Pest control using virus as control agent: A mathematical model

Sweta Pathak[a1], **Alakes Maiti**[b]

[a]Belur Girls' High School
Belurmath, Howrah-711202, India
sweta_bally@rediffmail.com

[b]Department of Mathematics, Presidency University
Kolkata-700073, India
alakesh_maity@hotmail.com

Received: 29 August 2010 / **Revised:** 11 November, 2011 / **Published online:** 24 February 2012

Abstract. It is now well recognised that biocontrol of pests is one of the best ecofriendly alternative for pest control. In this paper we have studied dynamical behaviours of a model for biocontrol of pests, where it is assumed that the pest is affected by a virus. Boundedness and stability of the model are studied. The effect of time-delay is investigated. Numerical simulations are carried out to illustrate our analytical findings. It is observed that the time-delay has a regulatory impact on the system. Biological implications of our results are discussed.

Keywords: pest, pesticide, biopesticide, virus, stability, time-delay.

1 Introduction

"The amount of food for each species of course gives the extreme limit to which each can increase but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species."– Darwin [1].

We are sharing the planet earth with some 10 million species of organisms. All species are interconnected to some extent, with some organisms more dependent on others, especially those higher in the food chain. Human have quite a dominant position in many ecosystems and they also compete with many organisms and we generally think of many of these competitors as "pests". A pest can be formally defined as any organism that reduces the availability, quality, or value of some human resource [2]. The resources in question can be a plant or animal grown for food, fiber or pleasure (e.g., pets, plants in recreation areas). Another resource is human health, and well-being, making organisms directly affecting human health, such as mosquitoes, pests too. Plant pests such as diseases, insects, and weeds invade our agricultural crops, forests, and home gardens causing

[1]Corresponding author.

significant losses in plant yield and quality. To combat these pests, a strong reliance on chemical pesticides has developed over the years as the main solution to these problems.

In fact, through the ages pest control practices have changed dramatically. The earliest known record for the use of naturally occuring compounds for pest control was in about 1000 BC, when the Greek Homer mentioned using sulfur as a fumigant. In the 1800s, tobacco extracts and nicotine smoke were applied for insect control. Bordeaux mix, a combination of copper sulphate and hydrated lime, was developed in 1882 in Bordeaux, France, for control of plant pathogenic fungi on grapes and other fruits. Between World Wars I and II, several developments took place, setting the stage for major changes in pest control. In 1939, both DDT for control of insects and 2,4-D for control of weeds came on the scene. These extremely effective compounds revolutionized pest control [3]. Since that time, a cascade of different compounds, belonging to an increasing number of chemical classes, have been synthesized for pest control. However, pesticides are not always the correct answer; sometimes they cannot control pests effectively. Besides that target pest resurgence, secondary pest outbreaks, development of resistance in pest populations, and poisonous effects on human health have directed the scientists searching for other useful pest control methods. Biological control is a strategy where living organisms are only used to control pests. Microbial pest control is a special kind of biological control in which microbial control agents (such as bacteria, algae, fungi, protozoa, viruses, mycoplasmae or rickettsiae, and related organisms) are used to control specific insects under certain conditions. Use of microbial control agents for pest control has focused on their application as biopesticides. Actually, the term biopesticide is used for microbial biological pest control agents that are applied in a similar manner to chemical pesticides. Biopesticides for use against crop diseases have already established themselves on a variety of crops. In this paper, we have focused on such a biological control method where virus is taken as a pest control agent.

Viruses have been used for long- as well as short-term insect pest control. Those with the greatest microbial control potential are in the Baculoviridae (nucleopolyhedroviruses [NPV] and granuloviruses [GV]) [4, 5]. CpGV (Cydia pomonella granulosis virus) is a virus of invertebrates – specifically *Cydia pomonella* or the *Codling moth*. CpGV is highly pathogenic, it is frequently used as a biological pesticide. More than 400 insect species, mostly in the Lepidoptera and Hymenoptera, have been reported as hosts for baculoviruses. Granados and Federici [6], Tanada and Hess [7], Tanada and Kaya [8], Vail [9], Cunningham [10], Hunter-Fujita et al. [4], and Vail et al. [11] summarize the literature on the nature of baculoviruses, their mode of action, epizootiology, and use for control of pest insects in forestry and agroecosystems. Compared with parasitoids and predators, pathogens have not been used frequently for classical biological control. The European spruce sawfly was permanently controlled through introduction of an nuclear polyhedrosis viruses (NPVs). The principal development of baculoviruses has been for use in inundative releases. While viruses can be applied with the same spray equipment as chemical pesticides, they do not kill immediately, as do chemical pesticides. For example, to control Velvetbean caterpillars (a major pest of soybean in Brazil), farmers are encouraged to spray NPVs when the Velvetbean caterpillar population is not greater than 40 larvae of under less than 1.5 cm in length per ground cloth sample [3].

Viruses are non-cellular genetic elements, containing either DNA or RNA, whose energy is derived from the host. Because viruses can only replicate themselves within a living cell, all viruses are obligate intracellular parasites. After they replicate their DNA or RNA genomes in host cells, viruses are then packaged into particles called virions that form the extracellular state that is infectious and is needed to reach new hosts. In nature, the infection by Baculovirus begins when an insect consumes virus particles on a plant perhaps from a sprayed treatment. Virus infection causes the cell lysis in host body and produces more virus particles (virus replication), until the cell, and ultimately the insect, dies out. The fluid inside a dead insect is composed largely of virus polyhedra or Polyhedral inclusion bodies (PIB) on an average $6.5 \pm 2.7 \times 109$ PIB per insect [12, 13], though in vivo the production of the viruses is more than the above value. Within the baculoviruses, the nuclear polyhedroses viruses (NPVs) have many-sided occlusion bodies ($c.0.5$–15 μm) that can contain many virions [3]. It should be mentioned that the production of PIB varies from virus to virus. There are many literatures in support of virus replication and infection mechanism [12,14,15]. A large number of viruses offer potential as microbial control agents of insects [16]. The virus *Oryctes virus* is used for control of Rhinoceros Beetle in the Pacific Islands [17]. One classic example of the successful use of baculoviruses as biopesticides is found in Brazil [18]. The Brazilian success should encourage other nations to implement biopesticides in their own programs, taking into consideration their regional crops, cropping systems and culture.

A chief task of theoretical ecologists is to focus on suitable non-linear models that can help us to understand the diverse array of observed scenarios in the field. In this paper we have introduced a mathematical model consisting of a plant, the pest and a virus. But there are only a few papers on mathematical models of the dynamics of microbial disease in pest control [19–25]. The literature abounds with many such evidences (see [3, 26–30], and references therein).

The main aim of this paper is to study the mutual relations occurring in an ecosystem where virus affects a pest population feeding on a plant, the latter being unaffected by the virus. We formulate a time-delayed model for this purpose. A blend of detailed analysis of the model is presented. The rest of the paper is structured as follows. In the next section, we introduce the basic mathematical model. In Section 3, positivity and boundedness of solutions of our model are established. The dynamical behaviours of the model in absence and presence of time-delay are presented in Section 4 and 5, respectively. In Section 6, computer simulations are carried out to illustrate our analytical findings. Section 7 contains the general discussion of the paper and biological significance of our analytical findings.

2 The basic mathematical model with time-delay and boundedness

The model we analyze in this paper has four populations:

(i) The plant, whose population density is denoted by X.

(ii) The uninfected pest, whose population density is denoted by Y.

(iii) The infected pest, whose population density is denoted by Z.

(iv) The virus, which attacks the pest population is denoted by V.

In construction of the model the following assumptions are made:

(A1) In the absence of the pest the plant population density grows according to a logistic curve with carrying capacity K ($K > 0$) and with an intrinsic growth rate constant r ($r > 0$).

(A2) The plant-pest interaction is studied with the Michaelis–Menten type (or Holling type II) functional response [31–34].

(A3) The virus attacks the pest population only and the infected population does not recover or become immune. The virus transmission is governed by the so-called mass-action incidence. The lysis death rate (i.e., mortality rate of infected pest) is the constant d_2.

(A4) It is now well established that in an improved analysis, the effect of time-delay is to be taken into account. Time-delays occur so often, in almost every situation, that to ignore them is to ignore reality. Detailed arguments on importance and usefulness of time-delays in realistic models may be found in the classical books of Macdonald [35], Gopalsamy [36] and Kuang [37]. It is now beyond doubt that delay in the infection process influences the other part of the underlined ecosystem. When the uninfected pest are converted to infected pest, we assume that they remain in this stage of development for σ units of time, decaying exponentially at the rate d_2. In other words, the individuals that are newly infected at time $T - \sigma$, the probability of surviving from time $T - \sigma$ to time T is $e^{-d_2\sigma}$. (More generally, the survival probability is given by some non-increasing function $f(\sigma)$ with $0 \leq f(\sigma) \leq 1$.)

On the above considerations we introduce a model under the framework of the following set of nonlinear ordinary differential equations:

$$\begin{aligned}
\frac{\mathrm{d}X}{\mathrm{d}T} &= rX\left(1 - \frac{X}{K}\right) - \frac{b_1XY}{a_1 + X} - \frac{b_2XZ}{a_2 + X}, \quad X(0) > 0,\\
\frac{\mathrm{d}Y}{\mathrm{d}T} &= \frac{c_1XY}{a_1 + X} - d_1Y - p_1YV, \quad Y(0) > 0,\\
\frac{\mathrm{d}Z}{\mathrm{d}T} &= \frac{c_2XZ}{a_2 + X} - d_2Z + p_1YV - p_1e^{-d_2\sigma}Y(T - \sigma)V(T - \sigma), \quad Z(0) > 0,\\
\frac{\mathrm{d}V}{\mathrm{d}T} &= \beta_1 - \gamma_1V - p_1YV + \alpha p_1e^{-d_2\sigma}Y(T - \sigma)V(T - \sigma), \quad V(0) > 0.
\end{aligned} \tag{1}$$

Here b_1 is the predation rate of uninfected pest, b_2 is the predation rate for the infected pest, a_1 and a_2 are the half saturation constants, c_1 and c_2 are the conversion factors. d_1 is the virus-independent predator background mortality rate, and p_1, is the infection rate, α (≥ 1) is the virus replication factor. β_1 is the amount of virus sprayed in the field. γ_1 is the mortality rate of the virus species (due to temperature changes, enzymatic attack, UV radiation etc.). It is obvious to assume that all the parameters are positive.

Now we study the boundedness of positive solutions of the above system (1). To this end we use the following scaling to the system.

$$x = \frac{X}{K}, \quad y = \frac{Y}{K}, \quad z = \frac{Z}{K} \quad v = \frac{V}{K} \quad \text{and} \quad t = rT.$$

Then the system (1) reduces to

$$\begin{aligned}
\frac{\mathrm{d}x}{\mathrm{d}t} &= x(1-x) - \frac{axy}{b+x} - \frac{hxz}{n+x}, \quad x(0) > 0, \\
\frac{\mathrm{d}y}{\mathrm{d}t} &= \frac{gxy}{b+x} - sy - dyv, \quad y(0) > 0, \\
\frac{\mathrm{d}z}{\mathrm{d}t} &= \frac{cxz}{n+x} - mz + dyv - e^{-m\tau}dy(t-\tau)v(t-\tau), \quad z(0) > 0, \\
\frac{\mathrm{d}v}{\mathrm{d}t} &= \beta - \gamma v - dyv + \alpha e^{-m\tau}dy(t-\tau)v(t-\tau), \quad v(0) > 0,
\end{aligned} \tag{2}$$

and

$$\begin{aligned}
&a = \frac{b_1}{r}, \quad b = \frac{a_1}{K}, \quad g = \frac{c_1}{r}, \quad s = \frac{d_1}{r}, \\
&h = \frac{b_2}{r}, \quad n = \frac{a_2}{K}, \quad m = \frac{d_2}{r}, \quad d = \frac{p_1 K}{r}, \quad c = \frac{c_2}{r}, \\
&\beta = \frac{\beta_1}{rK}, \quad \gamma = \frac{\gamma_1}{r} \quad \text{and} \quad \tau = r\sigma.
\end{aligned}$$

We make an obvious assumption that all the parameters are positive and $\tau \in \mathbb{R}_+$. The initial conditions are given by

$$x(\theta) = \phi_1(\theta), \quad y(\theta) = \phi_2(\theta), \quad z(\theta) = \phi_3(\theta), \quad v(\theta) = \phi_4(\theta), \tag{3}$$

where $\theta \in [-\tau; 0]$ with $\phi_i(\theta) > 0$ for $i = 1, 2, 3, 4$.

3 Positivity and boundedness of the solutions

In this section, we present results on positivity and boundedness of solutions of the system (2) with initial conditions (3). These are very important so far as the validity of the model is concerned.

Theorem 1. *Each component of the solution of* (2) *with initial conditions* (3)*, remains positive for all* $t > 0$*.*

The proof is deferred to the appendix.

We can further prove the results regarding boundedness of $x(t)$, $y(t)$, $z(t)$, $v(t)$.

Lemma 1. *Define the function* $W(t) = \frac{g}{a}x(t) + y(t)$, $t \in [0, +\infty)$*. Then for all* $t > 0$*,* $0 \le W \le \frac{2g}{a\delta}$ *where* $\delta = \min\{1, s\}$*.*

Proof is deferred to the appendix.

Lemma 2. *Define the function $W_1(t) = \alpha z(t) + v(t)$, $t \in [0, +\infty)$. Since, $y(t)$ is bounded, so there exists $M > 0$ and a time $t_1 > 0$ such that $y(t) > M$ for all $t > t_1$. Assume further that $\alpha < \alpha^* = 1 + \frac{\gamma}{dM}$ and L is any positive constant such that $L > \frac{\beta}{\mu_m - (\alpha-1)dM}$ where $\mu_m = \min\{(m - \frac{c}{n}) + (\alpha - 1)dM, \gamma\}$. Then there is a $t_2 = t_2(L) > t_1$ such that for all $t > t_2(L) > t_1 > 0$, $W_1(t) < L$.*

Proof is deferred to the appendix.

Theorem 2. *All the solutions of the system* (2) *that start in $\mathbb{R}^4_+$ are uniformly bounded.*

The proof is directly follows from Lemma 1 and Lemma 2.

4 Dynamics of system (2) when $\tau = 0$

4.1 Boundary equilibria and stability

The objective of this section is to study the stability of the boundary equilibrium points of the system (2). In the following lemma the equilibrium points and the conditions for their existence are mentioned.

The system (2) always have the equilibrium point $E_0(0, 0, 0, \frac{\beta}{\gamma})$, the pest-free equilibrium point $E_1(1, 0, 0, \frac{\beta}{\gamma})$, the equilibrium points $E_2(x_2, 0, z_2, \frac{\beta}{\gamma})$, $E_3(x_3, y_3, 0, v_3)$. E_2 exists if and only if $c - m - mn > 0$. When this condition is satisfied, x_2, z_2 are given by

$$x_2 = \frac{mn}{c - m}, \quad z_2 = \frac{cn(c - m - mn)}{h(c - m)^2}.$$

In terms of the original parameters of the system, the condition $c - m - mn > 0$ is equivalent to $d_2 < \frac{c_2 K}{a_2 + K}$. This indicates that if the death rate of the infected pest is low, then E_2 exists.

Now v_3 exists if the following equation in v has a positive real root:

$$\begin{aligned} a\gamma d^2 v^3 + \big[-a\beta d^2 - 2a\gamma d(g - s) + d^2 bg(\alpha - 1)(b + 1)\big]v^2 \\ + \big[a\gamma(g - s)^2 - dbg(\alpha - 1)(g - s - bs) + 2d(g - s)a\beta\big]v - a\beta(g - s)^2 = 0, \end{aligned}$$

and of course, v_3 is a positive real root of this equation.

The above equation can also be rewritten as

$$v^3 + g_1 v^2 + g_2 v + g_3 = 0, \tag{4}$$

where

$$\begin{aligned} g_1 &= \frac{-a\beta d^2 - 2a\gamma d(g - s) + d^2 bg(\alpha - 1)(b + 1)}{a\gamma d^2}, \\ g_2 &= \frac{a\gamma(g - s)^2 - dbg(\alpha - 1)(g - s - bs) + 2d(g - s)a\beta}{a\gamma d^2}, \\ g_3 &= -\frac{a\beta(g - s)^2}{a\gamma d^2}. \end{aligned}$$

Depending on the determinant of the above equation $U = (\frac{t_3}{2})^2 + (\frac{r_1}{3})^3$, where $r_1 = g_2 - \frac{1}{3}g_1^2$, $t_1 = \frac{2}{27}g_1^3 - \frac{1}{3}g_1g_2 + g_3$, there are three cases for solutions of (4).

(i) If $U > 0$, (4) has a real root and a pair of conjugate complex roots. The real root is positive and is given by $\delta_1 = \sqrt[3]{-\frac{t_3}{2} + \sqrt{U}} + \sqrt[3]{-\frac{t_3}{2} - \sqrt{U}} - \frac{1}{3}g_1$.

(ii) If $U = 0$, (4) has three real roots, of which two are equal. In particular, if $g_1 > 0$, there exists only one positive root, $\delta_1 = 2\sqrt[3]{-\frac{t_3}{2}} - \frac{1}{3}g_1$; If $g_1 < 0$, there exists a positive root $\delta_1 = 2\sqrt[3]{-\frac{t_3}{2}} - \frac{1}{3}g_1$ for $\sqrt[3]{-\frac{t_3}{2}} > -\frac{1}{3}g_1$, and there exist three positive roots for $\frac{g_1}{6} < \sqrt[3]{-\frac{t_3}{2}} < -\frac{1}{3}$, $\delta_1 = 2\sqrt[3]{-\frac{t_3}{2}} - \frac{1}{3}g_1$, $\delta_2 = \delta_3 = \sqrt[3]{-\frac{t_3}{2}} - \frac{1}{3}g_1$.

(iii) If $U < 0$, there are three distinct real roots, $\delta_1 = 2\sqrt{\frac{|r_1|}{3}}\cos\frac{\alpha_1}{3} - \frac{g_1}{3}$, $\delta_2 = 2\sqrt{\frac{|r_1|}{3}}\cos(\frac{\alpha_1}{3} + \frac{2\pi}{3}) - \frac{g_1}{3}$, $\delta_3 = 2\sqrt{\frac{|r_1|}{3}}\cos(\frac{\alpha_1}{3} + \frac{2\pi}{3}) - \frac{g_1}{3}$, where $\cos\phi_1 = \frac{t_3}{2\sqrt{(\frac{|r_1|}{3})^3}}$. Furthermore, if $g_1 > 0$, there exists only one positive root. Otherwise, if $g_1 < 0$, there may exist either one or three positive real roots. If there is only one positive real root, it is equal to $\max(\delta_1, \delta_2, \delta_3)$. Clearly the number of positive real roots of (4) depends on the sign of g_1.

If $g - s - bs - dv_3 - bdv_3 > 0$, then x_3, y_3 exist, and are given by

$$x_3 = \frac{b(s + dv_3)}{g - s - dv_3}, \quad y_3 = \frac{bg(g - s - bs - dv_3 - bdv_3)}{a(g - s - dv_3)^2}.$$

The variation matrix $V(E_0)$ at the equilibrium point $E_0(0, 0, 0, \frac{\beta}{\gamma})$ is given by

$$V(E_0) = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & -s - \frac{d\beta}{\gamma} & 0 & 0 \\ 0 & 0 & -m & 0 \\ 0 & -\frac{d(1-\alpha)\beta}{\gamma} & 0 & -\gamma \end{bmatrix}.$$

Clearly $V(E_0)$ has three negative and one positive eigenvalues. This indicates that E_0 is always unstable.

The variation matrix $V(E_1)$ at the equilibrium point $E_1(1, 0, 0, \frac{\beta}{\gamma})$ is given by

$$V(E_1) = \begin{bmatrix} -1 & -\frac{a}{b+1} & -\frac{h}{n+1} & 0 \\ 0 & \frac{g}{b+1} - s - \frac{d\beta}{\gamma} & 0 & 0 \\ 0 & 0 & \frac{c}{n+1} - m & 0 \\ 0 & \frac{d(1-\alpha)\beta}{\gamma} & 0 & -\gamma \end{bmatrix}.$$

Clearly $V(E_1)$ has two negative eigenvalues. Therefore, E_1 is stable if and only if $\frac{g}{b+1} - s - d\frac{\beta}{\gamma} < 0$ (i.e., $d_1 > (\frac{c_1K}{a_1+K} - \frac{\beta_1}{\gamma_1 K})$) and $c - m - mn < 0$ (i.e., $d_2 > \frac{c_2K}{a_2+K}$).

These two conditions indicate that if the death rates are high, then the system may stabilize to a pest-free steady state. Further, we notice that existence of E_2 destabilizes E_1.

The variation matrix $V(E_2)$ at the equilibrium point $E_2(x_2, 0, z_2, \frac{\beta}{\gamma})$ is given by

$$V(E_2) = \begin{bmatrix} p_{11} & p_{12} & p_{13} & 0 \\ 0 & p_{22} & 0 & 0 \\ p_{31} & 0 & 0 & 0 \\ 0 & p_{42} & 0 & -\gamma \end{bmatrix},$$

where

$$p_{11} = 1 - 2x_2 - \frac{hnz_2}{(n+sx_2)^2}, \quad p_{12} = -\frac{ax_2}{b+x_2}, \quad p_{13} = -\frac{hx_2}{n+x_2},$$
$$p_{22} = \frac{gx_2}{b+x_2} - s - dv_2, \quad p_{31} = \frac{cnz_2}{(n+x_2)^2}, \quad p_{42} = -d(1-\alpha)v_2.$$

The characteristic equation of $V(E_2)$ is

$$\left\{\lambda^2 + \lambda(-p_{11}) + (-p_{13}p_{31})\right\}(\lambda - p_{22})(\lambda + \gamma) = 0$$

or

$$\left\{\lambda^2 + S_1\lambda + S_2\right\}(\lambda - p_{22}) = 0,$$

and the corresponding eigenvalues are

$$\lambda_{1,2} = \frac{-S_1 \pm \sqrt{S_1^2 - 4S_2}}{2}, \quad \lambda_3 = p_{22} = \frac{gmn}{b(c-m)+mn} - s - \frac{d\beta}{\gamma}, \quad \text{and} \quad \lambda_4 = -\gamma,$$

where

$$S_1 = \frac{m(c-m-mn) - cmn}{c(c-m)}, \quad S_2 = \frac{m(c-m-mn)}{c} > 0.$$

This implies that E_2 is locally asymptotically stable if $(c - m - mn) - cn < 0$ and $\frac{gmn}{b(c-m)+mn} - s - \frac{d\beta}{\gamma} < 0$. In terms of the original parameters of the system we have $d_2 + \frac{d_2 a_2[\gamma_1(c_1-d_1)-p_1\beta_1]}{a_1(p_1\beta_1+\gamma_1 d_1)} < c_2 < \frac{d_2(K+a_2)}{K-a_2}$ which means that when the conversion rate (c_2) of the pest governs a moderate value, and the virus infection rate (p_1) are high, then it is expected that the system will stabilize at the steady state where all the pest become infected.

The variation matrix $V(E_3)$ at the equilibrium point $E_3(x_3, y_3, 0, v_3)$ is given by

$$V(E_3) = \begin{bmatrix} q_{11} & q_{12} & q_{13} & 0 \\ q_{21} & 0 & 0 & q_{24} \\ 0 & 0 & q_{33} & 0 \\ 0 & q_{42} & 0 & q_{44} \end{bmatrix},$$

where

$$q_{11} = 1 - 2x_3 - \frac{aby_3}{(b+x_3)^2}, \quad q_{12} = -\frac{ax_3}{b+x_3}, \quad q_{13} = -\frac{hx_3}{n+x_3},$$
$$q_{21} = \frac{gby_3}{(b+x_3)^2}, \quad q_{24} = -dy_3,$$
$$q_{33} = \frac{cx_3}{(n+x_3)} - m, \quad q_{42} = d(\alpha-1)v_3, \quad q_{44} = -\gamma + d(\alpha-1)y_3.$$

and all other $q_{ij} = 0$.

The characteristic equation of $V(E_3)$ is $\lambda^4 + \lambda^3 A_1 + \lambda^2 A_2 + \lambda A_3 + A_4 = 0$, where

$$A_1 = -q_{11} - q_{33} - q_{44},$$
$$A_2 = q_{33}q_{44} + q_{11}q_{44} + q_{11}q_{33} - q_{24}q_{42} - q_{21}q_{12},$$
$$A_3 = -q_{11}q_{33}q_{44} + q_{11}q_{24}q_{42} + q_{12}q_{21}q_{44} + q_{12}q_{21}q_{33} + q_{24}q_{42}q_{33},$$
$$A_4 = -q_{11}q_{24}q_{42}q_{33} - q_{12}q_{21}q_{33}q_{44}.$$

If $A_1 > 0$, $A_4 > 0$, $A_1A_2 - A_3 > 0$ and $A_3(A_1A_2 - A_3) - A_1^2A_4 > 0$, then from Routh–Hurwitz criterion it follows that E_3 is locally asymptotically stable.

4.2 Interior equilibrium and stability when $\tau = 0$

The interior equilibrium point $E_4(x_4, y_4, z_4, v_4)$ of the system (2) exists if $g - s - dv - s - dv > 0$, $\gamma v - \beta > 0$, $c > m$, $mng - s(bc - bm + mn) > 0$, and $(\alpha-1)bgdv(g - s - dv - bs - bdv) - a(\gamma v - \beta)(g - s - dv)^2 > 0$ and are given by

$$x_4 = \frac{mn}{c-m}, \quad y_4 = \frac{\gamma v - \beta}{dv(\alpha-1)}, \quad v_4 = \frac{mng - s(bc - bm + mn)}{d(bc - bm + mn)},$$
$$z_4 = \frac{n(g - s - dv) + b(s + dv)}{h(g - s - dv)^2(\alpha-1)bgdv}$$
$$\times \big\{(\alpha-1)bgdv(g - s - dv - bs - bdv) - a(\gamma v - \beta)(g - s - dv)^2\big\}.$$

The variation matrix $V(E_4)$ at the equilibrium point $E_4(x_4, y_4, z_4, v_4)$ is given by

$$V(E_4) = \begin{bmatrix} s_{11} & s_{12} & s_{13} & 0 \\ s_{21} & 0 & 0 & s_{24} \\ s_{31} & 0 & 0 & 0 \\ 0 & s_{42} & 0 & s_{44} \end{bmatrix},$$

where

$$s_{11} = 1 - 2x_4 - \frac{aby_4}{(b+x_4)^2} - \frac{hnz_4}{(n+x_4)^2}, \quad s_{12} = -\frac{ax_4}{b+x_4}, \quad s_{13} = -\frac{hx_4}{n+x_4},$$
$$s_{21} = \frac{gby_4}{(b+x_4)^2}, \quad s_{24} = -dy_4,$$
$$s_{31} = \frac{cnz_4}{(n+x_4)^2}, \quad s_{42} = d(\alpha-1)v_4, \quad s_{44} = -\gamma + d(\alpha-1)y_4.$$

and all other $s_{ij} = 0$.

The characteristic equation of $V(E_4)$ is

$$\eta^4 + \eta^3 L_1 + \eta^2 L_2 + \eta L_3 + L_4 = 0,$$

where

$$\begin{aligned}
L_1 &= -s_{11} - s_{44},\\
L_2 &= -s_{13}s_{31} + s_{11}s_{44} - s_{24}s_{42} - s_{21}s_{12},\\
L_3 &= s_{11}s_{24}s_{42} + s_{44}s_{13}s_{31} + s_{12}s_{21}s_{44},\\
L_4 &= s_{13}s_{31}s_{24}s_{42}.
\end{aligned}$$

If $L_1 > 0$, $L_4 > 0$, $L_1L_2 - L_3 > 0$ and $L_3(L_1L_2 - L_3) - L_1^2L_4 > 0$, then from Routh–Hurwitz criterion it follows that E_4 is locally asymptotically stable.

5 The interior equilibrium point with $\tau \neq 0$

The main purpose of this section is to study the stability behavior of $E_\tau^*(x_\tau^*, y_\tau^*, z_\tau^*, v_\tau^*)$ in the presence of delay ($\tau \neq 0$). v_τ^* of the interior equilibrium point $E_\tau^*(x_\tau^*, y_\tau^*, z_\tau^*, v_\tau^*)$ of the system (2) exists if $R_5v_\tau^5 + R_4v_\tau^4 + R_3v_\tau^3 + R_2v_\tau^2 + R_1v_\tau + R_0 = 0$ has a unique positive real root where

$$\begin{aligned}
&G = g - s, \quad H = mn(g - s) + bs(m - c), \quad I_1 = bd - nd,\\
&J = ng - ns + bs, \quad T = bd(m - c) - mnd, \quad L = d\big(1 - e^{-m\tau}\big),\\
&Q = d\big(1 - \alpha e^{-m\tau}\big), \quad Q_1 = \frac{hL}{bcQ}, \quad Q_2 = \frac{a}{bgQ},\\
&B_1 = (Q_2d - Q_1)d^2\gamma,\\
&B_2 = Q_2d^2(\gamma s - \beta d - 2\gamma G) - d^2(b + 1) + Q_1d(\beta d + 2\gamma G),\\
&B_3 = dQ_2G(\gamma G - 2s\gamma + 2d\beta) - ds(\beta dQ_2 + 2b + 1) + Gd - Q_1G(\gamma Q_1G + 2d\beta),\\
&B_4 = Q_2G(s\gamma G - \beta dG + 2\beta sd) + \beta Q_1G^2 + s(G - bs),\\
&R_0 = -H\beta sQ_2G^2,\\
&R_1 = HB_4 - T\beta sQ_2G^2 - m\beta JQ_1G^2,\\
&R_2 = HB_3 + TB_4 - m\gamma Q_1G^2(\beta I_1 - \gamma J) + 2md\beta Q_1GJ,\\
&R_3 = HB_2 + TB_3 + mQ_1\big(\gamma I_1G^2 - \beta Jd^2\big) + 2dmQ_1G(\beta I_1 - \gamma J),\\
&R_4 = HB_1 + TB_2 - 2dm\gamma Q_1GI_1 - d^2mQ_1(\beta I_1 - \gamma J),\\
&R_5 = TB_1 + m\gamma d^2Q_1I_1.
\end{aligned}$$

If $\gamma v_\tau^* - \beta > 0$, $\alpha e^{-m\tau} - 1 > 0$, $g - s - dv_\tau^* > 0$ and $(\alpha e^{-m\tau} - 1)bgdv_\tau^*(g - s - dv_\tau^* - bs - bdv_\tau^*) - a(\gamma v_\tau^* - \beta)(g - s - dv_\tau^*)^2 > 0$, then x_τ^*, y_τ^* and z_τ^* exist and are given by

$$x_\tau^* = \frac{b(s + dv_\tau^*)}{g - s - dv_\tau^*}, \quad y_\tau^* = \frac{\gamma v_\tau^* - \beta}{d(\alpha e^{-m\tau} - 1)v_\tau^*},$$

$$z_\tau^* = \frac{n + x_\tau^*}{hbgdv_\tau^*(g - s - dv_\tau^*)(\alpha e^{-m\tau} - 1)} \times \left\{(\alpha e^{-m\tau} - 1)bgdv_\tau^*(g - s - dv_\tau^* - bs - bdv_\tau^*) - a(\gamma v_\tau^* - \beta)(g - s - dv_\tau^*)^2\right\}.$$

Again, if $\gamma v_\tau^* - \beta < 0$, $\alpha e^{-m\tau} - 1 < 0$, $g - s - dv_\tau^* > 0$ and $(\alpha e^{-m\tau} - 1)bgdv_\tau^*(g - s - dv_\tau^* - bs - bdv_\tau^*) - a(\gamma v_\tau^* - \beta)(g - s - dv_\tau^*)^2 < 0$, then x_τ^*, y_τ^* and z_τ^* also exist.

Now we present an interesting theorem, which gives a condition for eradication of pest.

Theorem 3. *If $s > g$ and $m > c$, then $(x(t), y(t), z(t), v(t)) \to E_1(1, 0, 0, \frac{\beta}{\gamma})$ as $t \to +\infty$.*

The proof of the theorem is given in the appendix.

We use the following transformations:

$$x = x_\tau^* + x_1, \quad y = y_\tau^* + y_1, \quad z = z_\tau^* + z_1, \quad v = v_\tau^* + v_1.$$

Then the linear system is given by

$$\frac{\mathrm{d}u}{\mathrm{d}t} = Mu(t) + Nu(t - \tau), \tag{5}$$

where

$$u(t) = [x_1, y_1, z_1, v_1]^{\mathrm{T}}, \quad M = (m_{ij})_{4\times 4}, \quad N = (n_{ij})_{4\times 4},$$

where

$$m_{11} = 1 - 2x_\tau^* - \frac{aby_\tau^*}{(b + x_\tau^*)^2} - \frac{hnz_\tau^*}{(n + x_\tau^*)^2}, \quad m_{12} = -\frac{ax_\tau^*}{b + x_\tau^*}, \quad m_{13} = -\frac{hx_\tau^*}{n + x_\tau^*},$$
$$m_{21} = \frac{gby_\tau^*}{(b + x_\tau^*)^2}, \quad m_{24} = -dy_\tau^*,$$
$$m_{31} = \frac{cnz_\tau^*}{(n + x_\tau^*)^2}, \quad m_{32} = dv_\tau^*, \quad m_{33} = \frac{-dy_\tau^* v_\tau^*}{z_\tau^*}, \quad m_{34} = dy_\tau^*,$$
$$m_{42} = -dv_\tau^*, \quad m_{44} = -\gamma - dy_\tau^*,$$
$$n_{32} = -e^{-m\tau}dv_\tau^*, \quad n_{33} = \frac{e^{-m\tau}dy_\tau^* v_\tau^*}{z_\tau^*}, \quad n_{34} = -e^{-m\tau}dy_\tau^*,$$
$$n_{42} = \alpha e^{-m\tau}dv_\tau^*, \quad n_{44} = \alpha e^{-m\tau}dy_\tau^*,$$

and all other $m_{ij}, n_{ij} = 0$.

The characteristic equation is given by

$$P(\lambda, \tau) + Q^{(1)}(\lambda, \tau)e^{-\lambda\tau} + Q^{(2)}(\lambda, \tau)e^{-2\lambda\tau} = 0, \tag{6}$$

where

$$P(\lambda, \tau) = \lambda^4 + p_3(\tau)\lambda^3 + p_2(\tau)\lambda^2 + p_1(\tau)\lambda + p_0(\tau),$$
$$Q^{(1)}(\lambda, \tau) = q_3^{(1)}(\tau)\lambda^3 + q_2^{(1)}(\tau)\lambda^2 + q_1^{(1)}(\tau)\lambda + q_0^{(1)}(\tau),$$
$$Q^{(2)}(\lambda, \tau) = q_2^{(2)}(\tau)\lambda^2 + q_1^{(2)}(\tau)\lambda + q_0^{(2)}(\tau),$$

and

$$
\begin{aligned}
p_3(\tau) &= -(m_{11}+m_{33}+m_{44}),\\
p_2(\tau) &= m_{11}m_{44}+m_{33}m_{44}+m_{11}m_{33}-m_{12}m_{21}-m_{13}m_{31},\\
p_1(\tau) &= -m_{11}m_{33}m_{44}+m_{12}m_{21}m_{33}+m_{12}m_{21}m_{44}-m_{13}m_{21}m_{32}\\
&\quad +m_{13}m_{31}m_{44},\\
p_0(\tau) &= -m_{12}m_{21}m_{33}m_{44}+m_{13}m_{21}m_{32}m_{44}-m_{13}m_{21}m_{34}m_{42},\\
q_3^{(1)}(\tau) &= -n_{33}-n_{44},\\
q_2^{(1)}(\tau) &= m_{33}n_{44}+n_{33}m_{44}+m_{11}n_{44}+m_{11}n_{33},\\
q_1^{(1)}(\tau) &= -m_{11}m_{33}n_{44}-m_{11}m_{44}n_{33}+m_{12}m_{21}n_{44}+m_{12}m_{21}n_{33}-m_{13}m_{21}n_{32}\\
&\quad +m_{13}m_{31}n_{44},\\
q_0^{(1)}(\tau) &= -m_{12}m_{21}m_{33}n_{44}-m_{12}m_{21}m_{44}n_{33}+m_{13}m_{21}m_{32}n_{44}+m_{13}m_{21}m_{44}n_{32}\\
&\quad -m_{13}m_{21}m_{42}n_{34}-m_{13}m_{21}m_{34}n_{42},\\
q_2^{(2)}(\tau) &= n_{33}n_{44},\\
q_1^{(2)}(\tau) &= -m_{11}n_{33}n_{44},\\
q_0^{(2)}(\tau) &= -m_{12}m_{21}n_{33}n_{44}+m_{13}m_{21}n_{32}n_{44}-m_{13}m_{21}n_{34}n_{42},
\end{aligned}
$$

A necessary condition for a stability change of E_τ^* is that the characteristic equation (6) has purely imaginary solutions. Here we notice that the coefficients in $P(\lambda,\tau)$, $Q^{(1)}(\lambda,\tau)$ and $Q^{(2)}(\lambda,\tau)$ are delay-dependent as the equilibrium components x_τ^* are also delay-dependent. Characteristic equations with delay-independent coefficients are comparatively more simple to deal with. The theory in such cases are well developed [35, 37]. In our case, the main complication arises when we proceed to investigate the existence of purely imaginary roots $\lambda = i\omega$ of (6).

However, we follow with the approach developed by Beretta and Tang [38]. Let $\tau_{\max}$ be the maximum value of τ for which E_τ^* exists. We assume the following:

(i) $p_0(\tau)+q_0^{(1)}(\tau)+q_o^{(2)}(\tau)\neq 0 \quad \forall\tau\geq 0,$

either

(ii) $P_R(i\omega,\tau)+Q_R^{(2)}(i\omega,\tau)=p_4(\tau)\omega^4-p_2(\tau)\omega^2+p_0(\tau)+q_0^{(2)}(\tau)-q_2^{(2)}(\tau)\omega^2\neq 0,$
$P_R(i\omega,\tau)+Q_R^{(1)}(i\omega,\tau)+Q_R^{(2)}(i\omega,\tau)$
$=p_4(\tau)\omega^4-p_2(\tau)\omega^2+p_0(\tau)+q_0^{(1)}(\tau)-q_2^{(1)}(\tau)\omega^2+q_0^{(2)}(\tau)-q_2^{(2)}(\tau)\omega^2$
$\neq 0 \quad \forall\tau\geq 0,$

or

(iii) $P_I(i\omega,\tau)+Q_I^{(2)}(i\omega,\tau)=p_1(\tau)\omega-p_3(\tau)\omega^3+q_1^{(2)}(\tau)\omega\neq 0,$
$P_I(i\omega,\tau)+Q_I^{(1)}(i\omega,\tau)+Q_I^{(2)}(i\omega,\tau)$
$=p_1(\tau)\omega-p_3(\tau)\omega^3+q_1^{(1)}(\tau)\omega-q_3^{(1)}(\tau)\omega^3+q_1^{(2)}(\tau)\omega\neq 0 \quad \forall\tau\geq 0.$

Now, it is easy to see that

$$
\begin{aligned}
&F(\omega,\tau)\\
&\quad=\big[\big|P(i\omega,\tau)\big|^2-\big|Q^{(2)}(i\omega,\tau)\big|^2\big]^2\\
&\qquad-\big[Q_R^{(1)}(i\omega,\tau)\big(Q_R^{(2)}(i\omega,\tau)-P_R(i\omega,\tau)\big)+Q_I^{(1)}(i\omega,\tau)\big(Q_I^{(2)}(i\omega,\tau)-P_I(i\omega,\tau)\big)\big]^2\\
&\qquad-\big[Q_R^{(1)}(i\omega,\tau)\big(P_I(i\omega,\tau)+Q_I^{(2)}(i\omega,\tau)\big)-Q_I^{(1)}(i\omega,\tau)\big(Q_R^{(2)}(i\omega,\tau)+P_R(i\omega,\tau)\big)\big]^2,
\end{aligned}
$$

i.e.,

$$
\begin{aligned}
&F(\omega,\tau)\\
&\quad=\big[\big(p_4(\tau)\omega^4-p_2(\tau)\omega^2+p_0(\tau)\big)^2+\big(p_1(\tau)\omega-p_3(\tau)\omega^3\big)^2\\
&\qquad-\big(q_0^{(2)}(\tau)-q_2^{(2)}(\tau)\omega^2\big)^2-\big(q_1^{(2)}(\tau)\omega\big)^2\big]^2\\
&\qquad-\big[\big(q_0^{(1)}(\tau)-q_2^{(1)}(\tau)\omega^2\big)\big(q_0^{(2)}(\tau)-q_2^{(2)}(\tau)\omega^2-p_4(\tau)\omega^4+p_2(\tau)\omega^2-p_0(\tau)\big)\\
&\qquad\quad+\big(q_1^{(1)}(\tau)\omega-q_3^{(1)}(\tau)\omega^3\big)+\big(q_1^{(2)}(\tau)\omega-p_1(\tau)\omega+p_3(\tau)\omega^3\big)\big]^2\\
&\qquad-\big[\big(q_0^{(1)}(\tau)-q_2^{(1)}(\tau)\omega^2\big)\big(p_1(\tau)\omega-p_3(\tau)\omega^3+q_1^{(2)}(\tau)\omega\big)-\big(q_1^{(1)}(\tau)\omega-q_3^{(1)}(\tau)\omega^3\big)\\
&\qquad\quad\times\big(p_4(\tau)\omega^4-p_2(\tau)\omega^2+p_0(\tau)+q_0^{(2)}(\tau)-q_2^{(2)}(\tau)\omega^2\big)\big]^2 \qquad (7)
\end{aligned}
$$

is a polynomial of degree 16. Therefore, we have

(iv) $F(\omega,\tau)=0$ has a finite number of zeros.

Finally, by implicit function theorem, we have

(v) each positive root $\omega(\tau)$ of $F(\omega,\tau)=0$ is continuous and differentiable at τ whenever it exists.

To obtain the stability criterion of E_τ^*, we set $\lambda=i\omega$. Substituting it in $F(\omega,\tau)=0$ we have the real and imaginary parts as

$$
\cos\omega\tau=\frac{c_3(f_3-b_3)+a_3(e_3-d_3)}{d_3^2+b_3^2-e_3^2-f_3^2},\quad \sin\omega\tau=\frac{a_3(b_3+f_3)-c_3(d_3+e_3)}{d_3^2+b_3^2-e_3^2-f_3^2}, \qquad (8)
$$

where

$$
\begin{aligned}
a_3&=q_0^{(1)}(\tau)-q_2^{(1)}(\tau)\omega^2, & d_3&=p_4(\tau)\omega^4-p_2(\tau)\omega^2+p_0(\tau),\\
b_3&=p_1(\tau)\omega-p_3(\tau)\omega^3, & e_3&=q_0^{(2)}(\tau)-q_2^{(2)}(\tau)\omega^2,\\
c_3&=q_1^{(1)}(\tau)\omega-q_3^{(1)}(\tau)\omega^3, & f_3&=q_1^{(2)}(\tau)\omega.
\end{aligned}
$$

We notice that $d_3^2+b_3^2-e_3^2-f_3^2=|P(i\omega,\tau)|^2-|Q^{(2)}(i\omega,\tau)|^2=R(\omega(\tau),\tau)\neq 0$. (Because $R(\omega(\tau),\tau)=0$ would imply either $P_R(i\omega,\tau)+Q_R^{(2)}(i\omega,\tau)=0$ or $P_I(i\omega,\tau)+Q_I^{(2)}(i\omega,\tau)=0$, a contradiction to (ii) or (iii) respectively.)

Now, $F(\omega,\tau)$ determines ω in terms of τ. For each τ, (7) has at most a finite number of real roots, which ensures that there might have only a finite number of "gates" for the roots to cross the imaginary axis.

Let $I = \{\tau\colon \tau > 0$ and $\omega(\tau)$ is a positive root of (7)$\}$. Then, if $\tau \notin I$, there are no positive solution of (7), and consequently we have the following theorem.

Theorem 4. *If $\tau \notin I$, no stability switches occur.*

Now, for any $\tau \in I$ (where $\omega(\tau)$ is a positive root of (7)), we can define $\theta(\tau) \in [0, 2\pi]$ as the solution of (7):

$$\begin{aligned} \cos\theta(\tau) &= \frac{c_3(f_3-b_3)+a_3(e_3-d_3)}{d_3^2+b_3^2-e_3^2-f_3^2} = \frac{\phi}{R(\omega(\tau),\tau)},\\ \sin\theta(\tau) &= \frac{a_3(b_3+f_3)-c_3(d_3+e_3)}{d_3^2+b_3^2-e_3^2-f_3^2} = \frac{\psi}{R(\omega(\tau),\tau)}. \end{aligned} \tag{9}$$

Substituting $\omega = \omega(\tau)$ in (9), $\theta(\tau) \in [0, 2\pi]$ can be determined as follows:

$$\theta(\tau) = \begin{cases} \arctan\frac{\phi}{\psi} & \text{if } \sin\theta > 0,\ \cos\theta > 0,\\ \frac{\pi}{2} & \text{if } \sin\theta = 1,\ \cos\theta = 0,\\ \pi + \arctan\frac{-\phi}{\psi} & \text{if } \cos\theta < 0,\\ \frac{3\pi}{2} & \text{if } \sin\theta = -1,\ \cos\theta = 0,\\ 2\pi + \arctan\frac{\phi}{\psi} & \text{if } \sin\theta < 0,\ \cos\theta > 0. \end{cases} \tag{10}$$

Here we notice that for $\tau \in I$, $\theta(\tau)$ defined above is continuous at τ. Furthermore if $\theta(\tau) \in (0, 2\pi)$, $\tau \in I$, then $\theta(\tau)$ is also differentiable at τ [21]. Now, the relation between the arguments "$\theta(\tau)$" in (9) and "$\omega(\tau)\tau$" in (7) for $\tau \in I$ must be

$$\omega(\tau)\tau = \theta(\tau) + 2n\pi, \quad n \in \mathbb{N}_0.$$

Hence, we can define the maps $\tau_n : I \to \mathbb{R}_{+0}$ given by

$$\tau_n(\tau) := \frac{\theta(\tau)+2n\pi}{\omega(\tau)}, \quad n \in \mathbb{N}_0, \quad \tau \in I,$$

where $\omega(\tau)$ is a positive simple root of $F(\omega,\tau) = 0$. Let us introduce the functions $I \to \mathbb{R}$

$$S_n(\tau) := \tau - \tau_n(\tau), \quad \tau \in I,\ n \in \mathbb{N}_0, \tag{11}$$

that are continuous and differentiable at τ. We notice that the values of τ ($\in I$) at which stability switches may occur, are the solutions of $S_n(\tau) = 0$ for some $n \in \mathbb{N}_0$ provided the corresponding transversality condition is satisfied. To find out the transversality condition, we differentiate the characteristic equation (6). Then, after some algebraic manipulations, we obtain

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\Big|_{\lambda=\mathrm{i}\omega} = \frac{K_1+\mathrm{i}L_1}{G_1+\mathrm{i}H_1},$$

where

$$\begin{aligned}
g_3 &= p_4'(\tau)\omega^4 - p_2'(\tau)\omega^2 + p_0'(\tau), & n_3 &= p_1(\tau) - 3p_3(\tau)\omega^2,\\
h_3 &= q_0^{(2)'}(\tau) - q_2^{(2)'}(\tau)\omega^2 + 2q_1^{(2)}(\tau)\omega^2, & q_3 &= 4p_4(\tau)\omega^3 - 2p_2(\tau)\omega,\\
l_3 &= p_3'(\tau)\omega^3 - p_1'(\tau)\omega, & u_3 &= 2q_2^{(2)}(\tau)\omega - 2\tau q_1^{(2)}(\tau),\\
m_3 &= q_1^{(2)'}(\tau)\omega + 2q_2^{(2)}(\tau)\omega^3 - 2q_0^{(2)}(\tau)\omega, & v_3 &= q_1^{(1)}(\tau) - 3q_3^{(1)}(\tau)\omega^2,
\end{aligned}$$

and where

$$\begin{aligned}
K_1 &= (c_3f_3 - b_3c_3 + a_3e_3 - a_3d_3)(g_3 + h_3) + (l_3 + m_3)(a_3b_3 + a_3f_3 - d_3c_3 - c_3e_3)\\
&\quad + \big(q_0^{(1)'}(\tau) - q_2^{(1)'}(\tau)\omega^2 - c_3\omega\big)\big(d_3^2 + b_3^2 - e_3^2 - f_3^2\big),\\
L_1 &= (c_3f_3 - b_3c_3 + a_3e_3 - a_3d_3)(m_3 - l_3) + (g_3 - h_3)(a_3b_3 + a_3f_3 - d_3c_3 - c_3e_3)\\
&\quad + \omega\big(q_1^{(1)'}(\tau) - q_3^{(1)'}(\tau)\omega^2 - 2e_3\big)\big(d_3^2 + b_3^2 - e_3^2 - f_3^2\big),\\
G_1 &= (c_3f_3 - b_3c_3 + a_3e_3 - a_3d_3)\big(n_3 + q_1^{(2)}(\tau) - 2\tau e_3\big)\\
&\quad + (q_3 + u_3)(a_3b_3 + a_3f_3 - d_3c_3 - c_3e_3) + (v_3 - \tau a_3)\big(d_3^2 + b_3^2 - e_3^2 - f_3^2\big),\\
H_1 &= (c_3f_3 - b_3c_3 + a_3e_3 - a_3d_3)(u_3 - q_3)\\
&\quad + \big(n - q_1^{(2)}(\tau) + 2\tau e_3\big)(a_3b_3 + a_3f_3 - d_3c_3 - c_3e_3)\\
&\quad + \big(2q_2^{(1)}(\tau) - \tau c_3\big)\big(d_3^2 + b_3^2 - e_3^2 - f_3^2\big).
\end{aligned}$$

("$'$" indicates derivative with respect to τ.)

Therefore,

$$\left\{\Re\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\Big|_{\lambda=\mathrm{i}\omega}\right\} = \frac{GK + HL}{K^2 + L^2}.$$

Let us define

$$\operatorname{sgn}\left\{\Re\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\Big|_{\lambda=\mathrm{i}\omega}\right\} =: \delta(\tau) \quad \text{(say)}.$$

Then we have the following theorem.

Theorem 5. *Let $\omega(\tau)$ be a positive root of* (7) *defined for $\tau \in I$, and at some $\tau^* \in I$, $S_n(\tau^*) = 0$ for some $n \in \mathbb{N}_0$. Then a pair of simple conjugate pure imaginary roots $\lambda_+(\tau^*) = \mathrm{i}\omega(\tau^*)$, $\lambda_-(\tau^*) = -\mathrm{i}\omega(\tau^*)$ of* (6) *exists at $\tau = \tau^*$ which crosses the imaginary axis from left to right if $\delta(\tau^*) > 0$ and crosses the imaginary axis from right to left if $\delta(\tau^*) < 0$.*

6 Numerical simulation

In this section we present computer simulation of some solutions of the system (2). From practical point of view numerical solutions are very important beside analytical study.

We take the parameters of the system as $a = 8.6$, $b = 1.4$, $h = 3.3$, $n = 2.4$, $g = 1.3$, $c = 12.2$, $\gamma = 4.3$, $s = 1.8$, $m = 0.9$, $d = 1.8$, $\alpha = 0.5$, $\beta = 8.7$, $\tau = 0$, and $(x(0), y(0), z(0), v(0)) = (0.5, 0.03, 0.4, 0.7)$. Then $E_2(x_2, 0, z_2, v_2) = (0.19, 0, 0.64, 2.03)$. Fig. 1(a) shows that x, y, z, v approach to their steady state values $(x_2, 0, z_2, v_2)$ in finite time.

We take the parameters of the system as $a = 10.6$, $b = 0.99$, $h = 3.3$, $n = 6.4$, $g = 10.9$, $c = 12.2$, $\gamma = 5.9$, $s = 1.8$, $m = 0.9$, $d = 1.8$, $\alpha = 3.5$, $\beta = 2.7$, $\tau = 0$, and $(x(0), y(0), z(0), v(0)) = (0.2, 0.1, 0.2, 0.7)$. Then $E_3(x_3, y_3, 0, v_3) = (0.31, 0.09, 0, 0.42)$. Fig. 1(b) shows that x, y, z, v approach to their steady state values $(x_3, y_3, 0, v_3)$ in finite time.

We take the parameters of the system as $a = 0.03$, $b = 1.4$, $h = 3.3$, $n = 2.4$, $g = 12.3$, $c = 12.2$, $\gamma = 13.3$, $s = 1.8$, $m = 2.9$, $d = 1.8$, $\alpha = 4.5$, $\beta = 9.7$, $\tau = 0$, and $(x(0), y(0), z(0), v(0)) = (0.2, 0.6, 0.02, 1.2)$. Then $E_4(x_4, y_4, z_4, v_4) = (0.7484, 0.9957, 0.2268, 1.3804)$. Fig. 1(c) shows that x, y, z, v approach to their steady state values (x_4, y_4, z_4, v_4) in finite time.

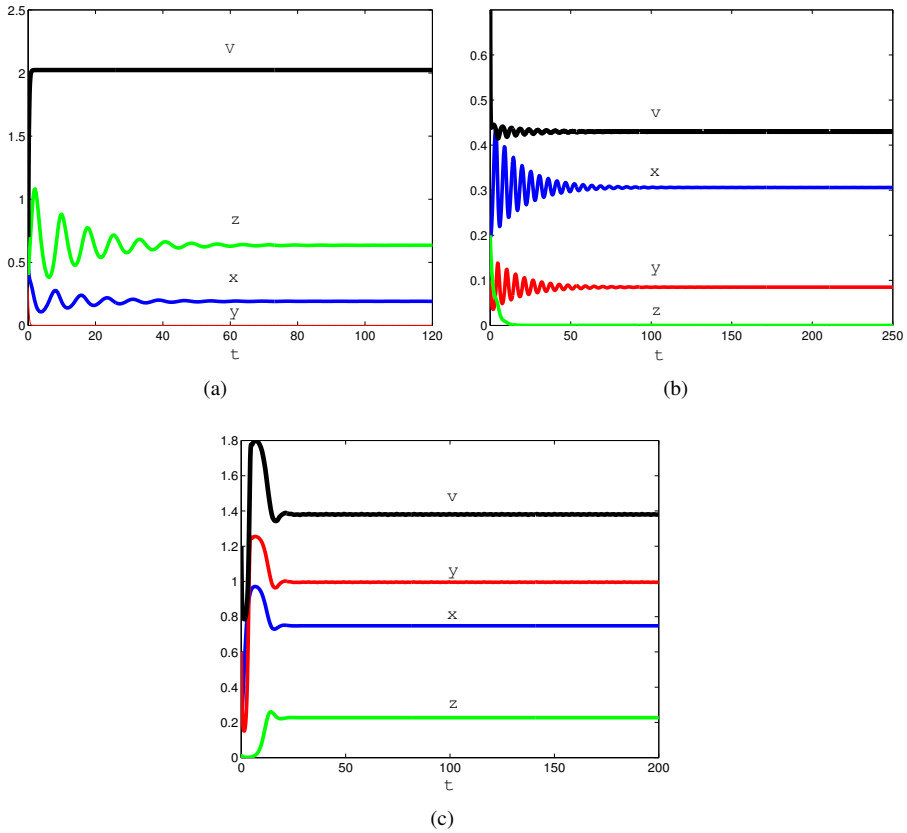
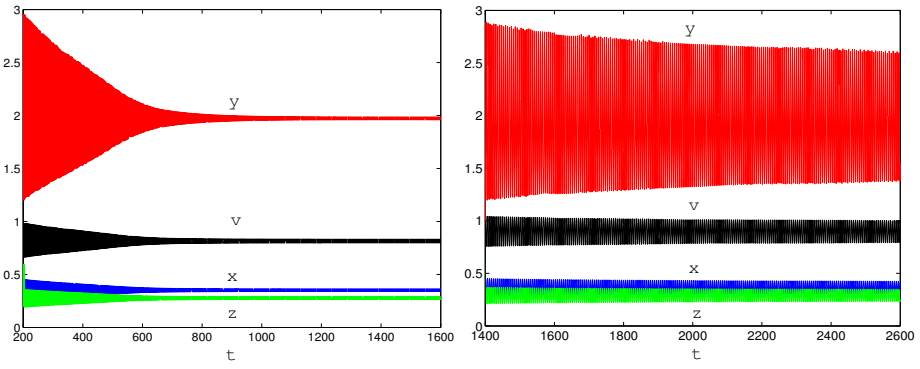


Fig. 1. x, y, z, v approach to their equilibrium values in finite time.

We take the parameters of the system as $a = 0.5$, $b = 1.4$, $h = 3.3$, $n = 10.4$, $g = 14.2$, $c = 7.6$, $\gamma = 2.1$, $s = 2.2$, $m = 4.9$, $d = 0.8$, $\alpha = 9.5$, $\beta = 3$, $\tau = 2.8$, and $(x(0), y(0), z(0), v(0)) = (0.4, 1.2, 0.6, 0.9)$. Then $E^*_\tau(x^*_\tau, y^*_\tau, z^*_\tau, v^*_\tau) = (0.3519, 1.973, 0.2765, 0.8158)$. Fig. 2(a) shows that x, y, z, v approach to their steady state values $(x^*_\tau, y^*_\tau, z^*_\tau, v^*_\tau)$ in finite time.

We take the parameters of the system as $a = 0.5$, $b = 1.4$, $h = 3.3$, $n = 10.4$, $g = 14.2$, $c = 7.6$, $\gamma = 2.1$, $s = 2.2$, $m = 4.9$, $d = 0.8$, $\alpha = 9.5$, $\beta = 3$, $\tau = 0.8$, and $(x(0), y(0), z(0), v(0)) = (0.4, 1, 0.8, 0.1)$. Then E^*_τ is unstable. The oscillations of x, y, z, v in finite time are depicted in Fig. 2(b).

Here Fig. 2(a) shows that for the above choices of parameters and $\tau = 2.8 > \tau^* = 0.9$, x, y, z, v populations approach to their equilibrium values $x^*_\tau, y^*_\tau, z^*_\tau, v^*_\tau$, respectively, in finite time. Keeping other parameters fixed, if we take $\tau = 0.8 < \tau^* = 0.9$, it is seen that the system is unstable (Fig.2(b)).



(a) (b)

Fig. 2. System is stable when $\tau > \tau^*$ and is unstable when $\tau < \tau^*$.

7 Concluding remarks

Farmers throughout the world have traditionally been encouraged by commercial, government and consumer interests to use synthetic chemical pesticides for a "fast and effective fix" to pest problems. But today they have understand that chemical insecticides have a limited life and that excessive and repeated use leads to resistance, resurgence and environmental problems and it is very expensive too. The baculovirus is a good example of an effective tool which allows diverse approaches that are in many ways more similar to chemical pesticides than to classical biocontrol agents. Their efficacy, specificity, and production of secondary inoculum make baculoviruses attractive alternatives to broad-spectrum insecticides [6,10,39]. This paper aims to provide a strong theoretical support to microbial pest control. In this paper we have studied the usefulness of this approach with the help of mathematical modelling. The basic model (1) is considered by analyzing the theoretical and experimental findings of several researchers. The details of the construction of the model is presented in Section 2. We have shown that the model is uniformly

bounded which implies that the system (1) is biologically well behaved. We have also observed that when $d_1 > (\frac{c_1K}{a_1+K} - \frac{\beta_1}{\gamma_1 K})$ and $d_2 > \frac{c_2K}{a_2+K}$, a complete eradication of pest is possible. This indicates that when the mortality rate of the infected pest due to virus is high then the system will be pest free. We have also found the condition when all pests become infected, which is $d_2 + \frac{d_2a_2[\gamma_1(c_1-d_1)-p_1\beta_1]}{a_1(p_1\beta_1+\gamma_1 d_1)} < c_2 < \frac{d_2(K+a_2)}{K-a_2}$, this means that when the conversion rate (c_2) of the infected pest is of moderate value, and if the virus infection rate (p_1) is high, then it is expected all the pests steadily converted to infected state. Theorem 3 also suggests that if the plant is attacked by a high capacity and aggressive pest, but due to virus infection pest becomes very low capacity consumers (conversion rate becomes lower than the mortality rate), then the pest species will go extinct and the plant species will persist. Another important result regarding plant fitness is also studied in this paper. We have observed that if $v_3 > v_\tau^*$, then $x_3 - x_\tau^* > 0$, i.e., if the number of viruses are high (by spraying or by replication process) in the field, then it will help to increase the production rate of the crops and will support the fundamental aim of microbial pest control. Besides that we have also noticed that fitness of the plant depends directly on the rate of infection of the virus (see Fig. 3).

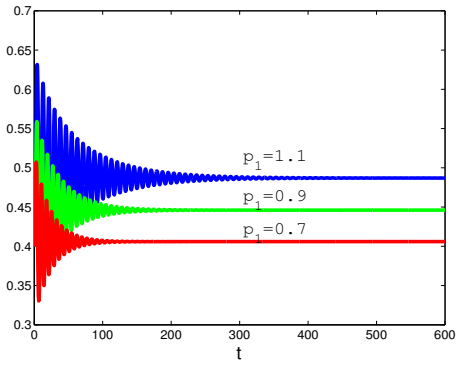


Fig. 3. Here $x(0) = 0.4$, $y(0) = 1.1$, $z(0) = 0.8$, $v(0) = 0.6$. $a = 0.5$, $b = 1.4$, $h = 3.3$, $n = 10.4$, $g = 8.3$, $c = 7.6$, $\gamma = 2.1$, $s = 1.2$, $m = 4.9$, $p_1 = f = 0.7/0.9/1.1$, $\alpha = 1.5$, $\beta = 3$, $\tau = 0.8$, and $(x(0), y(0), z(0), v(0)) = (0.4, 1.1, 0.8, 0.6)$. Fitness of the plant varies directly on the rate of infection of the virus in finite time.

So far, biological control has been successfully used in forestry and the greenhouse industry, where parasitoids, predatory mites/insects, and some microorganisms are used to control pests such as spider mites, thrips, aphids, whiteflies, scale, malybugs, moths, beetles, and some soil-borne fungi. The public awareness of biological control is slowly increasing as new products become available. Surveys have shown that about 30% of consumers would use biological control products if it were available. Insect viruses have a market in their natural form as biopesticides for forestry and field crops. Biotechnological research has focused on engineering of certain viruses to express genes whose toxin kills faster than the wild type of viruses.

Appendix

Proof of Theorem 1. Let $(x(t), y(t), z(t), v(t))$ be any solution of the system (2). It is easy to see that $x(t) > 0\ \forall t > 0$.

Now,

$$\begin{aligned}\frac{\mathrm{d}v}{\mathrm{d}t} &= \beta - \gamma v - dyv + \alpha e^{-m\tau} d\phi_2\big(-(\tau - t)\big)\phi_4\big(-(\tau - t)\big)\\ &\geq -\big(\gamma + dy(t)\big)v(t) \quad \forall t \in [0, \tau].\end{aligned}$$

Hence $v(t) \geq v(0)\exp\{-\int_0^t(\gamma + dy(T))\,\mathrm{d}T\} > 0$ as $t \in [0, \tau]$ and as long as

$$\int_0^t y(T)\,\mathrm{d}T < +\infty.$$

Again

$$\frac{\mathrm{d}y}{\mathrm{d}t} \geq -\big(s + dv(t)\big)y(t).$$

Hence $y(t) \geq y(0)\exp\{-\int_0^t(s + dv(T))\,\mathrm{d}T\} > 0$ as $t \in [0, \tau]$ and as long as

$$\int_0^t v(T)\,\mathrm{d}T < +\infty.$$

By repeating these arguments, we see that the positivity of $y(t)$ and $v(t)$ in $[0, \tau]$ can be used to infer positivity of $y(t)$ and $v(t)$ separately in $[0, +\infty)$.

Now we prove the positivity of $z(t)$ by contradiction. If possible, let there exists a $t_3 > 0$ such that $z(t_3) = 0$. But from the system (2)

$$z(t_3) = z(0)\int_0^{t_3} e^{\frac{cx(s)}{n+x(s)}}\,\mathrm{d}s + \int_0^{t_3}\left\{\int_{t-\tau}^{t} e^{-m(t-\theta)}y(\theta)v(\theta)\,\mathrm{d}\theta\right\}\mathrm{d}t > 0,$$

which is a contradiction (due to the positivity of $y(t)$ and $v(t)$).

Hence the theorem. □

Proof of Lemma 1. Let $(x(t), y(t), z(t), v(t))$ be any solution of the system (2).

Since

$$\frac{\mathrm{d}x}{\mathrm{d}t} \leq x(1 - x),$$

we have

$$\limsup_{t\to\infty} x(t) \leq 1.$$

Let

$$W = \frac{g}{a}x + y.$$

Then

$$\frac{\mathrm{d}W}{\mathrm{d}t} = \frac{g}{a}x(1-x) - \frac{ghxz}{a(n+x)} - sy - dyv \leq \frac{g}{a}x - sy \leq \frac{2g}{a} - \delta W,$$

where $\delta = \min\{1, s\}$. Therefore

$$\frac{\mathrm{d}W}{\mathrm{d}t} + \delta W \leq \frac{2g}{a}.$$

Applying a theorem on differential inequalities [40], we obtain

$$0 \leq W(x,y) \leq \frac{2g}{a\delta} + \frac{W(x(0),y(0))}{e^{\delta t}}. \qquad \square$$

Proof of Lemma 2. Let $W_1(t) = \alpha z(t) + v(t)$ for $t \in [0, +\infty)$. Then

$$\begin{aligned}\frac{\mathrm{d}W_1}{\mathrm{d}t} &= \frac{\alpha cxz}{n+x} - \alpha mz + (\alpha-1)dyv + \beta - \gamma v \\ &\leq \frac{\alpha cz}{n} - \alpha mz + (\alpha-1)dMv + \beta - \gamma v\end{aligned}$$

(since $y(t)$ is bounded, so a time $t_1 > 0$ exists such that $y(t) \leq M$ for all $t > t_1$)

$$\begin{aligned}&\leq \beta - \left(m - \frac{c}{n}\right)\alpha z - \gamma v + (\alpha-1)dM(W_1 - \alpha z) \\ &= \beta - \left[\left(m - \frac{c}{n}\right) + (\alpha-1)dM\right]\alpha z - \gamma v + (\alpha-1)dMW_1.\end{aligned}$$

Take $\mu_m = \min\{(m - \frac{c}{n}) + (\alpha-1)dM, \gamma\}$ and $mn - c > 0$.
If $\mu_m = \gamma$, then $\mu_m = \gamma > (\alpha-1)dM$.
If $\mu_m = (m - \frac{c}{n}) + (\alpha-1)dM$, then $\mu_m - (\alpha-1)dM = (m - \frac{c}{n}) > 0$.
This implies

$$\limsup_{t\to\infty} W_1(t) \leq \frac{\beta}{\mu_m - (\alpha-1)dM} < L \quad \forall t > t_2(L) > t_1 > 0. \qquad \square$$

Proof of Theorem 3. Before proving the theorem we first state a lemma known as Barbalat lemma [41].

Lemma 3. *Let $f(t)$ be a nonnegative function defined on $[0, +\infty)$ such that f is integrable on $[0, +\infty)$ and uniformly continuous on $[0, +\infty)$. Then $\lim_{t\to\infty} f(t) = 0$.*

We know that $x(0) > 0$, $y(0) > 0$, $z(0) > 0$, $v(0) > 0$.

Now,

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \frac{gxy}{b+x} - sy - dyv$$

can be rewritten as

$$y'(t) = -y\left(s - \frac{gx}{b+x}\right) - dyv = -y\left[\frac{x(s-g)+bs}{b+x}\right] - dyv.$$

If $s > g$ for all $t \geq 0$, then we can define a nonnegative function $f(t) = -y'(t)$ on $[0, +\infty)$.

So, $\int_0^t f(w)dw$ exists for all $t \in [0, +\infty)$ since negativity of $y'(t)$ implies $y(0) \geq \int_0^t f(w)dw = y(0) - y(t) \geq 0\ \forall t \geq 0$. So, by Barbalat lemma (Lemma 3) it follows that $\lim_{t\to\infty} f(t) = 0$, i.e., $\lim_{t\to\infty} y'(t) = 0$. Nonnegativity of $x(t)$, $y(t)$ and $v(t)$ implies that $\lim_{t\to\infty} y(t) = 0$ when $s > g$.

We have

$$\frac{\mathrm{d}v}{\mathrm{d}t} = -\gamma\left(v - \frac{\beta}{\gamma}\right) - dyv + \alpha e^{-m\tau} dy(t-\tau)v(t-\tau).$$

Since $v(t)$ is bounded, $\lim_{t\to\infty}[v'(t) + \gamma(v - \frac{\beta}{\gamma})] = 0$.

From this relation we can say that $\forall \epsilon > 0$, $\tau_\epsilon > 0$ exists such that

$$\left|v'(t) + \gamma\left(v - \frac{\beta}{\gamma}\right)\right| < \gamma\epsilon \quad \forall t > \tau_\epsilon.$$

It implies that $\limsup_{t\to\infty} |v(t) - \frac{\beta}{\gamma}| \leq \epsilon$.

Letting $\epsilon \to 0$ we get $\lim_{t\to\infty} v(t) = \frac{\beta}{\gamma}$.

Now

$$\frac{\mathrm{d}z}{\mathrm{d}t} = -z\frac{x(m-c)+mn}{n+x} - dyv(e^{-m\tau} - 1).$$

Since $v(t)$ is bounded and $y(t) \to 0$ as $t \to +\infty$, so $z(t) \to 0$ if $m > c$.

Again, we have

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x(1-x) - x\left[\frac{ay}{b+x} + \frac{hz}{n+x}\right].$$

As $y(t) \to 0$, $z(t) \to 0$ so $\exists t_1 > 0$ such that $y(t) < \epsilon_1/2$ if $t > t_1$ and $\exists t_2 > 0$ such that $z(t) < \frac{\epsilon_1}{2}$ for some $\epsilon_1 > 0$. Take $t > t' = max\{t_1, t_2\}$ and $\delta > 0$. So for $t > t'$,

$$\frac{\mathrm{d}x}{\mathrm{d}t} \geq x(1 - x - \delta\epsilon_1),$$

this implies that $\liminf_{t\to\infty} x(t) \geq 1 - \delta\epsilon_1$.

Letting $\epsilon_1 \to 0$, $\lim_{t\to\infty} x(t) = 1$.

Hence the theorem. □

Acknowledgment

The authors are grateful to Professor G. P. Samanta, Department of Mathematics, Bengal Engineering and Science University, Shibpur, for his valuable suggestions throughout the preparation of the paper. The authors also wish to thank the referees for their careful reading and constructive comments.

References

1. C. Darwin, *On the Origin of Species*, John Murray & Sons, London, 1859.
2. M.L. Flint, R. van den Bosch, *Introduction to Integrated Pest Management*, Plenum Press, New York, 1981.
3. A.E. Hajek, *Natural Enemies: An Introduction to Biological Control*, Cambridge Univ. Press, Cambridge, 2004.
4. P.F. Entwistle, A world survey of virus control of insect pests, in: F.R. Hunter-Fujita et al. (Eds.) *Insect Viruses and Pest Management*, John Wiley & Sons, Chichester, UK, 1998, pp. 188–204.
5. R.R. Grandos, B.A. Federici (Eds.), *The Biology of Baculoviruses*, CRC Press, Boca Raton, FL, 1986.
6. J. Huber, Use of baculoviruses in pest management programs, in: R.R. Granados, B.A. Federici (Eds.), *The Biology of Baculoviruses. II. Practical Application for Insect Control*, CRC Press, Boca Raton, FL, 1986, pp. 181–202.
7. Y. Tanada, R.T. Hess, Baculoviridae, Granulosis virus, in: J.R. Adams, J.R. Bonami (Eds.), *Atlas of Invertebrate Viruses*, CRC Press, Boca Raton, FL, 1991, pp. 227–257.
8. Y. Tanada, H.K. Kaya, *Insect Pathology*, Academic Press, New York, 1993.
9. P.V. Vail, Viruses for control of arthropod pests, in: R.D. Lumsden, J.L. Vaughn (Eds.), *ACS Proceedings Series, Pest Management: Biologically Based Technologies*, Am. Chem. Soc., Washington, DC, 1993, pp. 30–39.
10. J.C. Cunningham, Baculoviruses as microbial insecticides, in: R. Reuveni (Ed.), *Novel Approaches to Integrated Pest Management*, Lewis Publishers, Boca Raton, FL, 1995, pp. 261–292.
11. P.V. Vail, D.L. Hostetter, D.F. Hoffmann, Development of the multi-nucleocapsid nucleopolyhedroviruses (MNPVs) infectious to loopers (Lepidoptera: Noctuidae: Plusiinae) as microbial control agents, *Integrated Pest Management Reviews*, **4**, pp. 231–257, 1999.
12. E. Kurstak, *Microbial and Viral Pesticide*, Marcel Dekker, New York, 1982.
13. J.M. Vlak, Genetic engineering of baculoviruses for insect control, in: J. Oakeshott, M.J. Whitten (Eds.), *Molecular Approaches to Fundamental and Applied Entomology*, Springer-Verlag, New York, 1993, pp. 90–127.
14. J.R. Adams, J.R. Bonami, *Atlas of Invertebrate Viruses*, CRC Press, Boca Raton, 1971.

15. V.D. Amico, Baculoviruses, NEFES-Microbial Control, Hamden, CT, 1976, http://www.biocontrol.entomology.cornell.edu/pathogens/baculoviruses.html.

16. C.C. Payne, Insect viruses as control agents, *Parasitology*, **84**, pp. 35–77, 1982.

17. T.A. Jackson, The use of oryctes virus for control of rhinoceros beetle in the pacific islands, in: A.E. Hajek, T.Glare, M. O'Callaghan (Eds.), *Use of Microbes for Control and Eradication of Invasive Arthropods*, Progress in Biological Control, Vol. 6, Springer-Verlag, New York, 2008, pp. 133–140.

18. F. Moscardi, Assessment of the application of baculoviruses for control of Lepidoptera, *Annu. Rev. Entomol.*, **44**, pp. 257-289, 1999.

19. R.M. Anderson, R.M. May, Regulation and stability of host-parasite interactions. I. Regulatory processes, *J. Anim. Ecol.*, **47**, pp. 219-247, 1978.

20. E. Beretta, Y. Kuang, Modeling and analysis of a marine bacteriophage infection, *Math. Biosci.*, **149**, pp. 57–76, 1998.

21. E. Beretta, Y. Kuang, Modeling and analysis of a marine bacteriophage infection with latency period, *Nonlinear Anal., Real World Appl.*, **2**, pp. 35–74, 2001.

22. S. Bhattacharyya, D.K. Bhattacharya, Pest control through viral disease: Mathematical modeling and analysis, *J. Theor. Biol.*, **238**, pp. 177–197, 2006.

23. B.S. Goh, J. Leitman, T.L. Vincent, Optimal epidemic programs for pest control, in: B.S. Goh (Ed.), *Management and Analysis of Biological Populations*, Elsevier, 1980.

24. A. Maiti, S.P. Bera, G.P. Samanta, A prey-predator model with microparasite infection in the predator, *J. Biol. Syst.*, **16**, pp. 219–239, 2008.

25. S. Pathak, A. Maiti, Microbial pest control: A mathematical model, *J. Biol. Syst.*, **18**, pp. 455–478, 2000.

26. H.D. Burges, N.W. Hussey, *Microbial Control of Insects and Mites*, Academic Press, New York, 1971.

27. F. Fenner, F.N. Ratcliff, *Myxomatosis*, Cambridge Univ. Press, Cambridge, 1965.

28. P. Ferron, Pest control using the fungi beauveria and metarhizium, in: H.D. Burges (Ed.), *Microbial Control in Pests and Plant Diseases*, Academic Press, London, 1981.

29. A.E. Hajek, M.L. McManus, I.D. Junior, A review of introductions of pathogens and nematodes for classical biological control of insects and mites, *Biol. Control*, **41**, pp. 1–13, 2007.

30. L.A. Lacey, D.I. Shapiro-Ilan, The potential role for microbial control of orchard insect pests in sustainable agriculture, *J. Food Agric. Environ.*, **1**, pp. 326–331, 2003.

31. H.I. Freedman, *Deterministic Mathematical Models in Population Ecology*, Marcel Dekker, New Work, 1980.

32. A. Maiti, G.P. Samanta, Deterministic and stochastic analysis of a prey-dependent predator-prey system, *Int. J. Math. Educ. Sci. Technol.*, **36**, pp. 65–83, 2005.

33. R.M. May, *Stability and Complexity in Model Ecosystems*, Princeton Univ. Press, Princeton, 1974.

34. S. Ruan, D. Xiao, Global analysis in a predator-prey system with nonmonotonic functional response, *SIAM J. Appl. Math.*, **61**, pp. 1445–1472, 2001.

35. N. Macdonald, *Biological Delay Systems: Linear Stability Theory*, Cambridge Univ. Press, Cambridge, 1989.

36. K. Gopalsamy, *Stability and Oscillations in Delay Differential Equations of Population Dynamics*, Kluwer Academic, Dordrecht, 1992.

37. Y. Kuang, *Delay Differential Equations with Applications in Population Dynamics*, Academic Press, Boston, 1993.

38. E. Beretta, Y. Tang, Extension of a geometric stability switch criterion, *Funkc. Ekvacioj., Ser. Int.*, **46**, pp. 337–361, 2003.

39. A. Groner, Safety to nontarget invertebrates of baculoviruses. in: M. Laird, L.A. Lacey, E.W. Davidson (Eds.), *Safety of Microbial Insecticides*, CRC Press, Boca Raton, FL, 1990, pp. 135–147.

40. G. Birkhoff, G.C. Rota, *Ordinary Differential Equations*, Ginn, Boston, 1982.

41. I. Barbalat, Systems d'équations différentielles d'oscillations non linéaires, *Rev. Roum. Math. Pures Appl.*, **4**, pp. 267–270, 1959.

42. L.A. Lacey, M. Goettel, Current developments in microbial control of insect pests and prospects for the early 21st century, *Entomophaga*, **40**, pp. 3–27, 1995.

43. L.A. Lacey, R. Frutos, H.K. Kaya, P. Vail, Insect pathogens as biological control agents: Do they have a future?, *Biol. Control*, **21**, pp. 230–248, 2001.