RELAXATION OSCILLATIONS IN A SPRUCE-BUDWORM INTERACTION MODEL WITH HOLLING’S TYPE II FUNCTIONAL RESPONSE

YI-MING TAI
Department of Mathematics, National Tsing Hua University
No. 101, Sec. 2, Kuang-Fu Road, Hsinchu 300, Taiwan

ZHENGYANG ZHANG∗
School of Mathematical Sciences, Ocean University of China
No. 238 Songling Road, Laoshan District, Qingdao, Shandong Province, China

ABSTRACT. In this paper we study the spruce-budworm interaction model with Holling’s type II functional response. The existence, number and stability of equilibria are studied. Moreover, we prove the existence of relaxation oscillations by using singular perturbation method and give an asymptotic expression of the period of relaxation oscillations. Finally, the parameter ranges which allow the relaxation oscillations in several scenarios are explored and displayed by conducting numerical simulations.

Dedicated to Prof. Sze-Bi Hsu in acknowledgement of his helpful suggestions

1. Introduction. The spruce budworm (Choristoneura fumiferana) is a tortricid moth occurring along the North American boreal-forest zone, tending to concentrate more towards the eastern part [6]. The larva of this kind of moth feeds on needles of evergreen trees (such as spruce and balsam fir) and is one of the most destructive insects in the spruce-fir mixed forest [6]. Spruce budworm have been exhibiting periodic outbreaks at an average interval of about 35 years for the past three centuries [7], and the populations fluctuate between extreme levels. At outbreaks, the budworm larvae cause severe damages to spruce and fir stands and even kill trees. However, when larvae are scarce, even intensive sampling over a wide area may find only a few larvae [5].

A classical spruce-budworm interaction model where the fast dynamics of larval population and the slow dynamics of spruce foliage regrowth are separated is given as follows, which was originally proposed by Ludwig et al. [1]:

\[
\begin{align*}
\frac{dN}{dt} & = rN \left( 1 - \frac{N}{\kappa S} \right) - \beta \frac{PN^2}{\eta^2 S^2 + N^2}, \\
\frac{dS}{dt} & = \rho S \left( 1 - \frac{S}{S_{\text{max}}} \right) - \delta N.
\end{align*}
\]

2020 Mathematics Subject Classification. 34A34, 34C26, 34E15.
Key words and phrases. Spruce-budworm model, singular perturbation method, relaxation oscillations, Holling’s type II functional response.

∗ Corresponding author: Zhengyang Zhang.
In this model, \( N \) is the population density of the larvae, \( S \) is the average leaf area of the spruce. It is assumed that the intrinsic growth of both spruce and budworm follows the logistic equation, where \( r > 0 \) and \( \rho > 0 \) represent the intrinsic growth rate of budworm population and spruce leaf area, respectively. The terms \( \kappa S \) and \( S_{\text{max}} > 0 \) describe the carrying capacity of budworm population and spruce leaf area, respectively, where it is assumed that the carrying capacity of budworm population is proportional to the average leaf area of the spruce with \( \kappa > 0 \), a coefficient measuring to which degree the leaves can accommodate the larvae. The term

\[
\frac{\beta P N^2}{\eta^2 S^2 + N^2}
\]

is a loss term describing the predation pressure on budworm population by parasites, insectivorous birds, etc.. Here \( \beta^{-1} > 0 \) is the intrinsic timescale, \( P > 0 \) is the budworm population density at maximal predation pressure, and \( \eta S \) is the budworm population density at half of the maximal predation pressure, which is assumed to be proportional to the average leaf area with a regulating coefficient \( \eta > 0 \). The term \( \delta N \) describes the predation pressure on spruce leaves by the larvae, which is assumed to be proportional to the density of the larvae, where \( \delta^{-1} \) is a characteristic time scale denoted as the depletion time scale of the leaf population. More detailed explanations and information about this model can be found in Rasmussen et al. [4] and Murray [3] and the references therein.

Study of the periodicity of population fluctuation of budworms is essential in understanding the population dynamics of spruce-budworm interaction and in forest management. However, not much research has been done in this aspect. Ludwig et al. [1] has pointed out the possibility of this model exhibiting relaxation oscillations, corresponding to the population fluctuation between extreme levels in reality, which, was proved by Rasmussen et al. [4]. Moreover, Rasmussen et al. [4] gave an approximated formula of the period of relaxation oscillations. Based on this work, Wang et al. [9] introduced a distributed delay in the prey population, and proved the existence of relaxation oscillations and also gave an approximated formula of the period.

In this paper, based on the work in [1, 4], we study the following spruce-budworm model with Holling’s type II functional response

\[
\begin{align*}
\frac{dN}{dt} &= rN \left(1 - \frac{N}{\kappa S}\right) - \frac{\beta P N^2}{\eta^2 S^2 + N^2}, \\
\frac{dS}{dt} &= \rho S \left(1 - \frac{S}{S_{\text{max}}}\right) - \frac{\delta S}{K + S} N.
\end{align*}
\]

In this model, instead of using the linear predation \( \delta N \), the Holling’s type II functional response

\[
\frac{\delta S}{K + S} N
\]

is used to describe the predation pressure on spruce leaves due to budworm predation. With this kind of functional response, the rate of budworm predation pressure approaches a maximal value \( \delta > 0 \) when spruce leaf area increases, which seems more reasonable in reality. \( K > 0 \) is the spruce leaf area at half of the maximal predation pressure. Note that (1) becomes the previous one studied in [4] when \( K = 0 \). We list the biological interpretations of all the variables and parameters of model (1) in Table 1 for the readers’ convenience.
Variable/parameter | Biological interpretation
---|---
t | Time
N | Population density of the larvae
S | Average leaf area of the spruce
r | Intrinsic growth rate of budworm population
ρ | Intrinsic growth rate of spruce leaf area
κ | Coefficient measuring to which degree the leaves can accommodate the larvae
$S_{\text{max}}$ | Carrying capacity of spruce leaf area
β | Maximum consumption rate of budworms per budworm-predator per time
P | Budworm population density at maximal predation pressure
η | Regulating coefficient of the predation pressure
δ | Maximal rate of budworm predation pressure as spruce leaf area increases
K | Spruce leaf area at half of the maximal predation pressure

Table 1. The biological interpretations of the variables and parameters of model (1).

The paper is organized as follows. In Section 2 we study the equilibria of the model, including the existence, the number and the stability. Section 3 is devoted to the analysis of the existence of relaxation oscillations of the model by using perturbation theory. An asymptotic expression of the period of relaxation oscillations is also given. In Section 4 we study the conditions on parameters for having relaxation oscillations and the relation between the period of relaxation oscillations and parameters by conducting numerous numerical simulations.

2. Equilibria analysis. We make the following change of variables:

$X = \frac{N}{\kappa S}$,  \hspace{1em} $Y = \frac{r\kappa S}{\beta P}$,  \hspace{1em} $Z = XY = \frac{rN}{\beta P}$, \hspace{1em} $\tau = \rho t$,

and let

$\varepsilon = \frac{\rho}{r}$,  \hspace{1em} $\alpha = \frac{\eta}{\kappa}$,  \hspace{1em} $\varrho = \frac{\delta\kappa}{\rho}$,  \hspace{1em} $Y_{\text{max}} = \frac{r\kappa S_{\text{max}}}{\beta P}$, \hspace{1em} $A = \frac{r\kappa K}{\beta P}$.

Then system (1) is transformed into the following dimensionless form

$$
\begin{align*}
\varepsilon \frac{dZ}{d\tau} &= YF_0 \left( \frac{Z}{Y}, Y; \alpha^2 \right), \\
\frac{dY}{d\tau} &= Yf \left( \frac{Z}{Y}, \varrho, Y_{\text{max}}, A \right),
\end{align*}
$$

where

$F_0(X, Y; \alpha^2) := X(1 - X) - \frac{1}{Y} \frac{X^2}{X^2 + \alpha^2}$,

$f(X, Y; \varrho, Y_{\text{max}}, A) := 1 - \frac{Y}{Y_{\text{max}}} - \frac{\varrho XY}{A + Y}$.

According to [1], $\rho \ll r$, thus we have $0 < \varepsilon \ll 1$. 
2.1. **Existence of equilibria.** First it’s easy to deduce that there exists a semi-trivial equilibrium \((Z_{steq}, Y_{steq}) = (0, Y_{max})\) for system (2).

The possible positive equilibria \((X_{eq}, Y_{eq})\) are given by the solutions of the following nullcline equations:

\[
\begin{align*}
F_0(X, Y; \alpha^2) &= 0, \\
f(X, Y; \varrho, Y_{max}, A) &= 0.
\end{align*}
\]

First, the non-trivial solution of (3) is given as \(Y = \Psi(X; \alpha^2) := \frac{X}{(X^2 + \alpha^2)(1 - X)}\).

Since \(X, Y > 0\), then the possible positive equilibria \((X_{eq}, Y_{eq})\) is restricted in the strip \(S := \{(X, Y) \mid 0 < X < 1, Y > 0\}\).

Next, the non-trivial solution of (4) is given as \(X = \Theta(Y; \varrho, Y_{max}, A) := \frac{1}{\varrho} \left(1 - \frac{A + Y}{Y_{max} + A}\right)\).

Differentiation of (6) with respect to \(Y\) gives

\[
\Theta'(Y) = \frac{1}{\varrho} \left(-\frac{1}{Y_{max}} - \frac{A}{Y^2}\right) < 0,
\]

then the inverse function \(Y = \Theta^{-1}(X; \varrho, Y_{max}, A)\) exists and

\[
(\Theta^{-1})'(X) = \frac{dY}{dX} = \frac{1}{\frac{dY}{dX}} = \frac{1}{\Theta'(Y)} < 0.
\]

Moreover,

\[
\Theta''(Y) = \frac{2A}{\varrho Y^3} > 0.
\]

Therefore the function \(\Theta\) is decreasing and concave upward in the \(X-Y\) plane. Now observe that

\[
\Psi(0; \alpha^2) = 0, \quad \lim_{X \to 1^-} \Psi(X; \alpha^2) = +\infty.
\]

\[
\Theta(Y_{max}; \varrho, Y_{max}, A) = 0, \quad \lim_{Y \to 0^+} \Theta(Y; \varrho, Y_{max}, A) = +\infty.
\]

This implies that there exists at least one solution of system of equations (3)-(4) in the strip \(S\). Thus we always have at least one positive equilibrium for system (2).

2.2. **Number of positive equilibria.** Differentiation of (5) with respect to \(X\) yields

\[
\Psi'(X; \alpha^2) = \frac{P_3(X; \alpha^2)}{(X^2 + \alpha^2)^2(1 - X)^2},
\]

where \(P_3\) is the cubic polynomial

\[
P_3(X; \alpha^2) = 2X^3 - X^2 + \alpha^2.
\]

Then

(I) When \(\alpha^2 \geq 1/27\), we have \(P_3(X; \alpha^2) \geq 0\) for any \(X \in (0, 1)\). Thus \(\Psi\) is increasing, and system (2) has exactly one equilibrium (see Figure 1).
Figure 1. In this figure we show the nullclines when $\alpha^2 \geq \frac{1}{27}$. In this case there exists exactly one positive equilibrium. Other parameters are $\varepsilon = 0.001$, $\varrho = 5$, $Y_{\text{max}} = 20$, $A = 1$. 
(II) When $0 < \alpha^2 < 1/27$, $P_3(X; \alpha^2)$ changes sign for $X \in (0, 1)$. A simple analysis of the cubic polynomial $P_3$ shows that there exist $X_1(\alpha^2)$ and $X_2(\alpha^2)$ with the properties

$$0 < X_1(\alpha^2) < \frac{1}{3} < X_2(\alpha^2) < \frac{1}{2} < 1,$$

$$\frac{d}{d\alpha^2}X_1(\alpha^2) > 0,$$

$$\frac{d}{d\alpha^2}X_2(\alpha^2) < 0,$$

and

\[
\begin{cases}
    P_3(X; \alpha^2) = 0, & \text{if } X = X_1(\alpha^2) \text{ or } X_2(\alpha^2), \\
    P_3(X; \alpha^2) > 0, & \text{if } 0 < X < X_1(\alpha^2) \text{ or } X_2(\alpha^2) < X < 1, \\
    P_3(X; \alpha^2) < 0, & \text{if } X_1(\alpha^2) < X < X_2(\alpha^2). 
\end{cases}
\]

Thus the curve (5) exhibits an 8-shape in the phase plane, with increasing parts for $X \in (0, X_1(\alpha^2)) \cup (X_2(\alpha^2), 1)$ and decreasing parts for $X \in (X_1(\alpha^2), X_2(\alpha^2))$. Now we can choose the parameters $(\varrho, Y_{\max}, A)$ and move the curve (6) such that the system of equations (5)-(6) has one, two or three positive solutions (see Figure 2 for an example).

**Remark 2.1.** The case with two positive solutions of the system of equations (5)-(6) when $0 < \alpha^2 < 1/27$ can occur for point with $X$-coordinate satisfying $P_3(X; \alpha^2) < 0$ and

$$\Psi'(X; \alpha^2) = (\Theta^{-1})'(X; \varrho, Y_{\max}, A),$$

namely $\Psi$ and $\Theta^{-1}$ are tangential at this intersection point. This case can be viewed as a transition state between the one-solution and three-solution case when $0 < \alpha^2 < 1/27$.

2.3. **Computation of positive equilibria.** By replacing (5) into (6) we obtain that the $X$-coordinates of equilibria should satisfy the equation

$$P_6(X; \alpha^2, \varrho, Y_{\max}, A) = 0,$$

where

$$P_6(X; \alpha^2, \varrho, Y_{\max}, A) = AY_{\max}X^6 + Y_{\max}(\varrho - 2A)X^5 + [2AY_{\max}\alpha^2 + A + (A - 1 - \varrho)Y_{\max}]X^4 + [(\varrho - 4A)Y_{\max}\alpha^2 + Y_{\max} - A]X^3 + [AY_{\max}\alpha^4 + (A + 2AY_{\max} - Y_{\max} - \varrho Y_{\max})\alpha^2 - 1]X^2 + [-2AY_{\max}\alpha^4 + (Y_{\max} - A)\alpha^2]X + AY_{\max}\alpha^4.$$ 

Since

$$P_6(0; \alpha^2, \varrho, Y_{\max}, A) = AY_{\max}\alpha^4 > 0, \quad P_6(1; \alpha^2, \varrho, Y_{\max}, A) = -1 < 0,$$

we conclude that there exists at least one solution in the interval $(0, 1)$, consistent with our former result. Notice that not all the solutions of $P_6(X) = 0$ are the solutions of (5)-(6), since extra solutions might be introduced when we reduce the fraction to a common denominator.

We denote the equilibria of system (2) by $(Z_{eq}, Y_{eq})$ where $Z_{eq} = X_{eq}Y_{eq}$.
Figure 2. In this figure we show the nullclines when \( \alpha^2 = 0.0013 \in (0, 1/27) \) and the system of equations (5)-(6) has one positive solution. In this case there exists one positive equilibrium. Other parameters are: \( \varepsilon = 0.001, \varrho = 5, Y_{\text{max}} = 20, A = 1 \).

2.4. Stability of positive equilibria. The Jacobian \( J \) of system (2) is given as

\[
J = \begin{pmatrix}
\frac{1}{\varepsilon} \frac{\partial F_0}{\partial X} & \frac{1}{\varepsilon} \left( F_0 - X \frac{\partial F_0}{\partial X} + Y \frac{\partial F_0}{\partial Y} \right) \\
\frac{\partial f}{\partial X} & -X \frac{\partial f}{\partial X} + Y \frac{\partial f}{\partial Y}
\end{pmatrix},
\]

where

\[
\frac{\partial F_0}{\partial X} = 1 - 2X - \frac{1}{Y} \frac{2\alpha^2 X}{(X^2 + \alpha^2)^2}, \quad \frac{\partial F_0}{\partial Y} = \frac{1}{Y^2} \frac{X^2}{X^2 + \alpha^2},
\]

\[
\frac{\partial f}{\partial X} = -\frac{\varrho Y}{A + Y}, \quad \frac{\partial f}{\partial Y} = -\frac{1}{Y_{\text{max}}} - \frac{\varrho AX}{(A + Y)^2}.
\]

In order to obtain the stability of equilibria, we follow the standard argument of the qualitative analysis for planar system as follows. Consider on the \( X-Y \) plane and let \((X_{eq}, Y_{eq})\) be the equilibrium. Notice that \((X_{eq}, Y_{eq})\) satisfies (5), then we have the following simplified formula:

\[
\left. \frac{\partial F_0}{\partial X} \right|_{(X_{eq}, Y_{eq})} = -\frac{P_3(X_{eq}; \alpha^2)}{X_{eq}^2 + \alpha^2}.
\]

The trace and determinant of the Jacobian evaluated at \((X_{eq}, Y_{eq})\) can be computed explicitly as follows:

\[
tr(J) = -\frac{1}{\varepsilon} \frac{P_3(X_{eq}; \alpha^2)}{X_{eq}^2 + \alpha^2} + 1 - \frac{2Y_{eq}}{Y_{\text{max}}} - \frac{\varrho AX_{eq}Y_{eq}}{(A + Y_{eq})^2}.
\]
where the fact that \((X_{eq}, Y_{eq})\) satisfies (4) is also used in the computation. Then

(I) When \(\alpha^2 \geq 1/27\), there exists a unique equilibrium \((X_{eq}, Y_{eq})\) where \(0 < X_{eq} < 1\). Since \(P_3(X_{eq}; \alpha^2) > 0\), then \(det(J) > 0\), which implies that the equilibrium is a node or a focus. Moreover, we get \(tr(J) < 0\) for \(\varepsilon\) small enough, which means that the equilibrium is stable.

(II) When \(0 < \alpha^2 < 1/27\), consider the following two cases.

(i) There exists a unique equilibrium (see Figure 3 for an illustration).

If the \(X\)-coordinate \(X_{eq}\) of the equilibrium satisfies \(P_3(X_{eq}; \alpha^2) > 0\) (corresponding to situation (a) and (c) in Figure 3), then similar as in (I), the equilibrium is a node or a focus which is stable for \(\varepsilon\) small enough.

If \(P_3(X_{eq}; \alpha^2) < 0\) (corresponding to situation (b) in Figure 3), we must always have

\[
  (\Theta^{-1})(X_{eq}; \varrho, Y_{max}, A) < \Psi'(X_{eq}; \alpha^2) < 0.
\]

Next we try to determine the sign of \(det(J)\). Since by the fact that \((X_{eq}, Y_{eq})\) satisfies (4) and (5), we have

\[
  \frac{\varrho X_{eq} Y_{eq}}{A + Y_{eq}} = 1 - \frac{Y_{eq}}{Y_{max}}; \quad X_{eq} = Y_{eq}(X_{eq}^2 + \alpha^2)(1 - X_{eq}).
\]

Then by replacing them into the formula of \(det(J)\) and using (9) we get

\[
  det(J) = \frac{1}{\varepsilon} \left\{ \left( \frac{X_{eq}^2 + \alpha^2}{\varepsilon} \right) (1 - X_{eq})^2 \Psi(X_{eq}; \alpha^2) \left[ \frac{Y_{eq}}{Y_{max}} + \frac{A}{A + Y_{eq}} \left( 1 - \frac{Y_{eq}}{Y_{max}} \right) \right] \right. \\
  + \left. \frac{\varrho Y_{eq}^2 (X_{eq}^2 + \alpha^2)(1 - X_{eq})^2}{A + Y_{eq}} \right\}
\]

\[
  = \frac{1}{\varepsilon} \left[ \left( \frac{X_{eq}^2 + \alpha^2}{\varepsilon} \right) (1 - X_{eq})^2 \left( \frac{Y_{eq} + \alpha Y_{max}}{Y_{max} (A + Y_{eq})} \right)^2 \Psi'(X_{eq}; \alpha^2) \right. \\
  + \left. \frac{\varrho Y_{eq}^2 (X_{eq}^2 + \alpha^2)(1 - X_{eq})^2}{A + Y_{eq}} \right] \\
  = \frac{X_{eq}^2 + \alpha^2}{\varepsilon Y_{max} (A + Y_{eq})} (1 - X_{eq})^2 \left( \frac{Y_{eq} + \alpha Y_{max}}{Y_{max} (A + Y_{eq})} \right) \left( \Psi'(X_{eq}; \alpha^2) + \frac{\varrho Y_{eq}^2 Y_{max}}{Y_{eq} + \alpha Y_{max}} \right) \\
  = \frac{X_{eq}^2 + \alpha^2}{\varepsilon Y_{max} (A + Y_{eq})} (1 - X_{eq})^2 \left( \frac{Y_{eq} + \alpha Y_{max}}{Y_{max} (A + Y_{eq})} \right) \left( \Psi'(X_{eq}; \alpha^2) - \frac{\varrho}{Y_{max} + \alpha Y_{max}} \right) \\
  = \frac{X_{eq}^2 + \alpha^2}{\varepsilon Y_{max} (A + Y_{eq})} (1 - X_{eq})^2 \left( \frac{Y_{eq} + \alpha Y_{max}}{Y_{max} (A + Y_{eq})} \right) \left( \Psi'(X_{eq}; \alpha^2) - (\Theta^{-1})'(X_{eq}; \varrho, Y_{max}, A) \right)
\]

where in the last equality we have used (7) and (8). Then we can deduce that \(det(J) > 0\) and the equilibrium is also a node or a focus. Moreover, an \(\varepsilon\) small enough leads to \(tr(J) > 0\), which means that the equilibrium is unstable.

Finally, if \(P_3(X_{eq}; \alpha^2) = 0\), then \(det(J) > 0\) and the equilibrium is still a node or a focus, but the stability cannot be determined since the sign of \(tr(J)\) is uncertain.

(ii) There exists three equilibria. First, similar as in (I), the equilibria with the smallest and the largest \(X\)-coordinate will be stable node or focus.
for \( \varepsilon \) small enough. For the equilibrium in the middle, it holds that \( p_3(X_{eq};\alpha^2) < 0 \) and \( \Psi'(X_{eq};\alpha^2) < (\Theta^{-1})'(X_{eq};\varrho,Y_{\text{max}},A) < 0 \), then by (11) we deduce that \( \det(J) < 0 \), thus this equilibrium is a saddle point.

![Figure 3](image-url)

**Figure 3.** In this figure we show three possible situations producing only one equilibrium in the strip \( S \) when \( \alpha^2 = 0.0013 \in (0,1/27) \). Other parameters are: \( \varepsilon = 0.001, \varrho = 5 \) and \( Y_{\text{max}} = 10, A = 1 \) for (a), \( Y_{\text{max}} = 20, A = 1 \) for (b), \( Y_{\text{max}} = 55, A = 10 \) for (c).

### 3. Singular perturbation theory and relaxation oscillations

In this section we study the behavior of system (2) in the asymptotic limit \( \varepsilon \to 0 \). The following assumptions are made throughout this section.

**Assumption 3.1.** Assume that

(a) \( 0 < \alpha^2 < 1/27 \).

(b) There exists a unique equilibrium \((X_{eq},Y_{eq})\) satisfying that \( 0 < X_{eq} < 1 \) and \((\Theta^{-1})'(X_{eq};\varrho,Y_{\text{max}},A) < \Psi'(X_{eq};\alpha^2) < 0 \).

The nullclines under these assumptions correspond to situation (b) in Figure 3, namely the unique equilibrium (unstable node or focus) in the strip \( S \) is located at the intermediate branch of the nullcline (5) (namely the nullcline segment for which the \( X \)-coordinate is between \( X_1 \) and \( X_2 \)). In the next subsections we follow the standard procedure introduced in [2, 4, 8, 10] for singularly perturbed systems.

#### 3.1. Outer approximation

First, let \( \varepsilon = 0 \) in the predator equation in (2). We get the following system

\[
\begin{cases}
F_0(X,Y;\alpha^2) = 0, \\
\frac{dY}{d\tau} = Yf(X,Y;\varrho,Y_{\text{max}},A),
\end{cases}
\]
with $X = Z/Y$. System (12)-(13) is referred to as the degenerate or reduced system. Notice that equation (12) yields (5), which is referred to as the quasi-steady state of system (2), and is given as

$$Y_{qs} = \Psi(X_{qs}; \alpha^2) = \frac{X_{qs}}{(X_{qs}^2 + \alpha^2)(1 - X_{qs})}, \ 0 < X_{qs} < 1. \quad (14)$$

For clarity, in this section $(X_{qs}, Y_{qs})$ and the corresponding $(Z_{qs}, Y_{qs})$ with $Z_{qs} = X_{qs}Y_{qs}$ will denote the coordinates of the quasi-steady state. The evolution of $Y_{qs}$ is governed by the equation

$$\frac{dY_{qs}}{d\tau} = Y_{qs} \left(1 - \frac{Y_{qs}}{Y_{max}} - \frac{\varrho X_{qs}Y_{qs}}{A + Y_{qs}}\right).$$

Moreover, we obtain

$$\frac{dY_{qs}}{d\tau} = \frac{d\Psi(X_{qs}; \alpha^2)}{dX_{qs}} \frac{dX_{qs}}{d\tau},$$

hence

$$\frac{dX_{qs}}{d\tau} = \frac{1}{\Psi'(X_{qs}; \alpha^2)} \frac{dY_{qs}}{d\tau} = \frac{\Psi'(X_{qs}; \alpha^2)}{\Psi'(X_{qs}; \alpha^2)} \left(1 - \frac{\Psi(X_{qs}; \alpha^2)}{Y_{max}} - \frac{\varrho X_{qs}\Psi(X_{qs}; \alpha^2)}{A + \Psi(X_{qs}; \alpha^2)}\right)$$

$$= \frac{\Psi(X_{qs}; \alpha^2)}{\Psi'(X_{qs}; \alpha^2)} f \left(X_{qs}, \Psi(X_{qs}; \alpha^2); \varrho, Y_{max}, A\right). \quad (15)$$

We will refer to the quasi-steady state (14) together with the equation (15) as the outer approximation of system (2).

### 3.2. Inner approximation and stability of the quasi-steady state.

Next, in order to study the slow-fast system (2), we introduce the coordinate stretching

$$\xi = \frac{\tau}{\varepsilon}, \quad Z(\tau) = \tilde{Z}(\xi), \quad Y(\tau) = \tilde{Y}(\xi). \quad (16)$$

Then system (2) is rewritten as

$$\begin{cases} 
\frac{d\tilde{Z}}{d\xi} = \tilde{Y} F_0 \left(\tilde{Z}, \tilde{Y}; \alpha^2\right), \\
\frac{d\tilde{Y}}{d\xi} = \varepsilon \tilde{Y} f \left(\tilde{Z}, \tilde{Y}; \varrho, Y_{max}, A\right).
\end{cases} \quad (17)$$

From (18) we can see that asymptotically as $\varepsilon \to 0$, $\tilde{Y}$ is constant to the leading order, and the scalar equation (17) with the constraint $\tilde{Y} = \tilde{Y}_0 = \text{const.}$ describes the dynamical evolution of initial states located outside the quasi-steady state. Under this constraint, the solution of (17) is referred to as the inner approximation, which is represented by a line segment parallel to the $X$-axis in the phase plane.

In the remainder of this part we use means of standard methods to study the stability of the quasi-steady state within the framework of (17). The Jacobian of (17) evaluated at the quasi-steady state is given as

$$\lambda = \frac{\partial (\tilde{Y} F_0)}{\partial \tilde{Z}} \left(\tilde{Y} = \Psi(\tilde{X}; \alpha^2)\right) = \frac{\partial F_0}{\partial \tilde{X}} \left(\tilde{X}, \Psi(\tilde{X}; \alpha^2); \alpha^2\right) = -\frac{P_3(\tilde{X}; \alpha^2)}{\tilde{X}^2 + \alpha^2}. \quad (19)$$
By (10), the quasi-steady state is divided into three branches: the lower branch 
\( (0 < X < \tilde{X}_1) \), the intermediate branch \( (\tilde{X}_1 < X < \tilde{X}_2) \) and the higher branch 
\( (\tilde{X}_2 < X < 1) \). In addition, by (19), the lower branch and the higher branch are 
uniformly asymptotically stable, while the intermediate branch is unstable. The 
strip \( \mathcal{S} \) is thus decomposed into a union of two open disjoint sets, denoted by \( \Omega_1 \) 
and \( \Omega_3 \), where \( \Omega_1 \) and \( \Omega_3 \) are the attraction domain for the lower and higher branch, 
respectively. An illustration of the stability of the quasi-steady state is shown in 
Figure 4.

![Figure 4](image.png)

**Figure 4.** In this figure the stability of the quasi-steady state is 
shown (the tilde over \( X \) and \( Y \) is neglected here for a better look). 
The lower and higher branch (the blue part) of the quasi-steady 
state are uniformly asymptotically stable, while the intermediate 
branch (the pink part between \( \tilde{X}_1 \) and \( \tilde{X}_2 \)) is unstable. The arrows 
indicate the domains of attraction of the stable branches. The 
pink curve segments \( \Gamma_1^*, \Gamma_2^* \) and \( \Gamma_3^* \) indicate the common boundary 
between the attraction domains of the lower and higher branch (see 
Remark 3.3 in the following).

### 3.3. Existence of relaxation oscillations
In this subsection we construct a 
uniformly valid asymptotic approximation of the solution of system (2) by gluing 
together the inner and outer approximation. The common method is to restate 
the problem in terms of bifurcation theory. Consider the parameter \( Y_{qs} \) as a control 
parameter in the outer approximation (14)-(15). The stable branches and the un-
stable branch will meet in two bifurcation points denoted by \((X_i, Y_i)\), \(i = 1, 2\) and 
determined by the equations

\[
P_3(X_i; \alpha^2) = 0, \quad Y_i = \Psi(X_i; \alpha^2) = \frac{X_i}{(X_i^2 + \alpha^2)(1 - X_i)}.
\]  
(20)
It can be proved that the two bifurcation points \((X_i, Y_i), i = 1, 2\) are two saddle-node points (see [4, Appendix A] for a proof).

Now we can construct the asymptotic approximation of the solution. We start with an arbitrary initial condition \((X(0), Y(0))\). Then it is attracted to one of the stable branches of the quasi-steady state by the stability result in the previous subsection. This stage is described by the inner approximation, namely the equation (17) with the constraint \(Y = Y(0)\) and happens rapidly due to the coordinate stretching (16). From a biological point of view, this stage shows that there exists an explosive growth or decay in the predator population, while the prey population is not able to adjust to these changes so fast. The second stage consists of a motion along the stable branch of the quasi-steady state.

Next, when the state approaches one of the bifurcation points \((X_i, Y_i), i = 1, 2\), the dynamics has a remarkable change. Specifically speaking, the out approximation is invalidated (see (15)) since \(\Psi'(X; \alpha^2)\) tends to 0 by (20). We then speculate that the dynamical evolution can be approximately described by the inner approximation with the constraint \(Y = Y_i\) \((i = 1, 2)\). Since the points on the inner approximation curve in the phase plane will be attracted to the outer approximation, then the line segment \(Y = Y_i\) \((i = 1, 2)\) terminates on one of the stable branches of the quasi-steady state curve at the so-called drop-off points corresponding to the bifurcation points [2, 4, 8, 10]. Thus the dynamical evolution is resumed by the outer approximation in the zeroth-order approximation. Hence we construct a uniformly valid asymptotic approximation to the exact solution for all \(\tau \geq 0\), consisting of the outer and inner approximation in their respective regimes. Moreover, from the above process of construction, we can also see that an isolated closed orbit in the phase plane is obtained, representing the relaxation oscillation, due to the existence of the bifurcation points and the shape of the quasi-steady state.

Figure 5 shows the process of construction and the closed orbit in the above arguments.

**Remark 3.2.** The result on relaxation oscillations is consistent with Poincaré-Bendixson theorem on the existence of closed orbits in 2-d systems.

**Remark 3.3.** The existence of the bifurcation points \((X_i, Y_i), i = 1, 2\) also induces a discontinuous dependence on the initial conditions in the zeroth-order approximation in the following sense: Recall the attraction domain \(\Omega_1\) and \(\Omega_3\) in the study of the stability of the quasi-steady state (Sec. 3.2). Consider the common boundary between \(\Omega_1\) and \(\Omega_3\), which is given as a union of curve segments \(\Gamma^* = \Gamma_1^* \cup \Gamma_2^* \cup \Gamma_3^*\) and can be parameterized by \(\tilde{X}\) as follows

\[
\Gamma_1^*(\tilde{X}) = (\tilde{X}, Y_1), \quad 0 < \tilde{X} \leq \tilde{X}_1,
\]

\[
\Gamma_2^*(\tilde{X}) = (\tilde{X}, \Psi(\tilde{X}; \alpha^2)), \quad \tilde{X}_1 \leq \tilde{X} \leq \tilde{X}_2,
\]

\[
\Gamma_3^*(\tilde{X}) = (\tilde{X}, \tilde{Y}_2), \quad \tilde{X}_2 \leq \tilde{X} < 1.
\]

The behavior of attraction switches discontinuously when the initial condition changes and crosses the boundary curve \(\Gamma^*\). Since the solutions of (2) depend continuously on the initial conditions, we may conclude that for initial conditions in an \(\varepsilon\)-dependent layer around the common boundary curve \(\Gamma^*\), the zeroth-order dynamics will give a poor approximation of the full system. Other tools must be used to deal with the switching process in this case. We will not go deeper on this issue in this paper.
Figure 5. In this figure we show the construction of the closed orbit. The point $(X_1 + \delta, Y_1), \delta > 0$ is attracted to the higher stable branch of the quasi-steady state, while the point $(X_2 - \delta, Y_2), \delta > 0$ is attracted to the lower stable branch (indicated in (a)). As $\delta \to 0$, a closed orbit emerges, which represents the relaxation oscillations (indicated in (b)).
3.4. Asymptotic expression for the period of relaxation oscillation. In this subsection we derive an asymptotic expression for the period of relaxation oscillation by following the procedure in [2, 4, 8, 10]. The parameters in the expression of functions are neglected in this subsection for simplicity.

Denote $\xi_i, i = 1, 2$ to be the $X$-coordinates of the drop-off points corresponding to the bifurcation points, namely they satisfy

$$Y_1 = \Psi(\xi_2; \alpha^2) = \frac{\xi_2}{(\xi_2^2 + \alpha^2)(1 - \xi_2)}, \quad Y_2 = \Psi(\xi_1; \alpha^2) = \frac{\xi_1}{(\xi_1^2 + \alpha^2)(1 - \xi_1)}.$$  \hspace{1cm} (21)

Denote $\Gamma_1$ to be the segment starting at $(\xi_1, Y_2)$ and terminating at $(X_1, Y_1)$ of the lower stable branch of the quasi-steady state, and $\Gamma_2$ to be the segment starting at $(\xi_2, Y_1)$ and terminating at $(X_2, Y_2)$ of the higher stable branch of the quasi-steady state. The asymptotic expression for the period $T_0$ of the relaxation oscillation to the lowest order in the perturbation parameter $\varepsilon$ is given as in [2, 8, 10]

$$T_0 = \int_{\Gamma_1} d\tau + \int_{\Gamma_2} d\tau + \int_{\Sigma} d\tau,$$

where in the terminology of [2, 8, 10], $\Sigma$ includes the so-called junction time close to the bifurcation points, which is, the fast motion parts, namely the parts of the relaxation oscillation described by the inner approximation, and the drop parts close to the drop-off points (see Figure 6). However, when we deal with the zeroth-order theory, the contribution from $\Sigma$ is negligible compared to the contributions from $\Gamma_1$ and $\Gamma_2$. Then we get

$$T_0 = \int_{\Gamma_1} d\tau + \int_{\Gamma_2} d\tau = \int_{\Gamma_1} \frac{dY_{qs}}{\Psi'(X_{qs})f(X_{qs}, \Psi(X_{qs}))} dX_{qs} + \int_{\Gamma_2} \frac{dY_{qs}}{\Psi'(X_{qs})f(X_{qs}, \Psi(X_{qs}))} dX_{qs}.$$  \hspace{1cm} (22)

By using the formula (22) for $T_0$ we are able to estimate roughly the time interval between consecutive budworm outbreaks. Specific numerical results can be seen in the following section.

4. Numerical simulations.

4.1. The period $T_0$. From the last section we obtain an asymptotically estimated formula for this period, denoted by $T_0$. Moreover, numerical simulations of the original system (2) can also deduce a more accurate result of the period. We denote this one by $T_{num}$. In this subsection we are going to numerically calculate and compare the two results of the period of budworm outbreaks.

The procedures for computing the expression (22) are as follows:
(1) Choose $\alpha$ such that $0 < \alpha^2 < 1/27$.
(2) Determine the zeros $X_1$ and $X_2$ of the polynomial $P_3$.
(3) Compute $Y_1$ and $Y_2$ by using (5).
(4) Determine the $X$-coordinates $\xi_1$ and $\xi_2$ of the drop-off points by using (21).
(5) Choose the parameters $\varrho$, $Y_{\text{max}}$ and $A$.
(6) Evaluate the period $T_0$ by using (22).

For example, we choose parameters $\alpha^2 = 0.0013$, $\varrho = 5$, $Y_{\text{max}} = 20$ and $A = 1$. With this set of parameters, relaxation oscillations exist. Numerical evaluation of the integral (22) gives $T_0 = 3.3063$.

The procedures for estimating the period $T_{\text{num}}$ deduced by solving numerically the original system (2) are as follows:

(1) Find the extreme points of the solution curve $Z(\tau)$ and $Y(\tau)$ by finding the zeros of the derivative in system (2). Collect all the corresponding $\tau$ values.
(2) The first and the third $\tau$ value must correspond to either two maximal or two minimal points. The period can be estimated by the difference between the two $\tau$ values.

We choose the same parameters as above and $\varepsilon = 0.001$. Numerical simulations of system (2) are shown in Figure 7 and 8. Observe that the system spends a relatively longer time at low budworm density phase than at budworm outbreak phase (see the red curve in Figure 7). The part between the two phases looks like a vertical line segment, which reveals that the transition of the two phases is relatively fast. The simulation gives the period $T_{\text{num}} = 3.4467$. Moreover, we conduct the same numerical simulation with $\varepsilon = 10^{-6}$, and obtain the period $T_{\text{num}} = 3.3079$. In both cases $T_{\text{num}} > T_0$, because $T_{\text{num}}$ includes the fast motion parts (corresponding to the $\Sigma$-interval mentioned in the previous section) but $T_0$ does not. We show how the numerically estimated period $T_{\text{num}}$ varies with different $\varepsilon$ values in Figure 9.
Figure 7. In this figure we show how we compute the period of relaxation oscillation from numerical simulations of the original system (2). The period is estimated by the difference of time between two maximal (or minimal) points. The parameters are: $\alpha^2 = 0.0013$, $\varepsilon = 0.001$, $\varrho = 5$, $Y_{\text{max}} = 20$, $A = 1$.

Notice that $T_{\text{num}} > T_0$ for all values of the parameter $\varepsilon$ and that $T_{\text{num}} \to T_0$ as $\varepsilon \to 0$. We also plot the solutions as evolution in time and in the phase plane with different values of $\varepsilon$ in Figure 10. From the figures we can also observe that the period of the relaxation oscillations $T_{\text{num}}$ increases with the perturbation parameter $\varepsilon$, consistent with the increasing curve of $T_{\text{num}}$ in Figure 9.

4.2. A critical value $Y_{\text{cri}}$. The value $Y_{\text{cri}}$ is defined as the value of $Y_{\text{max}}$ when the graph of the function $X = \Theta(Y; \varrho, Y_{\text{max}}, A)$ passes through the points $(X_1, Y_1)$ and $(X_2, Y_2)$. It is dependent on $\varrho$ and $A$. Moreover, for each $Y_{\text{max}} > Y_{\text{cri}}$, we can always find some parameters $\varrho$ and $A$ such that Assumption 3.1-(b) is satisfied. A direct computation gives

$$Y_{\text{cri}} = \frac{Y_1 - Y_2}{X_1} \cdot \frac{1}{X_2} + A \left( \frac{1}{X_1} - \frac{1}{X_2} \right).$$

Observe that $Y_{\text{cri}}$ depends actually only on $A$. By (23), when $A = 0$,

$$Y_{\text{cri}} = \frac{X_2 Y_1 - X_1 Y_2}{X_2 - X_1}.$$
Figure 8. In Figure (a) we plot the budworm abundance (the lower curve) and the leaf area abundance (the upper curve) during one oscillation period. In Figure (b) we plot the budworm abundance against leaf area abundance on the phase plane. The closed orbit is displayed in (b). The period is divided into 20 equidistant time intervals indicated by rings. The parameters are: \(\alpha^2 = 0.0013, \varepsilon = 0.001, \varrho = 5, Y_{\text{max}} = 20, A = 1\).
Figure 9. In this figure we show the numerically estimated period $T_{num}$ as a function of $\varepsilon$. $T_{num}$ converges to $T_0$ as $\varepsilon \to 0$. The parameters are: $\alpha^2 = 0.0013$, $\varrho = 5$, $Y_{\text{max}} = 20$, $A = 1$.

In this case the function $\Theta$ becomes a straight line, and this result is consistent with [4]. When $A \to \infty$, we have

$$Y_{cri} \to \frac{1}{X_1} - \frac{1}{X_2}.$$ 

The variation of $Y_{cri}$ as a function of $A$ is shown in Figure 11. For different values of $A$, the nullclines satisfying that the graph of the function $X = \Theta(Y; \varrho, Y_{\text{max}}, A)$ passes through the points $(X_1, Y_1)$ and $(X_2, Y_2)$ are plotted in Figure 12.

4.3. Parameter ranges for exhibiting relaxation oscillations. In this subsection we fix $\alpha^2 = 0.0013$, then the graph of $(X, \Psi(X))$ is fixed, and so are the two extreme points $(X_i, Y_i), i = 1, 2$ of $\Psi(X)$.

Now for a fixed value of $Y_{\text{max}}$, the graph of $(\Theta(Y), Y)$ is determined by $\varrho$ and $A$. Next we investigate the conditions on $\varrho$ and $A$ when there exist relaxation oscillations.

For the nullclines to intersect at $(X_i, Y_i), i = 1, 2$, there must be

$$X_i \varrho + \left(\frac{1}{Y_{\text{max}}} - \frac{1}{Y_i}\right) A = 1 - \frac{Y_i}{Y_{\text{max}}},$$

namely the parameter pair $(A, \varrho)$ should be on a straight line (segment) since $Y_{\text{max}}$ is now fixed. In the following figures we fix different values of $Y_{\text{max}}$ and show the straight lines where the parameter pair $(A, \varrho)$ lies on.

For example, in Figure 13, we fix $Y_{\text{max}} = 16$. The nullclines will intersect at $(X_1, Y_1)$ for each parameter pair $(A, \varrho)$ taking value on the red line, and will intersect at $(X_2, Y_2)$ for $(A, \varrho)$ taking value on the green line. The intersection point $(A, \varrho)$
Figure 10. In this figure we show the variation of the relaxation oscillations with common initial condition $X(0) = 0.2$, $Y(0) = 8$ and different $\varepsilon$ values: 0.001, 0.0028, 0.0046, 0.0064, 0.0082 and 0.01. In Figure (a) the evolutions of the budworm and leaf area in time are displayed, while in Figure (b) the corresponding closed orbits in the phase plane are displayed. Notice that the period of oscillation increases with $\varepsilon$. The other parameters are: $\alpha^2 = 0.0013$, $\varrho = 5$, $Y_{\text{max}} = 20$, $A = 1$. 
Figure 11. In this figure we plot the variation of $Y_{cri}$ with different values of $A$. The other parameters are: $\alpha^2 = 0.0013$. When $A = 0$, $Y_{cri} = 15.2333$. When $A \to \infty$, $Y_{cri} \to 18.2349$.

Figure 12. In this figure we plot the nullclines such that the graph of the function $X = \Theta(Y; \varrho, Y_{max}, A)$ passes through the points $(X_1, Y_1)$ and $(X_2, Y_2)$. Five values of $A$ are selected: $A = 0, 1, 5, 20, 500$. The other parameters are: $\alpha^2 = 0.0013$. 
of the two straight lines indicates that the nullclines will intersect at both \((X_1, Y_1)\) and \((X_2, Y_2)\) at the same time. Thus for this \(A\) value we have \(Y_{\text{cri}} = Y_{\text{max}} = 16\). Observe that only when the parameter pair \((A, \varrho)\) takes value in the region between the two straight lines can we have an equilibrium lying on the intermediate branch (review the beginning of Sec. 3 for an explanation of intermediate branch), and thus the possibility of having relaxation oscillations. Now let’s look at another scenario. In Figure 14, we fix \(Y_{\text{max}} = 20\). Figure 14-(a) indicates that the nullclines will intersect at \((X_1, Y_1)\) for each parameter pair \((A, \varrho)\) taking value on the upper straight line, and will intersect at \((X_2, Y_2)\) for \((A, \varrho)\) taking value on the lower straight line. From this figure we can see that the two lines have no intersection in the first quadrant, that is to say, there doesn’t exist any parameter pair \((A, \varrho)\) such that the two nullclines can intersect at both \((X_1, Y_1)\) and \((X_2, Y_2)\) at the same time. Same as before, only when the parameter pair \((A, \varrho)\) takes value in the region between the two straight lines can we have relaxation oscillations. For example, for \(A = 0\), only the values of \(\varrho\) taken on the pink line segment shown in Figure 14-(a) can lead to relaxation oscillations. We plot the asymptotic period \(T_0\) versus \(\varrho\) in Figure 14-(b). In the following we try to explore the asymptotic period \(T_0\) by varying the parameters.

4.3.1. Fixed \(A\) and varied \(Y_{\text{max}}\). In this subsection we fix \(A = 0\) and repeat the above simulations with various \(Y_{\text{max}}\) values. Specifically speaking, we first plot the allowed regions of the parameter pair \((A, \varrho)\) for exhibiting relaxation oscillations.
Figure 14. In figure (a) we plot parameter $\varrho$ versus parameter $A$ for $Y_{\text{max}} = 20$. The upper line represents all the parameter pair $(A, \varrho)$ such that the nullclines intersect at $(X_1, Y_1)$. The lower line represents all the parameter pair $(A, \varrho)$ such that the nullclines intersect at $(X_2, Y_2)$. Relaxation oscillations are possible when the parameter pair $(A, \varrho)$ takes values in the quadrilateral region between the two straight lines. In figure (b) we plot the asymptotic period $T_0$ of relaxation oscillations as a function of $\varrho$ for $A = 0$, corresponding to the pink part in (a).
Then we plot the asymptotic period $T_0$ versus $\varrho$ for fixed $A = 0$. The results are shown in Figure 15-16. We notice that with the increase of $Y_{\text{max}}$, 

(i) the allowed region of the parameter pair $(A, \varrho)$ for exhibiting relaxation oscillations becomes larger and moves upwards slowly;

(ii) when $A = 0$, the smallest value of $\varrho$ for exhibiting relaxation oscillations is not changing much (becoming larger, though), while the largest value becomes larger in a noticeable manner, and the period $T_0$ has a decreasing trend in general.

![Figure 15](image.png)

Figure 15. In this figure we plot parameter $\varrho$ versus parameter $A$ for $Y_{\text{max}} = 20, 30, 40, 100$. The representations of upper lines and lower lines are the same as in Figure 14-(a).

4.3.2. *Fixed $Y_{\text{max}}$ and varied $A$*. In this subsection we fix $Y_{\text{max}} = 20$ and repeat the above simulations with various $A$ values. The results are shown in Figure 17-18. We notice that with the increase of $A$, the interval of possible $\varrho$ for exhibiting relaxation oscillations moves rightwards (i.e., a trend of becoming larger), and the length of interval becomes larger, too. The variation of the period $T_0$ becomes smaller.

4.3.3. *Fixed $Y_{\text{max}}$ and varied $\varrho$*. In this subsection we fix $Y_{\text{max}} = 20$ and repeat the above simulations with various $\varrho$ values. We plot the period $T_0$ as a function of $A$. The results are shown in Figure 19. We notice that with the increasing of $\varrho$, the interval of possible $A$ for exhibiting relaxation oscillations also moves rightwards (i.e., a trend of becoming larger), and the length of interval becomes larger, too. The period $T_0$ also seems to stay on the same level.

5. **Conclusions.** In this paper a type of spruce-budworm model is studied. The Holling’s type II functional response is included in this model in order to describe the interaction between budworm and spruce. This type of functional response imposes a limit on the predation rate of budworms on leaf areas. This is a reasonable
Figure 16. In this figure we plot the asymptotic period $T_0$ of relaxation oscillations as a function of $\varrho$ when $A = 0$ and $Y_{\text{max}} = 20, 30, 40, 100$, corresponding to the colored part on the $\varrho$-axis in Figure 15.

Figure 17. In this figure we plot parameter $\varrho$ versus parameter $A$ for $Y_{\text{max}} = 20$. The representations of upper lines and lower lines are the same as in Figure 14-(a). The colored vertical straight line segments indicate the possible $\varrho$ values for exhibiting relaxation oscillations for different $A$ value.
Figure 18. In this figure we plot the asymptotic period $T_0$ of relaxation oscillations as a function of $\varrho$ when $A = 0, 1, 5, 10$ and $Y_{\text{max}} = 20$, corresponding to the colored vertical straight line segments in Figure 17.

Figure 19. In this figure we plot the asymptotic period $T_0$ of relaxation oscillations as a function of $A$ when $\varrho = 2, 4, 6, 10, 20$ and $Y_{\text{max}} = 20$. 
assumption because intuitively we know that the budworms cannot always eat. The properties of existence, number and stability of equilibria are investigated by using standard method of qualitative analysis for planar systems. The main difference with [4] lies in the nullcline for the prey equation, which is a straight line in [4], but a curve which is concave upward in our paper. However, since the monotonicity is the same (which is crucial in the qualitative analysis here), the conclusion is also similar.

Next, we demonstrate that relaxation oscillations are possible when there exists a unique unstable equilibrium. The perturbation theory is used to find the asymptotic outer and inner approximations of solutions, and then relaxation oscillations can be constructed by gluing the outer and inner approximations together. We also give an asymptotic expression for the period of relaxation oscillations.

Finally, in order to explore numerically the relation between the period of relaxation oscillations and the parameters, we conduct various numerical simulations and display some examples of the parameter range of having relaxation oscillations. From the numerical simulations we see that the parameter $Y_{\text{max}}$ (representing the carrying capacity of spruce leaf area in the environment) makes a more remarkable influence on the period of relaxation oscillations. Generally, the more spruce the environment can carry, the shorter the outbreak period will be. Moreover, the parameter $A$ (appearing in the Holling’s type II functional response) also influences the period $T_0$ noticeably. With the increase of $A$, the variation of $T_0$ becomes smaller.

Acknowledgments. The authors are grateful to the anonymous referees for their useful suggestions and comments which improve the exposition of the paper. The authors would like to thank Prof. Je-Chiang Tsai for the instructions and suggestions. ZZ is supported by MOST (MOST 107-2811-M-007-1036 and 108-2811-M-007-536), and National Nature Science Foundation of China (grant number 11811530272 and 11471044).

REFERENCES

[1] D. Ludwig, D. D. Jones and C. S. Holling, Qualitative analysis of insect outbreak systems: The spruce budworm and forest, *J. Anim. Ecol.*, **47**(1) (1978), 315–332.
[2] E. F. Mishchenko and N. Kh. Rozov, *Differential Equations with Small Parameters and Relaxation Oscillations*, Mathematical Concepts and Methods in Science and Engineering, 13. Plenum Press, New York, 1980.
[3] J. Murray, *Mathematical Biology*, 2nd edition, Springer Verlag, Berlin Heidelberg, 1993.
[4] A. Rasmussen, J. Wyller and J. O. Vik, Relaxation oscillations in spruce-budworm interactions, *Nonlinear Anal. Real World Appl.*, **12** (2011), 304–319.
[5] T. Royama, Population dynamics of the spruce budworm *Choristoneura Fumiferana*, *Ecol. Monogr.*, **54** (1984), 429–462.
[6] T. Royama, *Analytical Population Dynamics*, Springer, Dordrecht, 1992.
[7] T. Royama, W. E. MacKinnon, E. G. Kettela, N. E. Carter and L. K. Hartling, Analysis of spruce budworm outbreak cycles in New Brunswick, Canada, since 1952, *Ecology*, **86** (2005), 1212–1224.
[8] N. Kh. Rozov, Asymptotic calculation of nearly discontinuous solutions of a second-order system of differential equations, (Russian) *Dokl. Akad. Nauk SSSR*, **145** (1962), 38–40.
[9] N. Wang and M. Han, Slow-fast dynamics of Hopfield spruce-budworm model with memory effects, *Adv. Differ. Equ.*, **2016** (2016), Paper No. 73, 12 pp.
[10] M. I. Zharov, E. F. Mishchenko and N. Kh. Rozov, Some special functions and constants that arise in the theory of relaxation oscillations (Russian), *Dokl. Akad. Nauk SSSR*, **261** (1981), 1292–1296.

Received July 2020; revised December 2020.

*E-mail address:* ben10640@yahoo.com.tw  
*E-mail address:* zhangzhengyang@ouc.edu.cn