth

Now we consider the case of

$$\Delta = \hat{G}(\bar{\hat{\tau}}) - \hat{G}(\hat{\tau}(t))$$

where $\hat{\tau}(t)$ is a periodic function, with period t_p; Δ is the growth rate defect between assuming $\hat{\tau}$ is constant at its average $\bar{\hat{\tau}}$ rather than oscillating. The Taylor expansion of Δ about $\bar{\hat{\tau}}$ is:

$$\Delta = -\hat{G}'(\bar{\hat{\tau}})(\hat{\tau}(t) - \bar{\hat{\tau}}) - \frac{\hat{G}''(\bar{\hat{\tau}})}{2}(\hat{\tau}(t) - \bar{\hat{\tau}})^2 - \frac{\hat{G}'''(\bar{\hat{\tau}})}{6}(\hat{\tau}(t) - \bar{\hat{\tau}})^3 \dots$$

If we write $\hat{\tau}(t) = \omega(t) + \bar{\hat{\tau}}$ - that is, isolating the oscillating component and the average component. The expansion is then

$$\Delta = -\hat{G}'(\bar{\hat{\tau}})\omega(t) - \frac{\hat{G}''(\bar{\hat{\tau}})}{2}\omega(t)^2 - \frac{\hat{G}'''(\bar{\hat{\tau}})}{6}\omega(t)^3 \dots$$

Our professed interest is in regions "near" inflection points, so let's consider for a moment (1) oscillation about one of those points and (2) the net resulting defect over a full period. The $\omega(t)$ term will vanish - it is defined to integrate to 0 over a period. The second term will also vanish by definition - G'' of an inflection point is 0. Leaving:

$$\int_{-t_p/2}^{t_p/2} \Delta dt = -\frac{\hat{G}'''(\bar{\hat{\tau}})}{6} \int_{-t_p/2}^{t_p/2} \omega(t)^3 dt \dots$$

Furthermore, if we choose our oscillating component ω to be an odd function - *e.g.*, a sine - then we have

$$\int_{-t_p/2}^{t_p/2} \Delta dt = -\sum_{m=2}^{\infty} \frac{\hat{G}^{(2m)}(\bar{\hat{\tau}})}{(2m)!} \int_{-t_p/2}^{t_p/2} \omega(t)^{2m} dt \dots$$

TODO: evaluate size of defect as a function of δ, n, and sine amplitude, divide by $\hat{G}(\bar{\hat{\tau}})$ to get as a percent defect.

5 CP Junk

clearly, we need some additional derivatives to understand the higher order terms:

$$\hat{G}'''(\hat{\tau}) = f'\hat{G}' + f\hat{G}'' + \hat{G}'f' + \hat{G}f''$$

$$\hat{G}'''(\hat{\tau}) = -2f^3 g\hat{G} + f\hat{G}'' + \hat{G}f''$$

$$\hat{G}'''(\hat{\tau}) = -2f^3 g\hat{G} + f\hat{G}'' + \hat{G}(2f^3g^2 - f^2g')$$

and, since we're interested in the behavior at the inflection point, let's simplify taking advantage of properties at the inflection point:

$$\hat{G}'''(\bar{\hat{\tau}}) = -f^2 g'\hat{G}$$

$$\hat{G}'''(\bar{\hat{\tau}}) = 2n\frac{1-\delta}{(\delta - \bar{\hat{\tau}})\bar{\hat{\tau}}^2(1-\bar{\hat{\tau}})^2}\hat{G}$$

For the moment, let's assume our even, periodic function is a cosine:

$$\hat{\tau}(t) = a\cos\frac{2\pi t}{t_p} + \bar{\hat{\tau}}$$

where $a \leq \min(\bar{\bar{\tau}}, 1-\bar{\bar{\tau}})$. In keeping with our dimensionless approach, $\hat{t} = \frac{2\pi}{t_p} t$ yields

$$\hat{\tau}(\hat{t}) = a \cos \hat{t} + \bar{\bar{\tau}}, \Delta = \hat{G}(\bar{\bar{\tau}}) - \frac{1}{\pi} \int_0^{\pi} \hat{G}(\hat{\tau}(\hat{t})) d\hat{t}$$

Applying our assumptions about temperature functional form to Δ:

$$\Delta = \left(\frac{\bar{\bar{\tau}}}{\delta}\right)^n \left(\frac{1-\bar{\bar{\tau}}}{1-\delta}\right)^{\frac{n}{\delta}-n} - \frac{1}{\pi \delta^n (1-\delta)^{\frac{n}{\delta}-n}} \int_0^{\pi} (a \cos \hat{t} + \bar{\bar{\tau}})^n (1 - a \cos \hat{t} - \bar{\bar{\tau}})^{\frac{n}{\delta}-n} d\hat{t}$$

our immediate interest is in the zero-defect case, so

$$\bar{\bar{\tau}}^n (1-\bar{\bar{\tau}})^{\frac{n}{\delta}-n} = \frac{1}{\pi} \int_0^{\pi} (a \cos \hat{t} + \bar{\bar{\tau}})^n (1 - a \cos \hat{t} - \bar{\bar{\tau}})^{\frac{n}{\delta}-n} d\hat{t}$$

References

[1] S Analytis. Über die relation zwischen biologischer entwicklung und temperatur bei phytopathogenen pilzen. *Journal of Phytopathology*, 90(1):64–76, 1977.

[2] Morris Cohen and CE Yarwood. Temperature response of fungi as a straight line transformation. *Plant Physiology*, 27(3):634–638, 1952.

[3] H Scherm and AHC Van Bruggen. Global warming and nonlinear growth: how important are changes in average temperature? *Phytopathology*, 84(12):1380–1384, 1994.


```
> delta <- 0.75
> s <- 1.5/delta
> taum<-function(s,delta) delta*(1-sqrt((1-delta)/(s-1)/delta))
> Gshift <- function(s,delta) {
+   off <- taum(s,delta)
+   G<-def.G(s,delta)
+   function(tau) G(tau+off)
+ }
> tester<-function(delta,s) {
+   sq <- sqrt((1-delta)/(s-1)/delta)
+   m <- (1-sq)
+   dm <- delta*m
+   mdm <- 1 - dm
+   c <- (((1-delta)*m/mdm)^(delta-1))^s
+   function(e) {
+     c*(m + e/mdm*(sq-e/mdm))^s
+   }
+ }
> tp<-tester(delta,s)
> off<-taum(s,delta)
> plot(tp,xlim=c(-off,1-off),ylim=c(0,1))
> f<-Gshift(s,delta)
> curve(f,add=T,col="red")
```