date
our three names, yours first

Diapause model for spruce budworms

Brief statement of what we want to achieve with this model.

Let's consider the following development frame, with t_0 is time when eggs hatch, t_d is time when diapause begins, t_p is time when post-diapause begins, and t_e is time at emergence (see figure 1).

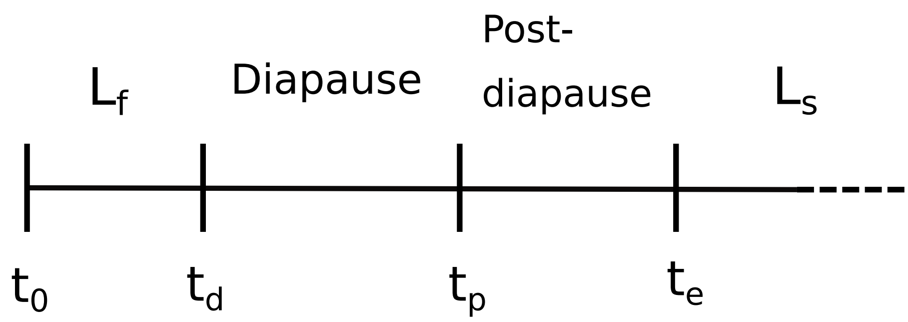

Figure 1: Time line of the model. L_f is Fall stages, and L_s are Summer stages.

1 Fall stages

One sentence about what happens in the fall: SBW eggs hatch and L1 stage develops. Larvae don't feed but use enerdy for development.

The population starts with a given abundance ($L_f(t_0)$) and a given amount of energy ($E_f(t_0)$). The system is:

$$\begin{cases} \dot{E}_f &= -\alpha_f T^{\beta_f} \\ \dot{L}_f &= -m_f(T) L_f \end{cases} \tag{1}$$

where T is temperature, m_f is temperature-dependent mortality (to account for early freeze, for example), α_f and β_f are constant that determine energy consumption according to temperature. Explicit solutions are:

$$E_f(t) = E_f(t_0) - \int_{t_0}^{t} \alpha_f T^{\beta_f} \, \mathrm{d}t \tag{2}$$

and

$$L_f(t) = \mathrm{e}^{-\int m_f(T(\sigma)) \, \mathrm{d}\sigma} L_f(t_0) \tag{3}$$

The system runs until $t = t_d$. This event may be a fixed point in time (e.g. determined by photoperiod). or it could be dependent on when the eggs were laid and how fast they developed. In the latter case, we might have to add an equation for the developmental rate. See question 5.1 below.

2 Diapause

One sentence about what is important: no feeding, low supercooling point, low temperature sensitivity...

The starting conditions are:

$$\begin{cases} E_d(t_d) &= E_f(t_d) \\ L_d(t_d) &= L_f(t_d) \end{cases} \tag{4}$$

and the system is:

$$\begin{cases} \dot{E}_d &= -\alpha_d T^{\beta_d} \\ \dot{L}_d &= -m_d(T) L_d \end{cases} \tag{5}$$

Explicit solutions are:

$$E_d(t) = E_d(t_d) - \int_{t_d}^{t} \alpha_d T^{\beta_d} \, \mathrm{d}t \tag{6}$$

and

I think the term is "supercooling point"

$$L_d(t) = \mathrm{e}^{-\int m_d(T(\sigma))\,\mathrm{d}\sigma} L_d(t_p) \tag{7}$$

I think there was a condition that T < \theta for at leasst 8 hours or so.

However, mortality is low. From an extreme simplification point of view, we may assume that $m_d = 0$, if $T \geqslant \theta$, and that the whole population dies if $T < \theta$, where θ is the freezing temperature. In that case, $L_d(t_p) = L_d(t_d)$ if there is no freeze, and 0 otherwise.

The system runs until $t = t_p$. This event may be triggered by:

I would be more explicit here. Suggestion below.

- **genetic**: the duration of the diapause stage is fixed~~, but if the beginning of diapause varies, the end of diapause varies as well~~.
  If the beginning of diapause is determined by external conditions (e.g. photoperiod) and the duration is fixed genetically, then the end of diapause is also fixed. If the beginning of diapause varies and the duration is fixed genetically, then the end varies accordingly.
- **photoperiod**: the end of diapause is a fixed moment in time (at a given location).
  Maybe a similar sentence to the one in blue could go here. The interesting thing is that the outcome is exactly opposite to the scenario above.
- **temperature**: the end of diapause varies from year to year.

I don't remember discussing temperature as end of diapause. I thought we discussed monitoring of energy level? But maybe temperature is also a factor. In that case, could you be more precise? For example: single warm event? Or cumulative warm events? Something like number of degree days (# of days were temp is above a threshold)?

3 Post-diapause

What is different from diapause: higher sensitivity to temperature. still no feeding, potentially different metabolism and hence energy use.

The starting conditions are:

$$\begin{cases} E_p(t_p) &= E_d(t_p) \\ L_p(t_p) &= L_d(t_p) \end{cases} \tag{8}$$

The system is:

$$\begin{cases} \dot{E}_p &= -\alpha_p T^{\beta_p} \\ \dot{L}_p &= -m_p(T) L_p \end{cases} \tag{9}$$

Explicit solutions are:

$$E_p(t) = E_p(t_p) - \int_{t_p}^{t} \alpha_p T^{\beta_p} \, \mathrm{d}t \tag{10}$$

and

$$L_p(t) = \mathrm{e}^{-\int m_p(T(\sigma))\,\mathrm{d}\sigma} L_p(t_p) \tag{11}$$

do we need a similar sumulative temperature below supercooling point here?

Mortality varies with temperature (very high mortality if temperatures are low, since this stage is assumed to be less freeze-resistant). The system runs until $t = t_e$. This event is triggered by:

- **temperature**: if $T > T_e$ Probably degree days again. In this case larvae emerge
- **energy**: if $E_p(t) < \phi$ Emergence or death?

We may stop the model here ~~of~~ or we can ~~pursue~~ continue to the next stage.

4 Summer stages

The starting conditions are:

$$L_s(t_e) = L_p(t_e) \tag{12}$$

We do not need to track energy anymore since larvae feed on the host. The model is:

Maybe we do if there is a mismatch, i.e. if the food is not ready when the larvae emerge?

$$\dot{L}_s = -m_s(T, F) L_s \tag{13}$$

where F is food availability.

In this case, do we need to include a model equation for the developmental rate?

5 Questions

5.1 Beginning of diapause

We assume that the beginning of the diapause stage (t_d) is a fixed point in time (early September). Is it a valid assumption?

Or should we assume that it may vary according to "hatching time" (t_0)? So, if eggs hatch (or are laid) later (earlier) in the year, diapause will occur later (earlier) as well. Or should we include inter-individual variability (which will increase the complexity of the model)?

I think that individual variability will need to enter the model eventually. Similar to the paper by Regniere maybe. This could be a separate discussion point.

5.2 Starting point of the model

Do we need to consider the Fall stages? The only advantage of doing so would be to include special events such as early freeze (that would increase death) or unusually warm temperatures (that would increase energy consumption).

I would not say that we ignore events prior to diapause,
I would say that we represent these events into the initial conditions
at the beginning of diapause. As you say in the second sentence.

Otherwise, we may start directly at diapause (t_d), and ignore former events. Hence, we may use different $L_d(t_d)$ and/or $E_d(t_d)$ to take Fall events into account as starting conditions instead of including them in the model explicitly.

If Fall stage is needed, then we should agree on t_0. Is it a fixed point in time?

5.3 End point of the model

Do we need to consider Summer stages? If we are only interested in the diapause stage and how much SBW can adapt to different climate/weather conditions, Summer stage may not be necessary. Hence, if we know when (within a year) food will be available at a given location, it should be enough knowing when larvae emerge from dormant stage to determine their ability to survive (i.e. how much time they will need to wait before food becomes available). Since we do not complete the full cycle, Summer stage may be ignored.

Maybe this question could start with what we can do with the model as is: With this model, we can relate the number of emerging larvae to the number of eggs laid or larvae entering diapause (see 5.2). If we want to know how many of the emerging larvae will survive if there is a possible mismatch with the resource, we will need to include the summer stage.