

Modeling Spruce Budworm Population Revisited: Impact of Physiological Structure on Outbreak Control

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Abstract Understanding the dynamics of spruce budworm population is very important for the protection of spruce and balsam fir trees of North American forests, and a full understanding of the dynamics requires careful consideration of the individual physiological structures that is essential for outbreak control. A model as a delay differential equation is derived from structured population system, and is validated by comparing simulation results with real data from the Green River area of New Brunswick (Canada) and with the periodic outbreaks widely observed. Analysis of the equilibrium stability and examination of the amplitudes and frequencies of periodic oscillations are conducted, and the effect of budworm control strategies such as mature population control, immature population control and predation by birds are assessed. Analysis and simulation results suggest that killing only budworm larvae might not be enough for the long-term control of the budworm population. Since the time required for development during the inactive stage (from egg to second instar caterpillar) causes periodic outbreak, a strategy of reducing budworms in the inactive stage, such as removing egg biomass, should also be implemented for successful control.

Keywords Delay differential equation · Larvae · Outbreak control · Predation · Spruce budworm · Structured populations

1. Introduction

The spruce budworm, *Choristoneura fumiferana*, is an insect common to North American forests, where white/black spruce and balsam fir trees grow (Fleming and Shoemaker, 1992; Felling and Dewey, 1982; Magnussen et al., 2005; Williams and Liebhold, 2000). Its larvae feed on young developing buds, needles, shoots, foliage and other plant parts causing damage to trees. In spite of several efforts such as use of insecticides (for example,

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dimethoate), outbreak occurs periodically (normally every 30–60 years lasting for about 10 years) causing billions of dollars loss to forest industry (Fleming and Shoemaker, 1992; Fogal and Plowman, 1989; Raske et al., 1991; Royama, 1984; Royama et al., 2005; Williams and Liebhold, 2000). Understanding the budworm population dynamics is very important to develop a strategy for their control.

The spruce budworm normally completes its life-cycle within a year producing one generation per year (Fleming and Shoemaker, 1992; Royama, 1984; Royama et al., 2005). However, depending upon temperature, environment and elevation, the life cycle can take up to 2 years or more to complete; and some species such as *Choristoneura biennis* have a 2-year life-cycle (Dunken, 2006). In the early summer months of July and August, females mate and lay eggs in clusters on the underside of the needles. In about 10 days, the eggs hatch to produce the first instar caterpillars (L_1). The first instar caterpillars develop into the second instar caterpillars (L_2), which move by wind and find sites under bark scales where they spend the winter in a small silk cocoon known as hibernaculum. There they remain dormant throughout the winter. In late April or May, L_2 budworms, which are yellowish with dark brown heads, develop to the next instar (L_3), which either bore into needles or buds or spin silken webbing around new shoots and begin to feed on the needles within. The most damage to the foliage normally occurs from early to mid-June when the larvae are in their stages L_4 , L_5 and L_6 of development. About 40 days after feeding begins in the spring, usually about the end of June, the budworms stop feeding and develop into brownish pupae, which in turn become moths. Adult moths usually emerge in July–August, migrate (females can fly as far as 50 miles), mate and then the females lay eggs.

A logistic model of budworm population with predation function is widely accepted in the literature because of the existence of a stable periodic orbit (Ledder, 2007; Ludwig et al., 1978, 1979; Murray, 2002). However, field observations in the Green River Project of New Brunswick, Canada (Royama, 1984) have observed that both predation and carrying capacity (tree foliage) are unlikely to be a primary cause of budworm population oscillation. Some other simulation and numerical approaches are found in Hassell et al. (1999); Jones (1976); Royama et al. (2005); Singh et al. (2000). However, none of the existing models have considered the important fact that only budworm after larval stage-3 (L_3) is responsible for damage to the foliage; from egg to L_2 , which is normally 9 months in duration (three quarters of the total life cycle), they are completely inactive and are not harmful to the trees. Moreover, birds mainly eat budworms after L_3 . Due to fluctuation in environment and temperature, this time duration from egg to L_2 can extend to 2 years. This huge delay compared to total duration of life cycle may have considerable impact on the long term dynamics of budworm population. Therefore, it is essential to take the delay into account in the model to better understand the population dynamics of budworm and its effects on forests.

In this paper, we derive a delay differential equation for the matured budworm population from a structured population model and by considering the inactive stage from egg to L_2 as the immature stage followed by the mature stage from L_3 . As such, unlike the classical logistic model, our model can be used to examine the effects of the birth process, the immature population survival, and the mature population mortality, which are observed as important components of budworm population fluctuation (Royama, 1984). Our results find excellent agreement with the real data from New Brunswick (Canada) and mimic closely periodic outbreaks observed in the real world. We perform a stability analysis of the equilibrium, corresponding to the extinction, of the model. This, together

with some numerical simulation results, suggests that along with destroying larvae, for example by insecticide, destruction of budworm in the inactive stage such as removal of egg biomass should be employed in an effective strategy for the successful control of budworm outbreak.

The rest of the paper is organized as follows. In Section 2, we derive a delay differential equation model governing the population of budworms from L_3 -stage to adult stage. Equilibrium analysis of the model is carried out in Section 3 followed by some simulation results in Section 4. We then conclude the paper with remarks and discussions for possible future work in Section 5.

2. Model

We derive a model of single species budworm population living in a closed environment with no spatial heterogeneity. Since even in a 10-year observation period the population of birds is found to be just doubled (Royama, 1984), we assume that the number of birds which act as the predator is fixed. We note that Moran effects, budworm migration and tree population can have an important impact on the dynamics of budworm population (Royama et al., 2005). However, at this stage, we have not considered these factors to simplify the discussion. The main focus of this paper is to study the effect of the maturation delay on the spruce budworm outbreak.

2.1. The delay differential equation

Let the size distribution of the budworm population be denoted by $N(t, a)$, where a is the age and t is the time. Let $\bar{D}(a)$ and P_a be the mortality rate and the predation rate, respectively, both depending on age. Then, we have the standard structured model of the budworm population as follows (So et al., 2001):

$$\frac{\partial N}{\partial t}(t, a) + \frac{\partial N}{\partial a}(t, a) = -\bar{D}(a)N(t, a) - P_a N(t, a). \quad (1)$$

From the life-cycle of budworms, it is clear that from egg stage to L_2 (i.e. second instar caterpillar), they are completely inactive and do not reproduce offsprings. They are not harmful to the trees in these stages. They spend about 9 months (normally from July–August to April–May) in this form. From L_3 , they become active and can damage the foliage. Also, birds mainly eat budworms after their L_3 stage. Therefore, for the damage to the trees as well as the predation by birds, the 9-month time (which may be extended to 2 years due to elevation, environmental and temperature fluctuation) acts as a delay to respond. This shows that the dynamic behavior of budworm population after L_3 is more important, as far as the damage to the foliage and the protection of the trees are concerned. Taking this factor into account, we divide the total budworm population into two classes: inactive stage as an immature stage from egg to L_2 , and active stage as a mature stage from L_3 to the adult.

We now derive a delay differential equation governing the dynamics of the mature budworm population. The maturation time, which varies from 9 to 24 months, acts as a delay for the delay differential equation. We assume that the birth rate only depends

upon the adult population and the maturation time is constant. Let $m(t)$ be the mature population density at time t . Then

$$m(t) = \int_{\tau}^{\infty} N(t, a) da,$$

where τ is the maturation time. We further assume that the predation rate for the matured population is a function $p = p(m)$ of the matured population, and this function describes the relationship between the matured budworms and the birds that consume them. Then, we have (So et al., 2001) from (1), after using $N(t, \infty) = 0$ that

$$\frac{dm(t)}{dt} = [-D - p(m(t))]m(t) + N(t, \tau), \quad (2)$$

where D , assumed to be a constant, is the average mortality rate of the mature budworms.

We obtain $N(t, \tau)$ by solving the age-structure model for immature population. Since the immature group is inactive and birds being lazy do not eat the immature budworms, we assume the predation rate $P_a = 0$ for $0 \leq a \leq \tau$. Using $\tilde{d} > 0$ for the average death rate of the immature population, it follows from the age-structure model (1) for the immature population subject to the boundary condition $N(t, 0) = b(m(t))$, by the method of integration along characteristics, that $N(t, a) = e^{-\tilde{d}a} b(m(t - a))$ which gives $N(t, \tau) = e^{-\tilde{d}\tau} b(m(t - \tau))$. Then the model becomes

$$\frac{dm(t)}{dt} = -Dm(t) - p(m(t))m(t) + e^{-\tilde{d}\tau} b(m(t - \tau)). \quad (3)$$

2.2. Birth function

The birth function can have different forms, subject to the following consideration: $b(0) = 0$ (No birth in the absence of the matured population), $b(\infty) = 0$ (Crowding effect) and $b(m) \sim qm$ (Logistic growth) when m is small. Examples of birth functions found in the biological literature satisfying these conditions are (i) $b_1(m) = q_1 m e^{-\alpha_1 m}$, $q_1 > D$, $\alpha_1 > 0$, and (ii) $b_2(m) = q_2 m / (m^2 + \alpha_2^2)$, $q_2, \alpha_2 > 0$, $q_2 > D\alpha_2^2$ (Cooke et al., 1999). The graphs of these birth functions are shown in Fig. 1(a). In this paper, we use the birth function b_1 .

2.3. Predation function

The predation rate $p(m)m$ is the rate at which the budworms are being consumed by the birds. It is a function of the mature budworm population size. In reality, when there is small budworm population, birds are not attracted and so the predation rate is also small. The more budworms there are, the more will be eaten. This means that the predation rate should be an increasing function. Also, there are only so many budworms that a bird can eat in a day. Consequently, we expect that the predation rate should level off at some point. This can be expressed mathematically by the predation rate function (Ludwig et al., 1978, 1979)

$$p(m)m = \frac{\beta m^2}{\gamma^2 + m^2},$$

where β is the maximum level of predation and γ describes how quickly this maximum is achieved as the budworm population grows. This predation function is plotted in Fig. 1(b).

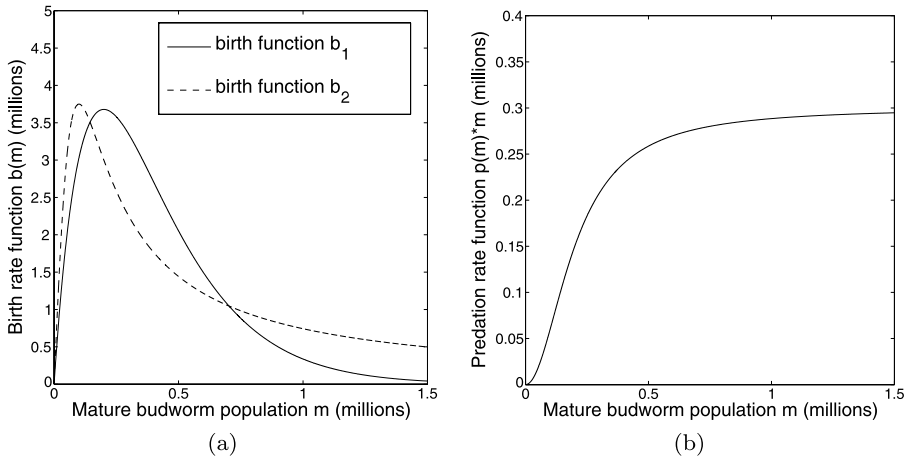


Fig. 1 (a) The birth functions $b_1(m) = q_1 m e^{-\alpha_1 m}$ and $b_2(m) = q_2 m / (m^2 + \alpha_2^2)$. (b) The predation rate function $p(m)m = \beta m^2 / (\gamma^2 + m^2)$.

3. Model analysis

In this section, we first carry out the dimensional analysis of the model followed by the equilibrium analysis of the non-dimensional model.

3.1. Dimensional analysis

We non-dimensionalize the model Eq. (3) with the birth function $b_1(m) = q_1 m e^{-\alpha_1 m}$ by changing the variables as $\hat{m}(t) = m(t)/\gamma$ and $\hat{t} = \beta t/\gamma$. Then, we define $\hat{m}(\gamma \hat{t}/\beta) = y(\hat{t})$. After removing the hat, we obtain the following non-dimensional model:

$$\frac{dy(t)}{dt} = -Ay(t) - \frac{y(t)^2}{1 + y(t)^2} + By(t - \tilde{\tau})e^{-Cy(t - \tilde{\tau})}, \tag{4}$$

where $A = D\gamma/\beta$, $B = q_1 \gamma e^{(-\tilde{d}\tau)}/\beta$, $C = \alpha_1 \gamma$ and $\tilde{\tau} = \beta\tau/\gamma$. While parameter A is related to the death of the matured population, parameters B and C are related to birth and survival of the immature population. Parameter A is thus relevant to the effect of insecticide as a control measure: insecticide increases the death rate D thereby increases the value of A . Parameter B decreases when the birth rate related parameter q_1 is decreased or when \tilde{d} is increased by natural death or control of the immature population. The reciprocal of α_1 in the parameter C is the size of the matured population when the birth function reaches its maximum.

3.2. Equilibrium analysis

An equilibrium of the model (4) $y(t) = y^*$, which is independent of time, is given by

$$-Ay^* - \frac{y^{*2}}{1 + y^{*2}} + By^* e^{-Cy^*} = 0.$$

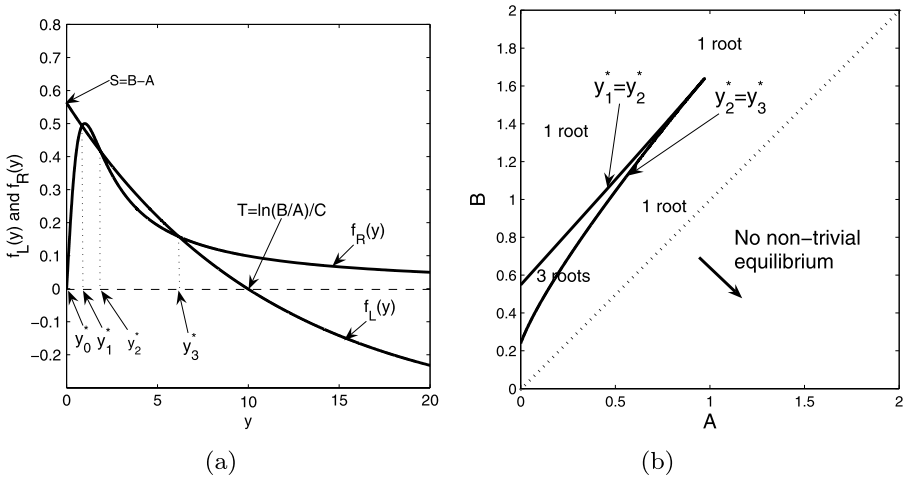


Fig. 2 (a) Curves $f_L(y) = Be^{-Cy} - A$ and $f_R(y) = y/(1 + y^2)$ plotted against y . The values of y corresponding to points of intersection give the equilibrium points. (b) $B - A$ diagram showing bifurcation curves of budworm density.

This implies $y^* = 0$ or, $f_L(y^*) = f_R(y^*)$, where

$$f_L(y^*) = Be^{-Cy^*} - A \quad \text{and} \quad f_R(y^*) = \frac{y^*}{1 + y^{*2}}.$$

$y^* = 0$ is always an equilibrium of (4), and the existence of non-trivial equilibria depends upon the values of parameters A , B and C . A closed form of the equation $f_L(y^*) = f_R(y^*)$ is not available, but the geometric interpretation of the curves $f_L(y)$ and $f_R(y)$ plotted in Fig. 2(a) provides a clear understanding of the role of these parameters in the structure of the set of non-trivial equilibria.

If $B \leq A$, both points $S = B - A$ and $T = \ln(B/A)/C$ are non-positive (see Fig. 2(a)). In this case, the curve f_L does not intersect the curve f_R at any $y > 0$. This implies that $y^* = 0$ is the only equilibrium for $B - A \leq 0$. As any non-negative solution of (4) satisfies $y'(t) \leq -Ay(t) + By(t - \tilde{\tau})$, we can easily show that the equilibrium $y^* = 0$ is asymptotically stable provided $B - A < 0$.

Bringing $B - A$ below zero should thus be a strategy for the control of spruce budworm population. To achieve this, one should reduce B or increase A , or do both. As noticed earlier, controlling the immature population such as removing egg biomass can reduce B and the use of insecticide to kill budworm can increase A . We should note that in reality using one of the above strategies may not be enough or may be too expensive for outbreak control. For example, the sole use of insecticide to kill budworm larvae might be very expensive or impossible to increase A to the level of B . The condition $B - A < 0$ indicates that it is sometimes much easier to bring A and B to the same level by destroying the immature population in combination with killing the mature population. We shall return to this issue later in our simulation analysis.

The condition $B = A$, i.e. $\tau = \ln(q_1/D)/\tilde{d}$ is very important for the eradication of budworm population. In reality, however, since each female lays about 200 eggs on average

(Fleming and Shoemaker, 1992; Sheehan et al., 1989; Royama, 1984), q_1 is very large compared to D and \bar{d} . This causes the delay τ to be less than $\ln(q_1/D)/\bar{d}$, which results in $B > A$.

From the graph (Fig. 2(a)), we can see that there may be 1, 2 or 3 positive equilibria (y_1^*, y_2^*, y_3^*) depending upon the value of parameters A, B and C . The graphical techniques to see the existence of non-trivial equilibria is similar to that employed in the classical logistic spruce budworm model (Ludwig et al., 1978, 1979), however unlike in the classical logistic model, the presence of delay in our model does not allow us to draw conclusions about stability by just looking over the height difference of the two curves.

In what follows, we abuse the notation and use S to denote the point $(0, S)$ and T for the point $(T, 0)$ of the Fig. 2(a). An increase in A moves the point S down and the point T to the left, causing y_1^* and y_3^* to move to the left and y_2^* to move to the right. Increasing A further, y_2^* and y_3^* coincide giving only two equilibria. For sufficiently large A , only the smallest non-trivial equilibrium y_1^* exists. The value of B has just opposite effect on the movement of points S and T , i.e. S moves up and T moves to the right due to an increase in B . This movement makes y_1^* and y_3^* move to the right and y_2^* move to the left. At some point, y_2^* coincides with y_1^* giving only two equilibria. A sufficiently large value of B causes unique existence of the nontrivial equilibrium y_3^* . This situation corresponds to an outbreak causing heavy destruction of the forest. Parameter C has no effect on the point S . An increase in C makes the point T move to the left and has the same effect as increasing A on equilibria y_1^*, y_2^* and y_3^* . Therefore, increasing A and C while decreasing B should be employed as a strategy of budworm control.

Keeping the parameter C fixed at some given value of C , we can plot bifurcation curves of budworm density showing the regions for the existence of 1, 2 and 3 equilibria in the $B - A$ diagram (Fig. 2(b)). The region below the diagonal line corresponds to $B - A < 0$, which gives no non-trivial equilibrium. Inside the critical region defined by two critical curves, there are three equilibria and there is only one equilibrium outside but above the diagonal line. Along the higher critical curve, y_1^* and y_2^* coincide giving two equilibria y_1^* ($= y_2^*$) and y_3^* . Above this curve equilibrium y^* jumps up and takes the high value $y^* = y_3^*$. Similarly, y_1^* and y_2^* ($= y_3^*$) are two equilibria along the lower critical curve, below which y^* jumps down and takes the low value $y^* = y_1^*$.

3.3. Oscillation and periodic outbreaks

To see the existence of periodic oscillations around the non-trivial equilibria $y^* > 0$, we first linearize Eq. (4) about the equilibrium value y^* to get the following equation.

$$\frac{dz(t)}{dt} = - \left[A + \frac{2y^*}{(1 + y^{*2})^2} \right] z(t) + B e^{-Cy^*} (1 - Cy^*) z(t - \bar{\tau}), \tag{5}$$

where $y(t) = y^* + \epsilon z(t)$, $\epsilon \ll 1$.

Scaling t further as $t = \varphi t_1$, where $\varphi = (1 + y^{*2})^2 / [A(1 + y^{*2})^2 + 2y^*]$ and defining $z(\varphi t_1) = w(t_1)$, we get

$$\frac{dw}{dt_1} = -w(t_1) + \zeta w(t_1 - \tau_1),$$

where $\zeta = B e^{-Cy^*} (1 - Cy^*) \varphi$ and $\tau_1 = \bar{\tau} / \varphi$.

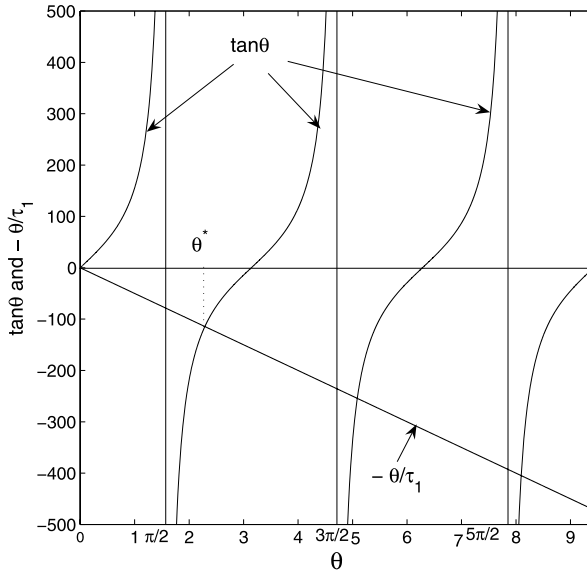


Fig. 3 Functions $\tan \theta$ and $-\theta/\tau_1$ vs. θ .

We now look for a solution in the form $w(t_1) = e^{\lambda t_1}$, which requires $\lambda = -1 + \zeta e^{-\lambda \tau_1}$. To obtain the condition for periodic oscillations to occur, we find λ with real part zero. Assuming $\lambda = iv$ with $v \neq 0$, we obtain

$$1 = \zeta \cos v\tau_1 \quad \text{and} \quad -v = \zeta \sin v\tau_1. \tag{6}$$

This gives $\zeta = \pm \sqrt{1 + v^2}$. This can also be obtained by using the formula provided in Beretta and Kuang (2002), which gives

$$v^2 = \zeta^2 - 1 \tag{7}$$

provided that $|\zeta| > 1$.

From Eq. (6), we get

$$\tan \theta = -\frac{\theta}{\tau_1},$$

where $\theta = v\tau_1 \neq 0$. A plot of the right and left-hand sides of this equation, as in Fig. 3, shows that the smallest non-zero solution is $\theta = \theta^* \in (\pi/2, \pi)$. The corresponding ζ is $\zeta = \zeta^* = -\sqrt{1 + (\theta^*/\tau_1)^2}$. Therefore, a bifurcation of periodic solution exists near $\zeta = -\sqrt{1 + (\theta^*/\tau_1)^2}$. More generally, as discussed in (Beretta and Kuang, 2002), if $\theta(\tau_1) \in I = \{\tau_1 : \tau_1 \geq 0 \text{ and } |\zeta| > 1\}$ is the solution of Eq. (6), then a stability switch may occur, through the roots $\lambda = \pm iv$, where $v > 0$ is given by Eq. (7), at the τ_1 values $\tau_{1,n} = [\theta(\tau_1) + 2\pi n]/v$ for $n \in N_0 := \{0, 1, 2, \dots\}$.

4. Simulation results

4.1. Parameter estimation

Estimation of parameter values is a very challenging task for spruce budworm models because most of the parameters depend on environment, temperature, weather, location, etc. Some parameters are available in the literature while others are calculated or estimated based on the information collected from the literature (Blais, 1981; Crawford and Jennings, 1989; Fleming and Shoemaker, 1992; Ludwig et al., 1978, 1979; Redak and Cates, 1984; Sheehan et al., 1989; Royama, 1984; Royama et al., 2005). As given in Ludwig et al., (1978, 1979) we use $\beta = 105,700$ larvae/hectare/year, $\gamma = 69,748$ larvae. Since the time delay to develop a budworm from egg to L_2 can vary from 9 months to 2 years (Fleming and Shoemaker, 1992; Sheehan et al., 1989; Royama, 1984), we take τ with $0.75 \leq \tau \leq 2$. Since the normal survival rate of the immature population is given to be approximately 15% (Sheehan et al., 1989; Royama, 1984), we adjust the value of the immature mortality rate \tilde{d} by using a formula $\tilde{d} = \ln(1/0.15)/\tau$. This gives $2.53 \geq \tilde{d} \geq 0.95$. The mature mortality rate D varies widely due to its dependence upon temperature, amount of tree foliage, dispersal rate, etc. (Sheehan et al., 1989; Royama, 1984). Based on the observation in Blais (1981); Sheehan et al. (1989), where the range of spruce budworm mortality was mentioned to be 0–48%, we use $D = 0.30$ for our baseline computation.

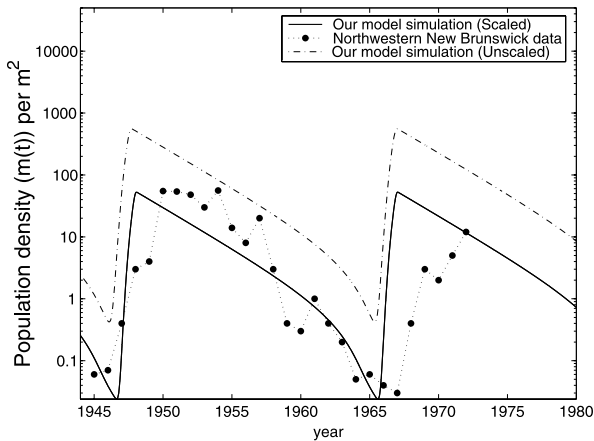
A maximum amount of eggs is produced when the temperature is suitable and there are plenty of foliages. This usually happens when there is a small population size. For our computation, we take the population size of $m_{\alpha_1} = 6,000$ corresponding to a maximum amount of total egg production. This gives $\alpha_1 = 0.00017$. Each female can lay 200 eggs (Fleming and Shoemaker, 1992; Sheehan et al., 1989; Royama, 1984) on average. This has occurred in a low budworm population, which we estimate to be $m_e = 50,000$ /hectare (Royama, 1984). Then using $q_1 e^{-50000\alpha_1} = 200$, we obtain $q_1 = 9.83 \times 10^5$. We note that these estimated values of q_1 and α_1 give a value of per capita birth rate high when the mature budworm population is extremely low. For example, population density of less than 0.9 per branch gives a per capita birth rate more than 400. However, in our computation, budworm population density lies between 0.9727 and 3930.8 per branch, which gives a per capita birth rate within a realistic range of 0–227.1. Therefore, we use these values for our computation and we provide the sensitivity analysis for these estimated values. Based on the information provided in Ludwig et al. (1978) that the maximum branch density of fully recovered forest is 25,440 per acre, we take 20,500 branches per acre (i.e. $\approx 50,635$ branches per hectare) in average for our calculation. Table 1 summarizes the data used in our computation.

4.2. Model validation

To validate our model, we run some simulations and compare these results with available real data, in particular, the data from the graph provided in Royama (1984); Royama et al. (2005). The data describes the yearly changes in the spruce budworm density (the third to fourth instar larvae) in the Green River area of Northwestern New Brunswick, Canada. The simulation results of our model along with the real data are shown in Fig. 4. For the purpose of comparison, we plot in the logarithmic scale

Table 1 Spruce budworm population model parameters

Symbol	Description	Value	Source
β	Max. budworms predated	105700 larvae/ha/yr	(Ludwig et al., 1979), (Ludwig et al., 1978)
γ	Related to predation function	69748 larvae	(Ludwig et al., 1979), (Ludwig et al., 1978)
τ	Maturation delay	0.75–2 yrs	(Fleming and Shoemaker, 1992), (Sheehan et al., 1989), (Royama, 1984)
\tilde{d}	Death rate of immature	0.95–2.53	(Sheehan et al., 1989), (Royama, 1984), Calculated
D	Death rate of mature	0.30	(Blais, 1981), (Sheehan et al., 1989), Estimated
α_1	Related to birth function	0.00017	Estimated
q_1	Related to birth function	9.83×10^5	(Royama, 1984), Estimated, Calculated

**Fig. 4** Changes of the spruce budworm density predicted by our model (solid line-scaled, dashed line-unscaled) along with the real data of the Green River area of New Brunswick, Canada (dotted line).

and express the population density in per square meter unit. Along with the population predicted by our model, we have also shown the population by scaling down to the level of the real data for the following reasons: (i) the population density in our model includes all stages from L_3 to the adult moths, and (ii) the real data provided in Royama (1984); Royama et al. (2005) are of a lower density case compared to the usual budworm population size. From the figure, we can see that the pattern of population distribution predicted by our model is in very good agreement with the real data.

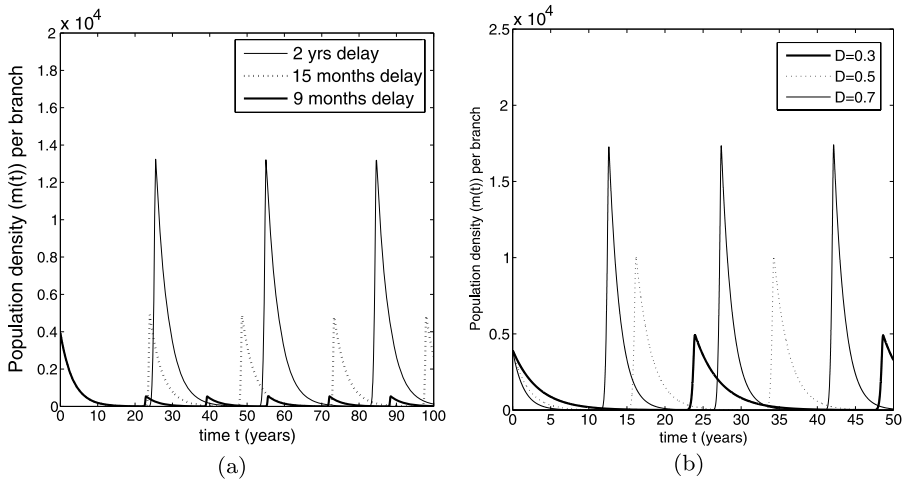


Fig. 5 (a) Temporal evolution of the Spruce Budworm mature population per branch with the maturation delay $\tau = 9$ months, 15 months and 2 years; (b) Temporal evolution of the Spruce Budworm mature population per branch with the mature population death rate $D = 0.3, 0.5$ and 0.7 .

4.3. The effect of delay

Temporal evolution of the mature budworm population density per branch is shown in Fig. 5(a). Despite the low level of population most of the time, periodic outbreaks are clearly seen from the graph. This is the realistic scenario in Canada and US. Figure 5(a) also shows the effect of maturation delay on the appearance of outbreaks. For a 9-month delay, which is the (usual) case given a normal environmental situation, outbreak appears approximately every 15 years and takes about 4–5 years to disappear. Due to variation in seasons resulting from environmental fluctuation, the maturation delay can go up to 2 years; for example, due to an unusually cool wet summer in 1956 in the *Gaspé Peninsula* of Quebec, Canada, the date of 50% adult emergence was delayed from mid-July in 1956 to the end of August in 1957 (Sheehan et al., 1989). Over the range of values of the delay corresponding to the real life situation (i.e. 0.75–2 years), an increase in delay increases the period of outbreak appearance, but more importantly, due to increase in delay the population level during outbreak increases drastically. Therefore, an increase in delay can cause more severe destruction of the forest even though the outbreak appears less frequently. For a 2-year delay, the outbreak appears approximately every 30 years and the population level falls down to a sufficiently low-level after about 9–10 years. This result is consistent with the outbreak appearance in the New-Brunswick forests of Canada.

To understand the effect of delay in more detail, we have plotted bifurcation diagrams (Fig. 6) by taking the delay τ as the bifurcation parameter and allowing it to vary over a wider range, i.e. $\tau \in [0.75, 9.5]$, similar to the technique used in Li et al. (2006); Li and Kuang (2007). As seen in Fig. 6(a), a bifurcation point has been detected at $\tau \approx 7.4$ years while varying the value of τ from 0.75 to 9.5 years. It can be seen that the oscillation is sustained for $\tau \in [0.75, 7.4]$. Figures 6(a) and (b) also help to understand the sensitivity of periods and amplitudes of the periodic solutions on the delay. For $\tau \in$

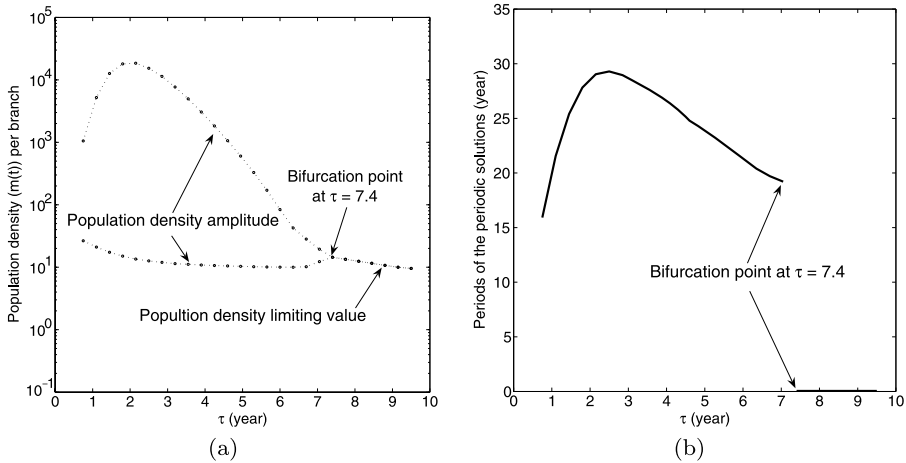


Fig. 6 (a) Bifurcation diagram of $\tau \in [0.75, 9.5]$; (b) Periods of the periodic solutions when $\tau \in [0.75, 9.5]$.

$[0.75, 7.4]$, the periods of the periodic solutions lie between 15 and 30 years. Both peak-to-peak amplitude and periods of the periodic solutions seem to have local maximum values in the interval $[0.75, 7.4]$. These occur at $\tau = 2.5$ years (approximate), which is higher than the usual delay occurring in the real-life scenario.

4.4. The effect of control strategies

There are control strategies for the protection of forests from budworm outbreak. We now examine the effects of these strategies on the budworm population dynamics.

4.4.1. The mature budworm control

One of the common practices to destroy the mature budworms is to use insecticides such as Dimethoate, Carbofuran, Acephate, etc. (Fogal and Plowman, 1989). The effect of the use of insecticide on budworm population can be studied via varying the mature population mortality rate D in our model; the use of effective insecticide kills the mature budworm, and hence increases the value of D . The mature population evolutions for three different values of D ($D = 0.3, 0.5, 0.7$) are shown in Fig. 5(b). By killing more mature budworms, i.e. by increasing the value of D from 0.3 to 0.7, the budworm population can be reduced quickly for the first few years. However, the outbreak takes place periodically for the long-term dynamics and more importantly, an increase in the mature budworm mortality makes the outbreak appearance more frequent and with the increased outbreak amplitudes. This result describes very well the real world phenomena, where it is found that despite the 100% disappearance of budworm due to insecticide spray in a certain year, the outbreak still appears later on. This result suggests that the use of insecticide can be only a short-term control strategy, but not a successful tool for the long-term eradication of the budworm population. We have also clarified this using some qualitative analysis of our model in Section 3.

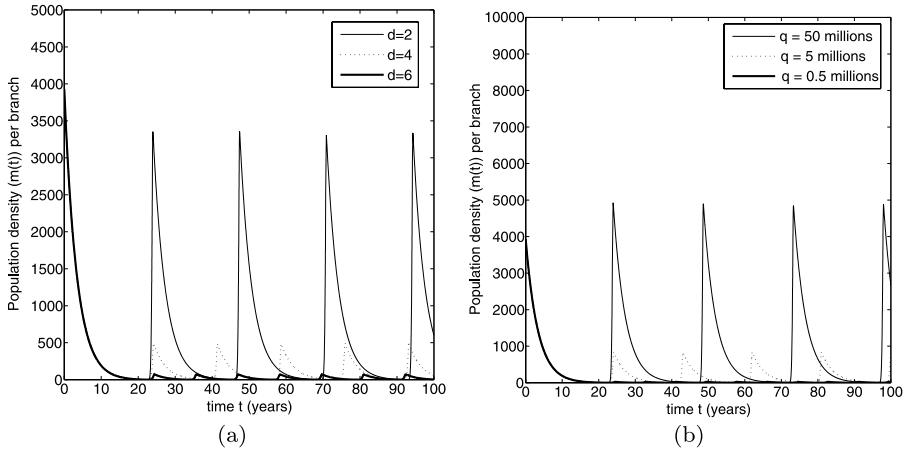


Fig. 7 (a) Temporal evolution of the Spruce Budworm mature population per branch with immature survival factor $\tilde{d} = 2, 4, 6$. (b) Temporal evolution of the Spruce Budworm mature population per branch with the birth factor $q_1 = 0.5, 5$ and 50 millions.

4.4.2. The immature budworm control

The control of the immature budworms can be reflected in our model via the parameters \tilde{d} and q_1 . The reduction in the immature survival rate such as the removal of egg biomass and the destruction of larvae in early stages (L_1 and L_2) increases the value of \tilde{d} . A decrease in the value of q_1 shows the control of birth of the immature population. Figures 7(a) and (b) show the effects of parameters \tilde{d} and q_1 , respectively, on the budworm population dynamics. The effect of the immature budworm control does not show up until the outbreak appears. However, by controlling the immature budworm population, either by increasing \tilde{d} or by decreasing q_1 , the outbreak magnitude can be drastically reduced. The result shows that periodic outbreaks can completely be put out by the sufficient control of the immature budworm population. Therefore, immature budworm control strategies should be incorporated in a long term policy of budworm control.

4.4.3. The predation by birds

The predation by birds has been considered to be one of the natural ways of controlling budworms. The β in our model, which represents the maximum value of the budworms eaten by birds, can be used to assess the effect of predation on budworm control. Our results (Figs. 8(a) and (b)) show that the predation influences the mean level of oscillations as mentioned in Royama (1984). If we observe the long-term dynamics of the budworm population, the predation factor does not help in controlling budworm; instead it increases the level of outbreak. For the short-term, the effect of predation depends upon the size of the budworm population. For a large budworm population size (Fig. 8(a)), there is no effect of the predation on the budworm population over a short period of time. However, as seen in Fig. 8(b), the predation is effective in controlling budworm for the short period of time if the budworm population size is small. This result is very much consistent with a finding of the survey study (Crawford and Jennings, 1989), where it was observed that the bird predation can effectively limit the budworm population if the population size is

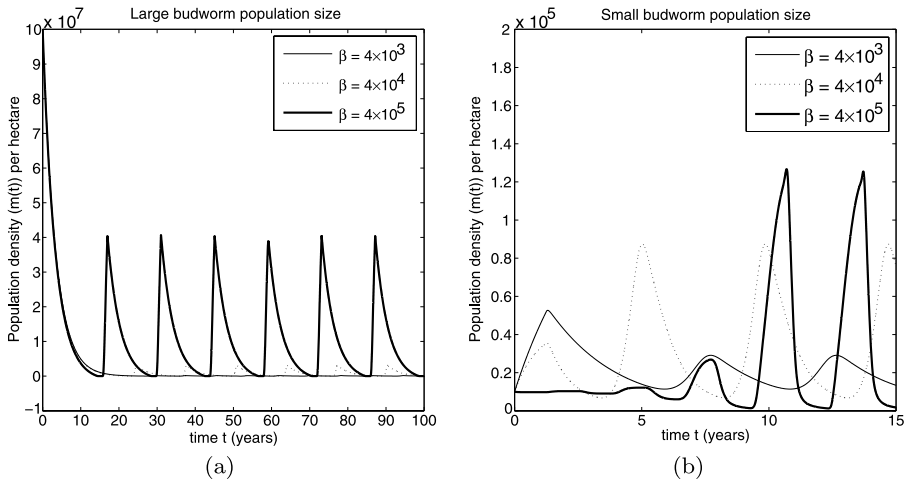


Fig. 8 Temporal evolution of the Spruce Budworm mature population per hectare with predation factor $\beta = 4 \times 10^3$, 4×10^4 and 4×10^5 for (a) the large population size and (b) the small population size.

low; once the size exceeds 10^6 per hectare, the bird predation becomes ineffective. We note that the budworm population size in Fig. 8(a) is more than 10^6 per hectare while it is less than 10^6 per hectare in Fig. 8(b).

4.5. Sensitivity analysis

We have also carried out the one-way sensitivity analysis of the effect of parameters m_{α_1} and m_e , which are used to estimate the values of $\alpha_1 = 1/m_{\alpha_1}$ and $q_1 = 200e^{m_e\alpha_1}$, respectively. Since q_1 exponentially depends on both m_e and α_1 , we allowed both m_{α_1} and m_e to vary from 10% below to 10% above the base case values of $m_{\alpha_1} = 6,000$ and $m_e = 50,000/\text{hectare}$. Over the range of values of m_{α_1} considered, the period of the periodic oscillation reached a maximum of 19.29 years and a minimum of 16.38 years, compared to the base case value of 17.99 years. Similarly, on varying the value of m_e , the period of the periodic oscillation varies from 16.41 to 19.5 years while the base case value is 17.99 years. In both cases, the peak amplitude (i.e. the peak-to-peak amplitude divided by 2) varies from 300 to 550 (approx.) per branch, compared to the base case value of 395.91 per branch. Moreover, changing the value of m_e with fixed α_1 is equivalent to changing the value of q_1 in our computation. We have presented above the effect of the change of q_1 on population dynamics by considering the change of q_1 as one of the control strategies.

5. Conclusions and future work

We present a delay differential equation model for the spruce budworm population by considering the budworm after larval stage-3 as a mature budworm. In the equilibrium analysis, we discuss the role of three parameters A , B , C of our non-dimensionalized

model on controlling budworm population. We validate the model by showing that the result of our model is in very good agreement with the real data from the Green River area of New Brunswick, Canada. Our model analysis demonstrates that the maturation delay causes periodic outbreak as seen in the real world. An increase in delay (within a realistic range) causes the outbreak to appear slightly less frequently but with a higher outbreak magnitude. We also assess the effects of three control strategies, namely the mature budworm control, the immature budworm control and the predation by birds. Our analytical discussions and simulation results suggest that the control of only mature budworms (for example, the use of insecticides) can be harmful for the long-term outcome, despite its effectiveness for the short-term control; an immature budworm control strategy (e.g. removing egg biomass) should be employed in combination with other successful budworm control measures.

Further research might be to treat the tree population as a variable and to incorporate some additional factors such as budworm migration and stochastic fluctuation due to Moran effect. It is worthwhile to mention that our approach should be useful to model the dynamics of other insects with physiological structures.

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