

Age-dependent toxicity in plant chemical defences and herbivore feeding behaviour

Stephen Gourley, University of Surrey

joint work with

Rongsong Liu, Donald L. DeAngelis, John P. Bryant

Betula glandulosa and snowshoe hares

- Plants defend themselves using chemicals that are toxic to herbivores.
- Herbivores (such as boreal snowshoe hares) regulate their intake of toxins to below lethal or acute poisoning levels.
- Boreal snowshoe hares eat segments of twigs of deciduous woody plants particularly the bog (shrub/scrub) birch *Betula glandulosa* in Kluane National Park, Yukon.
- *Betula glandulosa* is a rapidly growing plant that defends only its youngest twig segments.
- Hares have learned to counter this defence by biting a twig at an older segment, they start to chew it there and work towards the more poisonous younger segments which are then rejected.
- In some plants toxin concentration varies continuously for different parts of the twig. For example the evergreen spruces *Picea glauca* and *P. mariana* which are among the snowshoe hare's least preferred foods.



Figure 1: *Betula glandulosa*. Credit: Mary Ellen (Mel) Harte, Bugwood.org



Figure 2: Branch of *Picea glauca* spruce.



Figure 3: Snowshoe hare *Lepus americanus*. Credit: Terry Spivey, USDA Forest Service, Bugwood.org

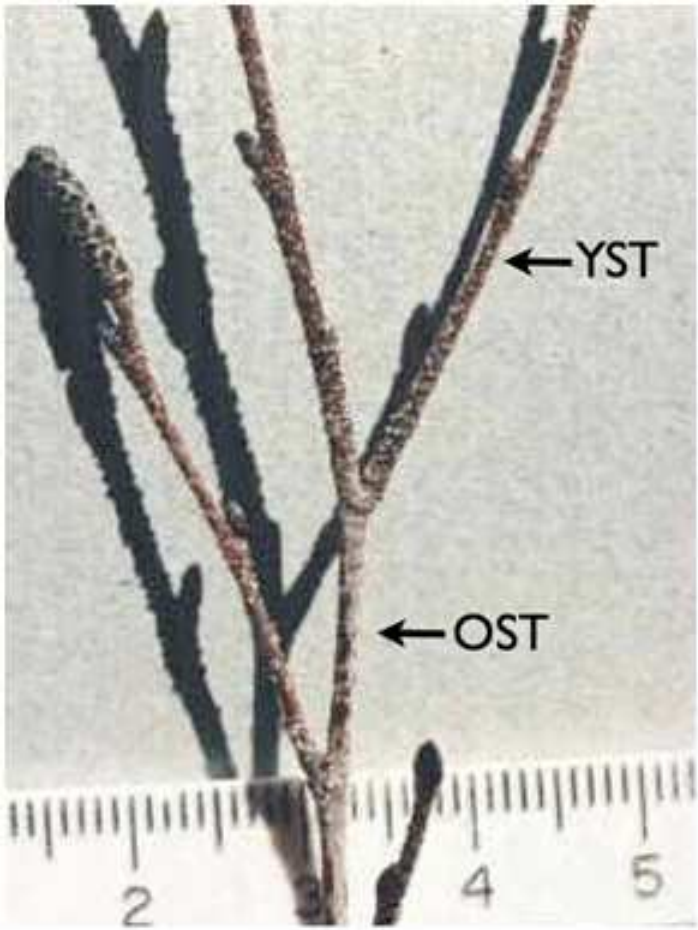


Figure 4: *Betula glandulosa* twig. Younger part densely covered with resin glands that produce toxin. Older part is much less toxic.



Figure 5: *B. glandulosa* twig tips rejected by snowshoe hares at Wiseman, Alaska.

Model derivation for two-segment twig

$n(t, a)$ = density of twig biomass at time t of age a

YST (younger segments of twigs) consists of twig biomass up to some age τ_1 .

OST (older segments of twigs) is older biomass that is still small enough in diameter to be consumed by hares. Total YST and OST biomass is given by

$$\text{YST:} \quad T_1(t) = \int_0^{\tau_1} n(t, a) da$$

$$\text{OST:} \quad T_2(t) = \int_{\tau_1}^{\tau_2} n(t, a) da$$

Twigs become major inedible branches after passing through age τ_2 . The plant is assumed to have such branches before browsing starts, and can always grow new twigs.

Birth rate of new twig biomass:

$$n(t, 0) = b(T_1(t)) \quad (1)$$

where $b(\cdot)$ is a decreasing function with $b(0) < \infty$. (If due to heavy browsing there are few YST-stage twigs on the plant, then it will try to optimise production of such twigs so the birth rate is higher in this case).

For YST twig biomass of age $a \in (0, \tau_1)$

$$\frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} = - \underbrace{\lambda_1 n(t, a)}_{\text{natural loss}} - \underbrace{\rho_1(t) P(t) n(t, a)}_{\text{direct loss of YST}} - \underbrace{\rho_2(t) P(t) n(t, a)}_{\text{indirect loss of YST}}$$

where $P(t)$ is the number of hares and

$$\rho_1(t) = \frac{e_1 \sigma_1}{1 + h_1 e_1 \sigma_1 T_1(t) + \frac{e_1 \sigma_1}{4G_1} T_1(t) + h_2 e_2 \sigma_2 T_2(t) + \frac{e_2 \sigma_2}{4G_2} T_2(t)}$$

$$\rho_2(t) = \frac{e_2 \sigma_2}{1 + h_1 e_1 \sigma_1 T_1(t) + \frac{e_1 \sigma_1}{4G_1} T_1(t) + h_2 e_2 \sigma_2 T_2(t) + \frac{e_2 \sigma_2}{4G_2} T_2(t)}$$

based on the Holling Type 2 functional response for a herbivore feeding on two different tissue (i.e. twig) types.

For OST twig biomass (of age $a \in (\tau_1, \tau_2)$)

$$\frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} = - \underbrace{\lambda_2 n(t, a)}_{\text{natural loss}} - \underbrace{\rho_2(t) P(t) n(t, a)}_{\text{direct loss of OST}}$$

λ_i	natural per-capita segments loss rate
e_i	rate of encounter per unit plant biomass $T_i, i = 1, 2$
σ_1	selection coefficient of $T_1, 0 \leq \sigma_1 \leq 1$
σ_2	selection coefficient of $T_2, 0 \leq \sigma_2 \leq 1$
h_i	time for handling one unit of the plant $T_i, i = 1, 2$
G_1	measure of plant toxicity for the YST, T_1
G_2	measure of plant toxicity for the OST, T_2
r	growth rate of YST
K	carrying capacity of new YST
d	per-capita death rate of the hare unrelated to plant toxicity
B_2	conversion constant (hare biomass per unit of plant T_2)
τ_1	duration of YST (effectively inedible) stage
τ_2	age beyond which twigs are too large to eat

For YST twig biomass, we can show

$$\begin{aligned}
T_1'(t) &= -(\lambda_1 + \rho_1(t)P(t) + \rho_2(t)P(t))T_1(t) + b(T_1(t)) \\
&\quad - b(T_1(t - \tau_1)) \\
&\quad \times \exp\left(-\int_0^{\tau_1} (\lambda_1 + (\rho_1(\eta + t - \tau_1) + \rho_2(\eta + t - \tau_1))P(\eta + t - \tau_1)) d\eta\right)
\end{aligned}$$

and the integral equation form

$$T_1(t) = \int_0^{\tau_1} b(T_1(t - a))e^{-\lambda_1 a} \exp\left(-\int_{t-a}^t (\rho_1(s) + \rho_2(s))P(s) ds\right) da.$$

For OST twig biomass

$$\begin{aligned}
T_2'(t) &= -(\lambda_2 + \rho_2(t)P(t))T_2(t) \\
&\quad + b(T_1(t - \tau_1)) \\
&\quad \times \exp\left(-\int_0^{\tau_1} (\lambda_1 + (\rho_1(\eta + t - \tau_1) + \rho_2(\eta + t - \tau_1))P(\eta + t - \tau_1)) d\eta\right) \\
&\quad - b(T_1(t - \tau_2))e^{-\lambda_1 \tau_1} \exp\left(-\int_{t-\tau_2}^{t-(\tau_2-\tau_1)} (\rho_1(s) + \rho_2(s))P(s) ds\right) \\
&\quad \times e^{-\lambda_2(\tau_2-\tau_1)} \exp\left(-\int_{t-(\tau_2-\tau_1)}^t \rho_2(s)P(s) ds\right)
\end{aligned}$$

and the integral equation form

$$\begin{aligned}
T_2(t) &= \int_0^{\tau_2} b(T_1(t - a)) \\
&\quad \times \exp\left(-\int_{t-a}^{\tau_1+t-a} (\lambda_1 + (\rho_1(s) + \rho_2(s))P(s)) ds - \int_{\tau_1+t-a}^t (\lambda_2 + \rho_2(s)P(s)) ds\right) da
\end{aligned}$$

For hares $P(t)$

$$P'(t) = B_2 \rho_2(t)T_2(t)P(t) - dP(t)$$

where B_2 is the conversion factor between plant biomass and the number of hares. We also introduce

$$\hat{h}_1 = h_1 + \frac{1}{4G_1}, \quad \hat{h}_2 = h_2 + \frac{1}{4G_2}$$

Positivity and boundedness

Theorem 1 (Boundedness) *Let $b(\cdot)$ be a positive decreasing function. Then $T_1(t) \geq 0$, $T_2(t) \geq 0$ and $P(t) \geq 0$ for all $t > 0$. Moreover, for all $t > 0$,*

$$T_1(t) \leq \frac{b(0)(1 - e^{-\lambda_1 \tau_1})}{\lambda_1}, \quad T_2(t) \leq \frac{b(0)e^{-\lambda_1 \tau_1}(1 - e^{-\lambda_2(\tau_2 - \tau_1)})}{\lambda_2}.$$

Also, if $T_1^{\text{inf}} = \liminf_{t \rightarrow \infty} T_1(t)$, then the following inequality implicitly yields a lower bound for T_1^{inf} :

$$\left(\lambda_1 + (e_1 \sigma_1 + e_2 \sigma_2) \frac{B_2 b(0) e^{-\lambda_1 \tau_1}}{\min(d, \lambda_2)} \right) T_1^{\text{inf}} \geq b(T_1^{\text{inf}})(1 - e^{-\lambda_1 \tau_1}).$$

Furthermore,

$$\begin{aligned} \liminf_{t \rightarrow \infty} T_2(t) &\geq b\left(\frac{b(0)(1 - e^{-\lambda_1 \tau_1})}{\lambda_1}\right) \exp\left[-\tau_1 \left(\lambda_1 + (e_1 \sigma_1 + e_2 \sigma_2) \frac{B_2 b(0) e^{-\lambda_1 \tau_1}}{\min(d, \lambda_2)}\right)\right] \\ &\times \left(\frac{1 - \exp\left[-(\tau_2 - \tau_1)(\lambda_2 + e_2 \sigma_2 B_2 b(0) e^{-\lambda_1 \tau_1} / \min(d, \lambda_2))\right]}{\lambda_2 + e_2 \sigma_2 B_2 b(0) e^{-\lambda_1 \tau_1} / \min(d, \lambda_2)}\right) \end{aligned}$$

Stability of hare-extinct equilibrium

If hares are absent, $P = 0$, and YST and OST twig population variables T_1 , T_2 can exist in a carrying capacity at levels T_1^* and T_2^* satisfying

$$\begin{aligned}\lambda_1 T_1^* &= b(T_1^*)(1 - e^{-\lambda_1 \tau_1}) \\ \lambda_2 T_2^* &= b(T_1^*)e^{-\lambda_1 \tau_1}(1 - e^{-\lambda_2(\tau_2 - \tau_1)})\end{aligned}$$

For realistic (ie positive decreasing) functions $b(\cdot)$, these equations can be solved uniquely for $T_1^* > 0$, $T_2^* > 0$.

Hares cannot kill the plant completely.

Theorem 2 (Linear stability of hare-free equilibrium) *Suppose that $b(\cdot)$ is a positive decreasing function and that*

$$d > \frac{B_2 e_2 \sigma_2 b(T_1^*) e^{-\lambda_1 \tau_1} (1 - e^{-\lambda_2(\tau_2 - \tau_1)}) / \lambda_2}{1 + \hat{h}_1 e_1 \sigma_1 T_1^* + \hat{h}_2 e_2 \sigma_2 b(T_1^*) e^{-\lambda_1 \tau_1} (1 - e^{-\lambda_2(\tau_2 - \tau_1)}) / \lambda_2} \quad (2)$$

Then the equilibrium $(T_1, T_2, P) = (T_1^, T_2^*, 0)$ is locally asymptotically stable.*

Inequality (2) is satisfied when

- τ_1 is sufficiently large (i.e. there is less edible twig biomass available). This is a strong effect, due to exponential decay (T_1^* depends on τ_1 but approaches a finite value as $\tau_1 \rightarrow \infty$; note also that we must have $\tau_2 > \tau_1$).
- G_1 is sufficiently small (i.e. \hat{h}_1 is large) (i.e. young twig segments are highly toxic). A weaker effect, due to algebraic decay
- conversion factor B_2 is low enough

- per-capita hare mortality d is large enough

Implication: better for the plant to prolong the duration of the YST phase than to increase the production of toxins. Toxins are expensive to produce.

Theorem 3 (Global stability of hare-free equilibrium) *Suppose that $b(\cdot)$ is a positive decreasing function and that*

$$\frac{B_2 e_2 \sigma_2 b(0) e^{-\lambda_1 \tau_1} (1 - e^{-\lambda_2 (\tau_2 - \tau_1)}) / \lambda_2}{1 + \hat{h}_1 e_1 \sigma_1 T_1^{**} + \hat{h}_2 e_2 \sigma_2 b(0) e^{-\lambda_1 \tau_1} (1 - e^{-\lambda_2 (\tau_2 - \tau_1)}) / \lambda_2} < d$$

where T_1^{**} is the solution of

$$\left(\lambda_1 + (e_1 \sigma_1 + e_2 \sigma_2) \frac{B_2 b(0) e^{-\lambda_1 \tau_1}}{\min(d, \lambda_2)} \right) T_1^{**} = b(T_1^{**}) (1 - e^{-\lambda_1 \tau_1}).$$

Then $(T_1, T_2, P) = (T_1^*, T_2^*, 0)$ is globally asymptotically stable.

Twig with N segments

$$\begin{aligned} \frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} &= -\lambda_1 n(t, a) - \left(\sum_{j=1}^N \rho_j(t) \right) P(t) n(t, a), \quad \text{for } a \in (0, \tau_1); \\ &\vdots \\ \frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} &= -\lambda_{i+1} n(t, a) - \left(\sum_{j=i+1}^N \rho_j(t) \right) P(t) n(t, a), \quad \text{for } a \in (\tau_i, \tau_{i+1}); \\ &\vdots \\ \frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} &= -\lambda_N n(t, a) - \rho_N(t) P(t) n(t, a), \quad \text{for } a \in (\tau_{N-1}, \tau_N) \end{aligned}$$

with

$$\rho_j(t) = \frac{e_j \sigma_j}{1 + \sum_{k=1}^N \left(h_k + \frac{1}{4G_k} \right) e_k \sigma_k T_k(t)}, \quad j = 1, \dots, N.$$

Total number of twigs in a particular age class is

$$T_i(t) = \int_{\tau_{i-1}}^{\tau_i} n(t, a) da, \quad i = 1, \dots, N,$$

and satisfies

$$T_i'(t) = n(t, \tau_{i-1}) - n(t, \tau_i) - \lambda_i T_i(t) - \left(\sum_{j=i}^N \rho_j(t) \right) P(t) T_i(t).$$

We write $n(t, \tau_{i-1})$ and $n(t, \tau_i)$ in terms of the birth rate:

$$n(t, 0) = b(T_1(t) + \dots + T_R(t))$$

where R is the number of “younger” age classes. Eventually, we get

$$\begin{aligned}
T'_i(t) &= -\lambda_i T_i(t) - \left(\sum_{j=i}^N \rho_j(t) \right) P(t) T_i(t) \\
&+ b \left(\sum_{l=1}^R T_l(t - \tau_{i-1}) \right) \mathcal{F}_{i-1} (T_{1t}(\cdot), T_{2t}(\cdot), \dots, T_{Nt}(\cdot), P_t(\cdot)) \\
&- b \left(\sum_{l=1}^R T_l(t - \tau_i) \right) \mathcal{F}_i (T_{1t}(\cdot), T_{2t}(\cdot), \dots, T_{Nt}(\cdot), P_t(\cdot)), \quad i = 1, \dots, N
\end{aligned}$$

where $\mathcal{F}_0 = 1$ and, for $i = 1, \dots, N$,

$$\begin{aligned}
\mathcal{F}_i (T_{1t}(\cdot), T_{2t}(\cdot), \dots, T_{Nt}(\cdot), P_t(\cdot)) &= \prod_{j=1}^i \exp(-\lambda_j(\tau_j - \tau_{j-1})) \\
&\times \exp \left(- \int_{t-\tau_i}^t (\rho_i(\eta) + \dots + \rho_N(\eta)) P(\eta) d\eta - \int_{t-\tau_i}^{t-(\tau_i-\tau_{i-1})} \rho_{i-1}(\eta) P(\eta) d\eta \right. \\
&\quad \left. - \int_{t-\tau_i}^{t-(\tau_i-\tau_{i-2})} \rho_{i-2}(\eta) P(\eta) d\eta - \dots - \int_{t-\tau_i}^{t-(\tau_i-\tau_1)} \rho_1(\eta) P(\eta) d\eta \right).
\end{aligned}$$

For hares $P(t)$:

$$P'(t) = -dP(t) + \sum_{i=1}^N B_i \left(\sum_{j=i}^N \rho_j(t) \right) T_i(t) P(t).$$

In the hare-extinct equilibrium, $P = 0$ and $T_i \equiv T_i^*$ where

$$T_i^* = b(T^*) \left(\frac{1 - e^{-\lambda_i(\tau_i - \tau_{i-1})}}{\lambda_i} \right) \prod_{j=1}^{i-1} \exp(-\lambda_j(\tau_j - \tau_{j-1})), \quad i = 1, \dots, N$$

and T^* satisfies

$$T^* = b(T^*) \sum_{i=1}^R \left[\left(\frac{1 - e^{-\lambda_i(\tau_i - \tau_{i-1})}}{\lambda_i} \right) \prod_{j=1}^{i-1} \exp(-\lambda_j(\tau_j - \tau_{j-1})) \right]$$

Theorem 4 (Hare-free equilibrium for N segments) *Suppose that $b(\cdot)$ is a positive decreasing differentiable function. If*

$$d > \sum_{i=1}^N B_i \left(\frac{\sum_{j=i}^N \frac{e_j \sigma_j}{1 + \sum_{k=1}^N \left(h_k + \frac{1}{4G_k} \right) e_k \sigma_k T_k^*}}{\sum_{j=i}^N \frac{e_j \sigma_j}{1 + \sum_{k=1}^N \left(h_k + \frac{1}{4G_k} \right) e_k \sigma_k T_k^*}} \right) T_i^*$$

and

$$\left| b' \left(\sum_{l=1}^R T_l^* \right) \right| \sum_{i=1}^R \left\{ \prod_{j=1}^{i-1} e^{-\lambda_j(\tau_j - \tau_{j-1})} \left(\frac{1 - e^{-\lambda_i(\tau_i - \tau_{i-1})}}{\lambda_i} \right) \right\} < 1$$

then the equilibrium with $T_i = T_i^*$, $i = 1, \dots, N$ and $P = 0$ is linearly asymptotically stable.

Twig toxicity varying continuously

Model becomes

$$\frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} = -\lambda(a)n(t, a) - \left(\int_a^{a_{\max}} \rho(t, s) ds \right) P(t)n(t, a)$$

where a_{\max} is the age beyond which twigs are too large to eat, and

$$\rho(t, s) = \frac{e(s)\sigma(s)}{1 + \int_0^{a_{\max}} \left(h(\bar{a}) + \frac{1}{4G(\bar{a})} \right) e(\bar{a})\sigma(\bar{a})n(t, \bar{a}) d\bar{a}}.$$

Total quantity of edible twig biomass is

$$N(t) = \int_0^{a_{\max}} n(t, a) da$$

Differentiation yields

$$\begin{aligned} \frac{dN(t)}{dt} &= n(t, 0) - n(t, a_{\max}) - \int_0^{a_{\max}} \lambda(a)n(t, a) da \\ &\quad - \int_0^{a_{\max}} \left(\int_a^{a_{\max}} \rho(t, s) ds \right) P(t)n(t, a) da. \end{aligned} \quad (3)$$

Birth law:

$$n(t, 0) = b \left(\int_0^{a_m} n(t, a) da \right)$$

where a_m is the upper age limit for which a twig is considered “young”.

Last term in (3) represents loss of twigs due to herbivory. Twigs are converted to hare biomass using a conversion factor $B_2(a)$ which depends on twig age

and is inserted into the integrand of the last term. Thus the equation for $P(t)$ is

$$\frac{dP(t)}{dt} = P(t) \int_0^{a_{\max}} B_2(a) \left(\int_a^{a_{\max}} \rho(t, s) ds \right) n(t, a) da - dP(t).$$

There is a hare-free equilibrium with $P = 0$ and $n(t, a) = n^*(a)$ where

$$n^*(a) = n^*(0) \exp \left(- \int_0^a \lambda(\xi) d\xi \right)$$

and $n^*(0)$ satisfies

$$n^*(0) = b \left(n^*(0) \int_0^{a_m} \exp \left(- \int_0^a \lambda(\xi) d\xi \right) da \right).$$

Theorem 5 *Suppose that $b(\cdot)$ is a positive decreasing function and that*

$$d > \frac{n^*(0) \int_0^{a_{\max}} B_2(a) \left(\int_a^{a_{\max}} e(s)\sigma(s) ds \right) \exp \left(- \int_0^a \lambda(\xi) d\xi \right) da}{1 + n^*(0) \int_0^{a_{\max}} \left(h(a) + \frac{1}{4G(a)} \right) e(a)\sigma(a) \exp \left(- \int_0^a \lambda(\xi) d\xi \right) da}$$

and

$$\left| b' \left(\int_0^{a_m} n^*(\tilde{a}) d\tilde{a} \right) \right| \int_0^{a_m} \exp \left(- \int_0^a \lambda(\eta) d\eta \right) da < 1.$$

Then the equilibrium $(n, P) = (n^(a), 0)$ is linearly asymptotically stable in the sense that small perturbations satisfy $P(t) \rightarrow 0$ and $\int_0^{a_m} n(t, a) da \rightarrow \int_0^{a_m} n^*(a) da$ as $t \rightarrow \infty$.*

Simulations for twig with two segments

Birth function chosen as $b(T_1) = r \exp(-T_1/K)$ for simulations.

- The effect of increasing τ_1 is a strong one. A thousand fold decrease in G_1 (increase in YST toxicity) is not sufficient to eradicate the hares, whereas increasing τ_1 by a factor of just 2.5 eradicates them (Figs. 6 and 7).
- If τ_1 is not too large then all three variables can persist and evolve to a limit cycle (snowshoe hare cycle) oscillation.
- Changes in G_2 (representing toxicity of older segments) do not have much effect on the dynamics because the proportion of contribution of G_2 to the handling time is small, for the range of values of G_2 that we considered.

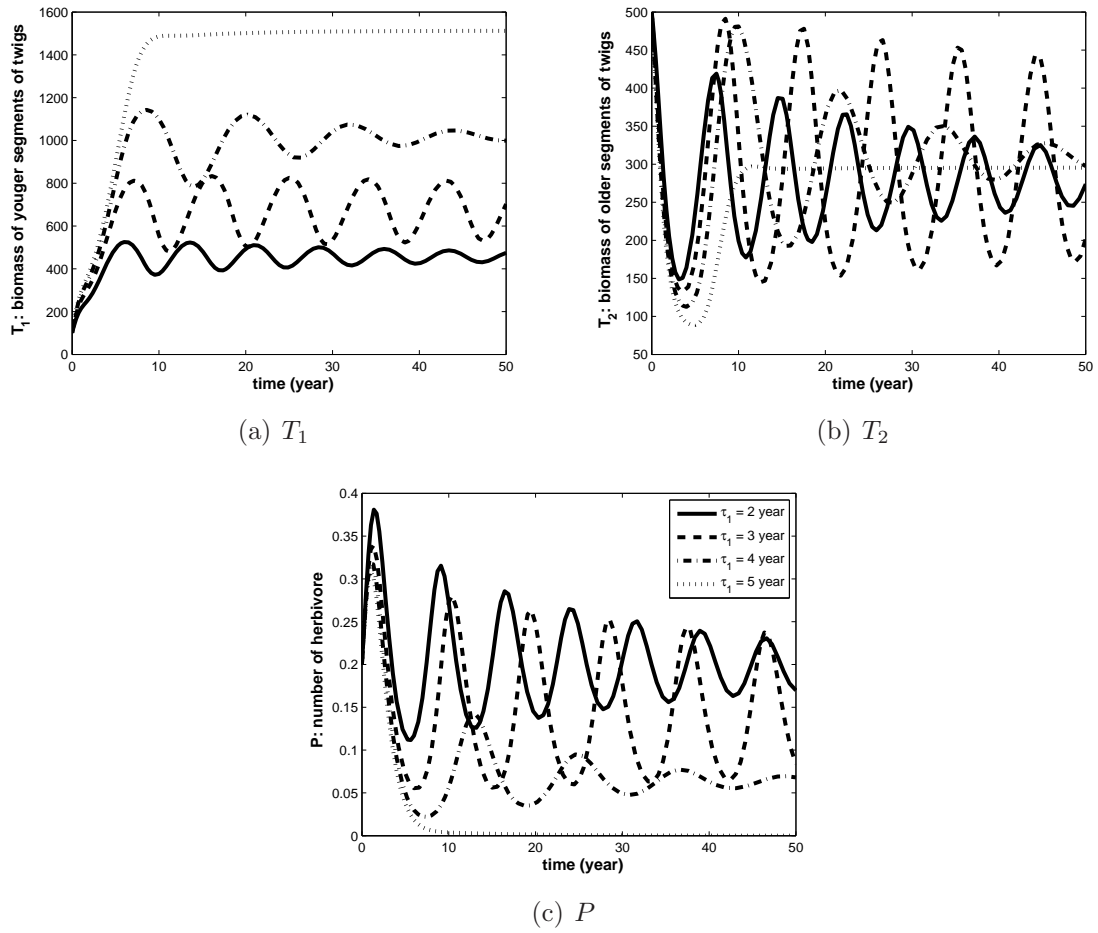
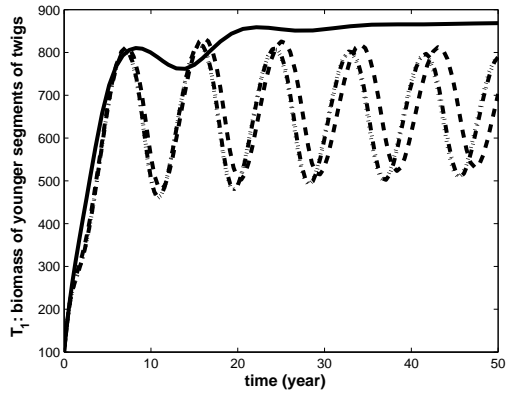
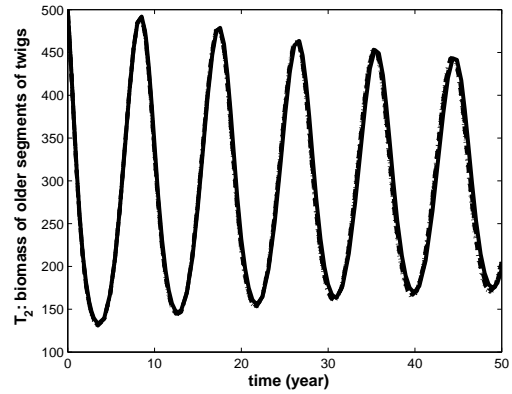


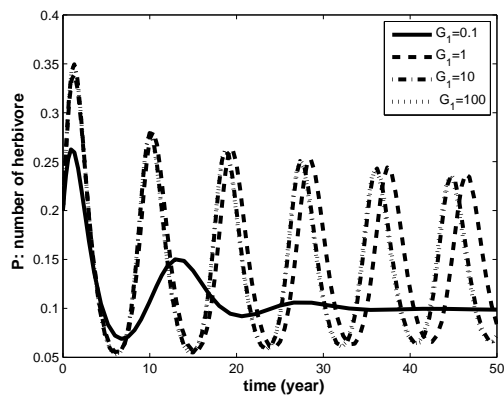
Figure 6: Panel (a): biomass of younger segments T_1 ; Panel (b): biomass of older segments T_2 ; Panel (c): number of hares P . Figure shows the dependence on τ_1 .



(a) T_1



(b) T_2



(c) P

Figure 7: Panel (a): biomass of younger segments T_1 ; Panel (b): biomass of older segments T_2 ; Panel (c): number of hares P . Figure shows the dependence on the toxicity $1/G_1$. Small G_1 means young twigs are highly toxic.

Summary

- Plants may defend some of their parts more strongly than others. Toxins are expensive to produce. Some rapidly growing plants, such as *Betula glandulosa*, defend only their youngest twig segments.
- When a hare feeds specifically on the older part of a twig, which is less toxic and more edible than the younger part, the hare must necessarily remove the younger part of the twig even though it may not ingest the younger part but merely discard it.
- An important prediction of the model is that it is better for a plant to prolong the duration of the toxic phase of twig development, than to evolve a more potent toxin that defends only young twigs. The prediction is particularly important for slowly growing plants (such as the spruces).
- Boreal snowshoe hares prefer *Betula glandulosa*. Evergreen spruce twigs are an alternative, less desirable, food source.
- Spruces are slowly growing evergreens that have a limited ability to replace the twigs eaten by hares. Therefore, though toxins are expensive to produce, spruce similarly defends YST and OST.
- In fact, spruce twigs retain needles on their OST until that OST exceeds the diameter that a hare can eat. These needles contain toxic monoterpenes such as camphor.
- There is evidence that increased consumption of spruce does indeed contribute to the decline of a snowshoe hare population.
- The variation in twig toxicity with age can generate plant-hare limit cycle behaviour. This is important because oscillatory dynamics are a common feature of the dynamics of snowshoe hare populations in boreal ecosystems. Our parameter values produce a cycle of about 5 or 6 years (slightly shorter than the true hare cycle).