Notes on germination model for Dan
By Lizzie & Megan so far

Megan and I discussed the changes needed to do simulations for Dan's germination questions. Specifically, Dan is interested in building from the data from his germination trials and competition experiment to do some forecasting of how climate change could shift competitive outcomes due to priority effects.

1 What needs to change

We need a model that has priority effects, and to add 'chilling' somehow to the model. Specifically we want a model where with maximum chilling you get your maximum germination at the earliest time. This means that lower chilling will have two effects: lower germination, and later germination.

How it compares to previous model: (1) In our previous model both species start at the same time ($\delta T = 0$). Now we will explicitly include the time-lag (but we may be able to make that within year part an equivalence) and now changes in timing become a f(x) of chilling and how that connects to resource pulse (so how the cues connect to the resource pulse timing).

In our original model, we had a start of season parameter (τ_p) that determined the germination amount for each species (depending on how close τ_i was to τ_p) and changed each year. Here, (2) we will keep τ_p constant and effectively allow the start of season to always be the same—what Lizzie is thinking of as a biological start of season—and species will germinate after that date depending on their species-level parameters + chilling that year.

Another way to put this ... last time we assumed τ_i was fixed and moved around τ_p (and what mattered was the distance); now we assume τ_p is fixed and species move around depending on chilling. **Do we need this?** we asked ourselves. Yes, because we need germination to not be instantaneous with τ_p. Also, Lizzie adds—it's nice as it's more equivalent to there being a biological start of the season and that there are 'early' and 'late' species relative to that.
One more important outcome of these changes—in our previous model tracking put you closer to pulse and you germinated more, here you can have a priority effect and get a big benefit without using so many seeds (before, with tracking, you germinated at a high fraction every year).

2 How to vary germination timing

How to vary germination time (relative to pulse) with more chilling?

Season starts at resource pulse (that's $t = 0$). And we introduce some new parameters...

- $\tau_{g,i}$ – **species-specific germination timing** given maximum chilling (must be after pulse)

- $\tau_{g,i}$ can be delayed due to chilling with $\tau_{c,i}$ – **species-specific delay** given less than maximum chilling
- So, $\tau_{g,i} + \tau_{c,i}$ would be **the realized germination date**, which we refer to as $\hat{\tau_{g,i}}$.

This model allows the following trade-offs:

- R^* versus $\tau_{g,i}$
- R^* versus $\tau_{c,i}$

Constraint: Species that do not delay with chilling should have a higher germination fraction.

We'll have a new germination equation, that depends on **chilling** (ξ): $g_i = g_{max,i}e^{(-\xi)^2/h}$
$\tau_c = f(\xi)$ [could just be linear with threshold, or exponential etc.]

While we agreed that g_{max} likely varies by species, and will generally be lower for species with later $\tau_{g,i}$, we decided not to vary this as we have enough to vary already.

Trade-offs inherent in the model:

- $R*$ vs. $\tau_{g,i}$
- $R*$ vs. $\tau_{c,i}$

3 Equations

We keep the year to year dynamics ...

$$N_i(t+1) = s_i(N_i(t)(1 - g_i(t)) + \phi_i B(t + \delta) \tag{1}$$

And the production of new biomass each season still follows a basic R^* competition model: new biomass production depends on its resource uptake ($f_i(R)$ converted into biomass at rate c_i) less maintenance costs (m_i), with uptake controlled by a_i and u_i:

$$\frac{\partial B_i}{\partial t} = [c_i f_i(R) - m_i]B_i \tag{2}$$

$$f_i(R) = \frac{a_i R^{\theta_i}}{1 + a_i u_i R^{\theta_i}} \tag{3}$$

The resource (R) itself declines across a growing season due to uptake by all species and abiotic loss (ϵ):

$$\frac{\mathrm{d}R}{\mathrm{d}t} = -\sum_{i=1}^{n} f_i(R)B_i - \epsilon R \tag{4}$$

With the initial condition (**second line is new**):

$$B(t + 0) = N_i(t)g_i(t)b_{0,i} \tag{5}$$

$$B_i(t = \hat{\tau_{g,i}}) = N_i(t)g_i(t)b_{0,i} \tag{6}$$

And germination is now dependent on chilling ...

$$g_i(t) = g_{max} e^{-\xi^2/h} \tag{7}$$

Though we have not defined the chilling function yet.

4 How to implement

Use a two-stage ODE: solve for the first species and resource for a fixed number of days, then use that as the initial conditions for the second stage, where you add the other species.
Stuff we do no longer need:

- tracking
- τ_i

5 Next steps

See `_READMEpriorityeff.txt`

- Adding in two-step ODE (Megan says this is very straightforward)
- Build an environment with heating, cooling and resource pulse and relate back to τ_i
  - Try species with same germination fraction no matter the environment
  - Try species with increasing fraction with more chilling
- Think on two strategies versus continuous (or is continuous low warming).
- Stick with our old parameters?

covar(pulse size, chill units) – discussed in relation to what happens in years when one species is early and draws down the resource below later species' $R*$ (we think that they still go but hopefully they don't germinate too much) or change covar(epsilon, chill units)