

# Simple model for spruce budworms

## 1 Features

The model should include a diapause. Emergence depends on temperature, but may also depend on internal energy (to be discussed). In a first step, the model includes only two stages. L1 and L2 stages are lumped together (i.e. Winter stage). Similarly, L3-L6 are lumped as well (i.e. Summer stage). Budworms emerge in Spring, they develop during Summer. Then they lay eggs that hatch into a Winter stage that goes into diapause.

Hence, the model considers a so-called Winter stage population ( $L_w$ ) that runs from egg stage until the end of the diapause. Then, a Summer stage population ( $L_s$ ) runs from the end of the diapause until reproduction.

$L_w$  individuals do not feed and rely on internal energy provided by the former generation.  $L_s$  individuals need food for survival. Forage during Summer also translates into internal energy for the future generation.

## 2 Model

### 2.1 Winter population ( $L_w$ )

$$\begin{cases} \dot{R}_w &= r_w(T(t)) \\ \dot{L}_w &= -m_w(\alpha_w(t))L_w \\ \dot{\alpha}_w &= -\alpha_1 T^{\alpha_2}(t) \end{cases} \quad (1)$$

The first equation is larval development, where  $R_w$  is the Winter life stage,  $r_w$  is the development rate that depends on temperature ( $T$ ) at any time ( $t$ ).  $R_w(t_0) = 0$  and development ends when  $R_w(t) = 1$ . It gives the duration of the life stage, and the time during which the two following equations run.

The second equation is larval survival. Larvae die at a rate  $m_w$  that depends on internal energy available ( $\alpha_w$ ). The third equation represents the decay of internal energy through time that increases with temperature, where  $\alpha_1$  and  $\alpha_2$  are data-derived parameters.

It is possible to write explicit solutions for the second and third equations. Winter population writes

$$L_w(t) = e^{-\int m_w(\alpha_w(t))dt} L_w(t_0) \quad (2)$$

Moreover,  $m_w$  is monotone decreasing in  $\alpha_w$  (i.e. the more energy larvae get, the less they

are likely to die). Available energy writes

$$\alpha_w(t) = \alpha_w(t_0) - \int_{t_0}^t \alpha_1 T^{\alpha_2}(t) dt \quad (3)$$

**A question remains:** if larvae run out of energy before the end of the diapause, do they emerge anyway even if the development is not fully completed, or do they die?

## 2.2 Summer population ( $L_s$ )

$$\begin{cases} \dot{R}_s &= r_s(T(t)) \\ \dot{L}_s &= -m_s(F)L_s \\ \dot{F} &= P(t) - dF - \beta FL_s \\ \dot{\alpha}_s &= c\beta FL_s - m_s(F)L_s\alpha_i \end{cases} \quad (4)$$

The first equation represents development during Summer stage.  $R_s(t_0) = 0$  and development ends when  $R_s(t) = 1$ . The second equation is larval survival during Summer. Death rate ( $m_s$ ) is now food-dependent.

The third equation is food (leaves) availability. Leaves are produced at a rate  $P$  that varies through time. There is a natural decay ( $d$ ) due to senescence and other sources of loss not related to budworms. Last, leaves are consumed by budworms at a rate  $\beta$ .

The last equation is energy storage ( $\alpha_s$ ) made by Summer stages and that will be given to Winter stages via eggs. Energy comes from consumed food, with a conversion efficiency ( $c$ ). When a given individual dies during Summer time (i.e. before it reproduces), all its energy is lost:  $\alpha_i$  represents individual energy storage.

For simplicity, we assume no tree mortality (i.e. the number of trees is constant). For a longer trend, this parameter will have to vary as well.

## 2.3 Reproduction

At the end of the Summer (once Summer stage is fully developed), reproduction occurs.

$$\begin{cases} L_w(t_n) &= g_i L_s(t_n) \\ \alpha_w(t_n) &= \frac{\alpha_s(t_n)}{L_w(t_n)} \end{cases} \quad (5)$$

Remaining Summer stage individuals produce a given number of offspring ( $g_i$ ) *per capita*. Each of these individuals will receive energy which is the total amount of energy stored divided by the number of offspring.

These new offspring are the next generation:

$$\begin{cases} L_w(t_0) &= L_w(t_n) \\ \alpha_w(t_0) &= \alpha_w(t_n) \end{cases} \quad (6)$$

**Two questions remain.**

- 1) Should we make food production ( $P$ ) dependent on temperature, or photoperiod, or both?
- 2) What would be the most relevant metrics for food ( $F$ )? Should we consider leaf area, leaf biomass ...?