Available online at http://scik.org
Commun. Math. Biol. Neurosci. 2018, 2018:8
https://doi.org/10.28919/cmbn/3634
ISSN: 2052-2541

PLANT RESPONSES TO DISEASE AND HERBIVORE ATTACK: A MATHEMATICAL MODEL

DEBASIS MUKHERJEE

Department of Mathematics, Vivekananda College, Thakurpukur, Kolkata- 700063, India

Communicated by M. Liu

Abstract. This paper presents a model for plants subject to a disease, harvested by (insect) herbivores and it also includes natural enemies of the latter. Basic results on boundedness, feasibility of equilibria, uniform persistence and local and global stability issues are investigated.

Keywords: plant defence; persistence; global stability.

2010 AMS Subject Classification: 34D23, 92B05, 92D30.

1. Introduction

In nature, plants interact in complex ways with herbivores and pathogens. Presently, 50% of 6 million insects species are herbivorous [17]. Plant pathogenic microbes are not estimated still they create major threats to plants [19]. Due to multiple attack, plants have developed sophisticated defence mechanism that allow them to identify herbivores or pathogens [13]. Two types of defence mechanism are employed by plant namely physical and chemical. In case of chemical defence, plant release volatile organic compounds (VOCs) that attract natural enemies

E-mail address: mukherjee1961@gmail.com

Received December 30, 2017

of herbivores to reduce enemy pressure [6,16]. In fact, VOCs mainly attract predatory mites and parasitic wasps. For example, lima bean and apple plants which release volatile that attract predatory mites when damaged by spider mites [20]. Several plant species such as cucumber, corn, cotton etc. release volatile when they are attacked by herbivores. This herbivore-induced plant volatile (HIPV) can control pest and reduce the use of artificial pesticides. HIPVs are the lipophilic liquids with high vapor pressures which are released from the different parts of the plant body namely leaves, flowers fruits etc.[7]. Thus the induced plant can protect forestry and agriculture. Though, VOCs can attract predatory arthropods and / or repel herbivores and thus promote plant fitness [1,5,21]. Volatile of any kind confer protection for damaged plants by attracting natural enemies of herbivores [15,16]. Studies either on plant-herbivore or plant-pathogen interaction has received much attention to the researchers. But the role of VOCs in mediating tritrophic interactions, when plants are attacked by herbivore and pathogen is still unknown. Recently Liu et al.[11] investigated the model involving plants, herbivores and natural enemies of herbivores in the form of tritrophic interactions without considering pathogenic effect on the plant population. They found that increase in attraction of strength of plant-induced volatile to the natural enemy leads to high fluctuation amplitude of plant biomass and herbivore population. It was observed that when the attack strength of natural enemies reaches a certain level, fluctuation amplitude of plant biomass and herbivore population decrease and plant biomass approach to its environmental carrying capacity. Fergola and Wang [8] improved the model of Liu et al. [11] and considered the effect of time delay. They established that for Volterra type interaction, the threshold value for persistence of herbivore and carnivore populations is not affected by the chemical attractions. It was remarked that presence of carnivores may decrease the density of herbivores and increase the density of plants. The model exhibits the fold bifurcation when the predation process follows Leslie type.

In view above discussion, we consider a system where pathogens co-occur with herbivory. The novelty of our work is to demonstrate the situation when plants are attacked by herbivorous insects and pathogens. Previous studies mainly focussed plant-insect and plant-pathogen interactions largely independent from one another, although plant defence against both is regulated by the same general mechanism.

One of the main findings of this work is the condition under which the positive (endemic) equilibrium is globally asymptotically stable. For this condition, the disease become endemic. To control disease such condition should not be accepted. On the other hand, one may remove infected plants to prevent disease. Local stability of boundary equilibria are derived. If these conditions are satisfied then one of the subpopulation faces extinction. In that case, either infected plants or herbivore population can be removed. To protect plant fitness, immigration rate of natural enemies of herbivores and pathogens play a major role. For a four species system, one critical condition demands that all boundary equilibria with one missing species can be invaded by the missing species. These conditions are obtained in system parameters.

This paper is structured as follows. In Section 2, we present our model. Positivity and boundedness of solutions of system are given in Section 3. Dynamical behavior of the system are investigated in Section 4. Uniform persistence criterion is described in Section 5. We discuss global stability of the positive equilibrium point in Section 6. A brief discussion follows in Section 7.

2. Model

Let $S(t), I(t)$ be the number of susceptible and infected plant respectively. $Y(t)$ and $Z(t)$ be the population sizes of herbivores and their natural enemies respectively. The model is described by :

$$\begin{aligned}
\frac{dS}{dt} &= S\{r(1-\frac{S}{k}) - \beta I - p_1 Y\},\\
\frac{dI}{dt} &= I(\beta S - \mu),\\
\frac{dY}{dt} &= Y(-d_1 + c_1 p_1 S - p_2 Z),\\
\frac{dZ}{dt} &= -d_2 Z + c_2 p_2 Y Z + \omega S
\end{aligned} \tag{2.1}$$

with initial conditions given by $S(0) = S_0 > 0, I(0) = I_0 > 0, Y(0) = Y_0 > 0$ and $Z(0) = Z_0 > 0$. Here r is the intrinsic growth rate of plants. k is the environmental carrying capacity. β is the

disease transmission rate. p_1 and p_2 are the predation rates for plant-herbivore and herbivore-natural enemies respectively. c_1 and c_2 are the corresponding conversion rates. d_1 is the death rate of herbivores, and μ is the death rate of infected plant. The term ω is the immigration rate of natural enemies of herbivores due to the attraction of defensive chemical from plants. Biological justification of the above model can be found in [3]. For example, lima bean plants (*Phaseolus lunatus* L. cv Sieva) emit volatile when attacked by spider mites (*Tetranychus urticae*) and attract predatory mite (*Phytoseiulus persimilis*), a specialized natural enemy of spider mites. Pod blight is caused to the lima bean plants by the fungus *Diaporthe phaselorum*.
All the model parameters are assumed to be positive.

3. Prelimineries

In this section, we shall first show positivity and boundedness of solutions of system (2.1). For system (2.1) to be biologically meaningful and well posed, it is necessary to prove that all solutions of system with positive initial data will remain positive for all times $t > 0$. This will be established by the following lemma.

Lemma 3.1. *All solutions* $(S(t), I(t), Y(t), Z(t))$ *of system (2.1) with initial value* $(S_0, I_0, Y_0, Z_0) \in \mathbb{R}^4_+$, *remains positive for all* $t > 0$.

Proof. The positivity of $S(t), I(t)$ and $Y(t)$ can be verified by the equations
$S(t) = S_0 \exp\{\int_0^t [r(1 - \frac{S(u)}{k}) - \beta I(u) - p_1 Y(u)] du\}$,
$I(t) = I_0 \exp\{\int_0^t [\beta S(u) - \mu] du\}$,
$Y(t) = Y_0 \exp\{\int_0^t [-d_1 + c_1 p_1 S(u) - p_2 Z(u)] du\}$
with $S_0, I_0, Y_0 > 0$. The positivity of $Z(t)$ can be easily deduced from the fourth equation of system (2.1). We observe that
$\frac{dZ}{dt} \geq Z(-d_2 + c_2 p_2 Y)$
$\Rightarrow Z(t) \geq Z_0 \exp\{\int_0^t [-d_2 + c_2 p_2 Y(u)] du\}$.
Also if $S(0) = I_0 > 0$, then $S(t) > 0$ for all $t > 0$. The same argument is valid for component

$I(t), Y(t)$ and $Z(t)$. Hence the interior of $\mathbb{R}^4_+$ is an invariant set of system (2.1).
In the theoretical eco-epidemiology, the boundedness of the system ensures that the system is biologically valid and well behaved. Biological validity of the model is shown by the following lemma.

Lemma 3.2. *All the solutions of system (2.1) will lie in the region* $B = \{(S,I,Y,Z) \in \mathbb{R}^4_+ : 0 \leq S + I + \frac{1}{c_1}Y + \frac{1}{c_1 c_2}Z \leq \frac{M}{\lambda}\}$ *as* $t \to \infty$ *for all positive initial values* $(S(0), I(0), Y(0), Z(0)) \in \mathbb{R}^4_+$ *where* $\lambda = min\{r, \mu, d_1, d_2\}$ *and* $M = \frac{k}{4r}(2r + \frac{\omega}{c_1 c_2})^2$.

Proof. Let us consider the function
$W(t) = S + I + \frac{1}{c_1}Y + \frac{1}{c_1 c_2}Z.$
The time derivative along a solution of (2.1) is
$\frac{dW(t)}{dt} = S\{r(1 - \frac{S}{k})\} - \mu I - \frac{d_1}{c_1}Y - \frac{d_2}{c_1 c_2}Z + \frac{\omega}{c_1 c_2}S.$
For each $\lambda > 0$ the following inequality is satisfied :

$$\frac{dW}{dt} + \lambda W \leq M + (\lambda - r)S + (\lambda - \mu)I + \frac{1}{c_1}(\lambda - d_1)Y + \frac{1}{c_1 c_2}(\lambda - d_2)Z. \tag{3.1}$$

Now choose λ such that $0 < \lambda = min\{r, \mu, d_1, d_2\}$. Then (3.1) can be written as
$\frac{dW}{dt} + \lambda W < M$.
By using the Comparison Theorem [2] we obtain
$0 \leq W(S(t), I(t), Y(t), Z(t)) \leq \frac{M}{\lambda} + W(S(0), I(0), Y(0), Z(0))/e^{\lambda t}$.
Taking limit when $t \to \infty$, we have, $0 < W(t) \leq \frac{M}{\lambda}$. Hence system (2.1) is bounded.
Since the total population is bounded, each subpopulation S, I, Y, Z is bounded as well for all future times. From above Lemma 3.2, we have $S(t) \leq k, I(t) \leq M, Y(t) \leq Mc_1, Z(t) \leq Mc_1c_2$.

4. Dynamical behaviour

Evidently, system (2.1) has the following boundary equilibrium points : $E_0 = (0,0,0,0), E_{14} = (k, 0, 0, \frac{\omega k}{d_2}), E_{124} = (\frac{\mu}{\beta}, \frac{r(\beta k - \mu)}{k\beta^2}, 0, \frac{\omega\mu}{\beta d_2})$ and $E_{134} = (\tilde{S}, 0, \tilde{Y}, \tilde{Z})$ where $\tilde{S}$ is the positive root of the equation

$rc_1c_2p_1p_2S^2+(c_1p_1kd_2-c_1c_2p_1p_2rk-d_1c_2p_2r-p_2k\omega)S-d_1k(d_2-c_2p_2r)=0,$

and $\tilde{Y}=r(1-\frac{\tilde{S}}{k}),\tilde{Z}=\frac{k\omega\tilde{S}}{kd_2-c_2p_2(k-\tilde{S})}$. Clearly, E_0 and E_{14} always exist. E_{124} is feasible if $\beta k>\mu$ and E_{134} is feasible if $\tilde{S}<k$ and $kd_2>c_2p_2r(k-\tilde{S})$.

The local stability of these equilibria is determined by the eigenvalues of the Jacobian matrix of (2.1),

$$J(S,I,Y,Z)=\begin{pmatrix} r-\frac{2rS}{k}-\beta I-p_1Y & -\beta S & -p_1S & 0\\ \beta I & \beta S-\mu & 0 & 0\\ c_1p_1Y & 0 & -d_1+c_1p_1S-p_2Z & -p_2Y\\ \omega & 0 & c_2p_2Z & -d_2+c_2p_2Y \end{pmatrix}$$

Theorem 4.1.$(i)E_0$ *is always unstable.*

$(ii)E_{14}$ *is locally stable if* $\beta k<\mu$ *and* $\frac{d_1d_2+p_2k\omega}{d_2}<c_1p_1k$.

$(iii)E_{124}$ *is locally stable if* $c_1p_1d_2\mu<\beta d_1d_2+p_2\omega\mu$.

$(iv)E_{134}$ *is locally stable if* $\beta\tilde{S}<\mu$.

Proof. It follows immediately by linearizing around the equilibria.

Next we interested about the existence of the interior equilibrium point of system (2.1) which is given by $E^*=(S^*,I^*,Y^*,Z^*)$ where

$S^*=\frac{\mu}{\beta},I^*=\frac{1}{\beta}\{r(1-\frac{S^*}{k})-p_1Y^*\},$

$Y^*=\frac{d_2(c_1p_1\mu-\beta d_1)-\omega\mu p_2}{c_1p_1\mu-\beta d_1},Z^*=\frac{c_1p_1\mu-\beta d_1}{d_2\beta}.$

E^* is feasible if $c_1p_1\mu d_2>\beta d_1d_2+\omega\mu p_2$ and $r(1-\frac{S^*}{k})-p_1Y^*>0$.

The Jacobian matrix of (2.1) at E^* is,

$$J(E^*)=\begin{pmatrix} -\frac{rS^*}{k} & -\beta S^* & -p_1S^* & 0\\ \beta I^* & 0 & 0 & 0\\ c_1p_1Y^* & 0 & 0 & -p_2Y^*\\ \omega & 0 & c_2p_2Z^* & -\frac{\omega S^*}{Z^*} \end{pmatrix}$$

whose characteristic equation is

$$\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0 \tag{4.1}$$

where

$A_1 = S^*(\frac{\omega}{Z^*} + \frac{r}{k}), A_2 = \beta^2 S^* I^* + c_2 p_2^2 Y^* Z^* + \frac{\omega r S^{*2}}{kZ^*} + p_1^2 c_1 S^* Y^*,$

$A_3 = \frac{\beta^2 S^{*2} I^* \omega}{Z^*} + \frac{c_2 p_2^2 Y^* Z^* S^* r}{k} + \frac{p_1 S^* Y^* \omega d_1}{Z^*},$

$A_4 = \beta^2 S^* I^* c_2 p_2^2 Y^* Z^*.$

From the Routh-Huwitz criteria, all the real parts of roots for (4.1) are negative if and only if

$A_3(A_1A_2 - A_3) - A_1^2 A_4 > 0$

which is equivalent to

$$\begin{aligned}(\frac{\beta^2 S^{*2} I^* \omega}{Z^*} + \frac{c_2 p_2^2 Y^* Z^* S^* r}{k} + \frac{p_1 S^* Y^* \omega d_1}{Z^*})\{\frac{\omega S^*}{Z^*}(c_2 p_2^2 Y^* Z^* + \frac{\omega r S^{*2}}{kZ^*}) + p_1 p_2 S^* Y^* \omega \\ + \frac{rS^*}{k}(\beta^2 S^* I^* + \frac{\omega r S^{*2}}{kZ^*} + p_1^2 c_1 S^* Y^*)\} - S^{*2}(\frac{\omega}{Z^*} + \frac{r}{k})^2 \beta^2 S^* I^* c_2 p_2^2 Y^* Z^* > 0.\end{aligned} \tag{4.2}$$

If the inequality (4.2) holds then E^* is locally asymptotically stable.

5. Uniform persistence

Biologically, uniform persistence of the system ensures the long term survival of all populations, none of them facing extinction. To establish uniform persistence of system (2.1) we use Butler-McGehee lemma [10]. Now we state coexistence condition for all the populations.

Theorem 5.1. *Suppose that*

i) $k > max\{\frac{\mu}{\beta}, \frac{d_1}{c_1 p_1}\}$,

ii) $c_1 p_1 d_2 \mu > \beta d_1 d_2 + p_2 \omega \mu$,

(iii) $\beta \tilde{S} > \mu$,

(iv) the equilibrium points E_{124} *and* E_{134} *are globally stable with respect to* $\mathbb{R}^+_{SIZ}$ *and* $\mathbb{R}^+_{SYZ}$

respectively.

Then system (2.1) is uniformly persistent.

Proof. Suppose that x is a point in the positive octant and $o(x)$ is the orbit through x and Ω is the omega limit set of the orbit through x. Note that $\Omega(x)$ is bounded. We show that $E_0 \notin \Omega(x)$.If $E_0 \in \Omega(x)$, then by Butler-McGehee lemma [10], there exists a point p in $\Omega(x) \cap W^s(E_0)$ where $W^s(E_0)$ denotes the strong stable manifold of E_0. Since $o(p)$ lies in $\Omega(x)$ and $W^s(E_0)$ is the $I-Y-Z$ plane and hence unbounded orbits lies in $\Omega(x)$ is unbounded, which is a contradiction.

Next we show that $E_{14} \notin \Omega(x)$. The condition $k > max\{\frac{\mu}{\beta}, \frac{d_1}{c_1 p_1}\}$, implies that E_{14} is a saddle point. $W^s(E_{14})$ is the $S-Z$ plane. Thus unbounded orbits lies in $\Omega(x)$ once more a contradiction. The condition $c_1 p_1 d_2 \mu > \beta d_1 d_2 + p_2 \omega \mu$ implies that E_{124} is a saddle point and $W^s(E_{124})$ is the $S-I-Z$ plane. So one easily show that unbounded orbits lies in $\Omega(x)$ once more a contradiction. Lastly, we can show that $E_{134} \notin \Omega(x)$ as $\beta\tilde{S} > \mu$. Thus , $\Omega(x)$ does not intersect any of the coordinate planes and hence system (2.1) is persistent. Since (2.1) is bounded, by main theorem in [4], this implies that the system is uniformly persistent.

6. Global stability of positive equilibrium point

If the inequality (4.2) holds then the positive equilibrium point E^* is locally asymptotically stable under certain restrictions. So natural question arises under what additional conditions it becomes globally asymptotically stable. To derive global stability condition it is sometimes difficult to find out a Lyapunov function. There is an alternative approach to show global stability due to Li and Muldowney [12]. Now we use a high-dimensional Bendixson's criterion of Li and Muldowney [12], which we briefly state next.

Let $D \subset \mathbb{R}^n$ be an open set and $F \in C^1$. Consider a system of differential equations

$$\frac{dX}{dt} = F(X). \tag{6.1}$$

According to the theory developed in [12], it is sufficient to show that the second compound equation

$$\frac{dU}{dt} = \frac{\partial F^{[2]}}{\partial X}(X(t,X_0))U(t) \tag{6.2}$$

with respect to a solution $X(t,X_0)$ of system (6.1) is equi-uniformly asymptotically stable, namely, for each $X_0 \in D$, system (6.2) is uniformly asymptotically stable, and the exponential decay rate is uniform for X_0 in each compact subset of D, where $D \subset R^n$ is an open connected set. Here $\partial F/\partial X^{[2]}$ is the second additive compound matrix of the Jacobian matrix $\partial F^{[2]}/\partial X$. It is an $\begin{pmatrix} n \\ 2 \end{pmatrix} \times \begin{pmatrix} n \\ 2 \end{pmatrix}$ matrix, and thus (6.2) is a linear system of dimension $\begin{pmatrix} n \\ 2 \end{pmatrix}$ (see Fiedler [9] and Muldowney [14]). For a general 4×4 matrix

$$P = \begin{pmatrix} p_{11} & p_{12} & p_{13} & p_{14} \\ p_{21} & p_{22} & p_{23} & p_{24} \\ p_{31} & p_{32} & p_{33} & p_{34} \\ p_{41} & p_{42} & p_{43} & p_{44} \end{pmatrix}$$

its second compound matrix $P^{[2]}$ is

$$P^{[2]} = \begin{pmatrix} p_{11}+p_{22} & p_{23} & p_{24} & -p_{13} & -p_{14} & 0 \\ p_{32} & p_{11}+p_{33} & p_{34} & p_{12} & 0 & -p_{14} \\ p_{42} & p_{43} & p_{11}+p_{44} & 0 & p_{12} & p_{13} \\ -p_{31} & p_{21} & 0 & p_{22}+p_{33} & p_{34} & -p_{24} \\ -p41 & 0 & p_{21} & p_{43} & p_{22}+p_{44} & p_{23} \\ 0 & -p_{41} & p_{31} & -p_{42} & p_{32} & p_{33}+p_{44} \end{pmatrix} \tag{6.3}$$

The equi-uniform asymptotic stability of (6.2) implies the exponential decay of the surface area of any compact two-dimensional surface D. If D is simply connected, this prevents the occurrence of any invariant simple closed rectifiable curve in D, including periodic orbits.The following result is proved in Li and Muldowney [12].

Proposition 6.1. Let $D \subset \mathbb{R}^n$ be a simply connected region. Assume that the family of linear systems (6.2) is equi-uniformly asymptotically stable. Then

(i) D contains no simple closed invariant curves including periodic orbits, homoclinic orbits, heteroclinic cycles;

(ii) each semi-orbit in D converges to a single equilibrium.

In particular, if D is positively invariant and contains an unique equilibrium $\bar{X}$, then $\bar{X}$ is globally asymptotically stable in D.

One can show uniform asymptotic stability of system (6.2) by constructing a Lyapunov function. For example, (6.2) is equi-uniformly asymptotically stable if there exists a positive definite function $V(U)$, such that $dV(U)/dt|_{(6.2)}$ is negative definite, and V and $dV(U)/dt|_{(6.2)}$ are both independent of X_0.

We now require the following assumptions to prove the global stability of positive equilibrium point of system (2.1).

$(\mathbf{A_1})$ There exist positive numbers $\alpha, \theta, \eta, \rho$, and σ such that
$max\{c_{11}+\frac{c_{14}\alpha}{\theta}, c_{22}+c_{23}\eta+\frac{c_{24}\eta}{\theta}, \frac{c_{32}}{\eta}+c_{33}+\frac{c_{35}}{\rho}+\frac{c_{36}}{\sigma}, \frac{c_{41}\alpha}{\theta}+\frac{c_{42}\theta}{\eta}+c_{44}+\frac{c_{45}\theta}{\rho}, \frac{c_{51}\rho}{\alpha}+c_{53}\rho+\frac{c_{54}\rho}{\theta}+c_{55}, \frac{c_{62}\sigma}{\eta}+c_{63}\sigma+c_{66}\} < 0$ and

$(\mathbf{A_2})$ Assumption of Theorem 5.1 be hold.

Assumption (A_2) implies that system (2.1) is uniformly persistent and hence there exists a time T such that $S(t), I(t), Y(t), Z(t) > \tilde{k}(0 < \tilde{k} < k)$ for $t > T$.

We again denote $X = (S, I, Y, Z)^T$ and $F(X) = (S\{r(1-\frac{S}{k}) - \beta I - p_1 Y\}, I(\beta S - \mu), Y(-d_1 + c_1 p_1 S - p_2 Z), -d_2 Z + c_2 p_2 Y Z + \omega S)^T$,

We have $\frac{\partial F}{\partial X} = J(S, I, Y, Z)$ and by (6.3) and we assume that

$$\frac{\partial F^{[2]}}{\partial X} = \begin{pmatrix} m_{11} & m_{12} & m_{13} & m_{14} & m_{15} & m_{16} \\ m_{21} & m_{22} & m_{23} & m_{24} & m_{25} & m_{26} \\ m_{31} & m_{32} & m_{33} & m_{34} & m_{35} & m_{36} \\ m_{41} & m_{42} & m_{43} & m_{42} & m_{43} & m_{45} \\ m_{51} & m_{52} & m_{53} & m_{54} & m_{55} & m_{56} \\ m_{61} & m_{62} & m_{63} & m_{64} & m_{65} & m_{66} \end{pmatrix} \tag{6.4}$$

where

$m_{11} = r - \frac{2rS}{k} - \beta I - p_1 Y + \beta S, m_{12} = 0, m_{13} = 0, m_{14} = p_1 S, m_{15} = 0, m_{16} = 0, m_{21} = 0, m_{22} = r(1-\frac{2S}{k}) - \beta I - p_1 Y - d_1 + c_1 p_1 S - p_2 Z, m_{23} = -p_2 Y, m_{24} = -\beta S, m_{25} = 0, m_{26} = 0, m_{31} = 0, m_{32} = c_2 p_2 Z, m_{33} = r - \frac{2rS}{k} - \beta I - p_1 Y - d_2 + c_2 p_2 Y, m_{34} = 0, m_{35} = -\beta S, m_{36} = -p_1 S, m_{41} =$

$-c_1p_1Y, m_{42} = \beta I, m_{43} = 0, m_{44} = \beta S - \mu - d_1 + c_1p_1S - p_2Z, m_{45} = -p_2Y, m_{46} = 0, m_{51} = -\omega, m_{52} = 0, m_{53} = \beta I, m_{54} = c_2p_2Z, m_{55} = \beta S - \mu - d_2 + c_2p_2Y, m_{56} = 0, m_{61} = 0, m_{62} = -\omega, m_{63} = c_1p_1Y, m_{64} = 0, m_{65} = 0, m_{66} = -d_1 + c_1p_1S - p_2Z - d_2 + c_2p_2Y.$

The second compound system

$$\begin{pmatrix} \dot{x_1} \\ \dot{x_2} \\ \dot{x_3} \\ \dot{x_4} \\ \dot{x_5} \\ \dot{x_6} \end{pmatrix} = \frac{\partial F^{[2]}}{\partial X} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \\ x_6 \end{pmatrix}$$

then becomes

$$\begin{aligned}
\dot{x_1} &= \{r + (\beta - \frac{2r}{k})S - \beta I - p_1Y - \mu\}x_1 + p_1Sx_4, \\
\dot{x_2} &= \{r - S(c_1p_1 - \frac{2r}{k}) - \beta I - p_1Y - d_1p_2Z\}x_2 - p_2Yx_3 - \beta Sx_4, \\
\dot{x_3} &= c_2p_2Zx_2 + \{r - \frac{2rS}{k} - \beta I + (c_2p_2 - p_1)Y - d_2\}x_3 - \beta Sx_5 - p_1Sx_6, \\
\dot{x_4} &= -c_1p_1Yx_1 + \beta Ix_2 + (\beta S - \mu - d_1 + c_1p_1S - p_2Z)x_4 - p_2Yx_5, \\
\dot{x_5} &= -\omega x_1 + \beta Ix_3 + c_2p_2Zx_4 + (\beta S - \mu - d_2 + c_2p_2Y)x_5, \\
\dot{x_6} &= -\omega x_2 + c_1p_1Yx_3 - (d_1 - c_1p_1S + p_2Z + d_2 - c_2p_2Y)x_6
\end{aligned} \tag{6.5}$$

where $X(t) = (S(t), I(t), Y(t), Z(t))^T$ is arbitrary solution of system (2.1) with $X_0(t) = (S_0(t), I_0(t), Y_0(t), Z_0(t))^T \in \mathbb{R}^4_+$. Set $W(Q) = max\{\alpha|x_1|, \eta|x_2|, |x_3|, \theta|x_4|, \rho|x_5|, \sigma|x_6|\}$.

The direct calculations lead to the following inequalities :

$\frac{d^+}{dt^+}\alpha|x_1| \leq c_{11}\alpha|x_1| + \frac{c_{14}\theta}{\theta}|x_4|,$

$\frac{d^+}{dt^+}\eta|x_2| \leq c_{22}\eta|x_2| + c_{23}\eta|x_3| + \frac{c_{24}\eta\theta}{\theta}|x_4|,$

$\frac{d^+}{dt^+}|x_3| \leq \frac{c_{32}\eta}{\eta}|x_2| + c_{33}|x_3| + \frac{c_{35}\rho}{\rho}|x_5| + \frac{c_{36}\sigma}{\sigma}|x_6|,$

$\frac{d^+}{dt^+}\theta|x_4| \leq \frac{c_{41}\theta\alpha}{\alpha}|x_1| + \frac{c_{42}\theta\eta}{\eta}|x_2| + c_{44}\theta|x_4| + \frac{c_{45}\rho\theta}{\rho}|x_5|,$

$\frac{d^+}{dt^+}\rho|x_5| \leq \frac{c_{51}\rho\alpha}{\alpha}|x_1| + c_{53}\rho|x_3| + \frac{c_{54}\rho\theta}{\theta}|x_4| + c_{55}\rho|x_5|,$

$\frac{d^+}{dt^+}\sigma|x_6| \leq \frac{c_{62}\sigma\eta}{\eta}|x_2| + c_{63}\sigma|x_3| + c_{66}\sigma|x_6|$

where d^+/dt denotes the right-hand derivative and

$c_{11} = r + \beta k - (\frac{2r}{k} + \beta + p_1)\tilde{k}, c_{14} = p_1 k, c_{22} = 3r - (c_1 p_1 + \beta + p_2)\tilde{k}) - d_1,$

$c_{23} = -p_2\tilde{k}, c_{24} = -\beta\tilde{k}, c_{32} = c_1 c_2^2 p_2 M, c_{33} = r - d_2 + c_1 c_2 p_2 M - (\frac{2r}{k} + \beta + p_1)\tilde{k},$

$c_{35} = -\beta\tilde{k}, c_{36} = -p_1\tilde{k}, c_{41} = -c_1 p_1 \tilde{k}^2, c_{42} = \beta M, c_{44} = \beta k - \mu - d_1 + c_1 p_1 k - p_2\tilde{k},$

$c_{45} = -p_2\tilde{k}, c_{51} = -\omega\tilde{k}, c_{53} = \beta M, c_{54} = c_1 c_2^2 p_2 M, c_{55} = \beta k - \mu - d_2 + c_1 c_2 p_2 M,$

$c_{62} = -\omega\tilde{k}, c_{63} = c_1^2 p_1 M, c_{66} = -d_1 + c_1 p_1 k - p_2\tilde{k} - d_2 + c_1 c_2 p_2 M.$

Therefore,

$\frac{d^+}{dt} W(Q(t)) \leq \psi W(Q(t))$

with

$\psi = max\{c_{11} + \frac{c_{14}\alpha}{\theta}, c_{22} + c_{23}\eta + \frac{c_{24}\eta}{\theta}, \frac{c_{32}}{\eta} + c_{33} + \frac{c_{35}}{\rho} + \frac{c_{36}}{\sigma}, \frac{c_{41}\alpha}{\theta} + \frac{c_{42}\theta}{\eta} + c_{44} + \frac{c_{45}\theta}{\rho}, \frac{c_{51}\rho}{\alpha} + c_{53}\rho + \frac{c_{54}\rho}{\theta} + c_{55}, \frac{c_{62}\sigma}{\eta} + c_{63}\sigma + c_{66}\}$. Thus, under assumptions (A_1) and (A_2) and by the boundedness of solutions of system (2.1), there exists a positive constant ξ such that $\psi \leq -\xi < 0$ and thus

$W(Q(t)) \leq W(Q(s)) \exp(-\xi(t-s)), t \geq s > 0.$

This proves the equi-uniform asymptotic stability of the second compound system (6.5), and hence the positive equilibrium point E^* of system (2.1) is globally stable due to Proposition 6.1.

From above analysis, we now state the sufficient conditions for the global asymptotic stability of the positive equilibrium.

Theorem 6.1 *If the assumptions (A_1) and (A_2) are satisfied then system (2.1) has no non-trivial periodic solution. Furthermore, the positive equilibrium point E^* is globally stable in $\mathbb{R}^4_+$.*

7. Discussion

In natural environment, plants are attacked simultaneously by herbivorous insects and pathogen. Though recent research work mainly focused on either plant-pathogen or plant-insect interactions. In respond to multiple attack, plant emit VOCs that attract natural enemies of herbivores which is important in planning crop plants with better protection against herbivores. Recently, it is observed that rapid usage of pesticides and fertilizers cause major damage on farmland. So it is important to reduce the requirement for harmful pesticides for insect control. The role of VOCs in mediating tritrophic interactions under multiple attack situation is still unexplored. In this work, we have tried to investigate the dynamics of plant-herbivore system in the presence of pathogen through mathematical model. The model includes carnivores as an indirect defence against herbivores. In our model, we assumed that herbivore preferentially feeds on the susceptible plant. This induces that infected plant remains in the system due to less attack by herbivore. Many herbivorous insects avoid infected plant [18] and such preferences may allow infected plants to survive until killed by disease. We note that disease is more likely to persist when the herbivores consume susceptible plant only. Our model is described by the four ordinary differential equations. Then we studied the dynamical behavior of the system at various equilibrium points and the stability of those equilibrium points. We obtain five equilibrium points of which E_0 is the population free equilibrium point. The system cannot collapse for any parametric values as the population free equilibrium point is never stable. The planar equilibrium point E_{14} always exist which may be stable or unstable under certain restrictions on the system parameters. When the disease transmission rate exceeds a certain threshold value, herbivore free equilibrium point E_{124} appears and it becomes stable as long as herbivore consumption rate remains below a certain threshold value. The disease free equilibrium point E_{134} can be stable for low disease transmission rate. Coexistence has shown to be possible in the case disease affecting the plant population. Global stability aspect of the positive equilibrium is developed. From biological point of view, this study gives the condition, written in terms of the parameters of the system, under which the disease cannot be eliminated from the community. Here, we employed the geometric approach developed by Li and Muldowney to global stability for four dimensional system.

Conflict of Interests

The author declares that there is no conflict of interests.

REFERENCES

[1] G. Arimura, C. Kost, W. Boland, Herbivore-induced, indirect plant defences, Biochimica et Biophysica. Acta. 1734 (2005), 91-111.

[2] G. Birkhoff, G.C. Rota, Ordinary Differential Equation, Ginn and Co. Boston, 1982.

[3] J. G. de Boer, C. A. Hordijk, M. A. Posthumus, M. Dicke, Prey and non-prey arthropods sharing a host plant : effects on induced volatile emission and predator attraction, J. Chem. Ecol. 34 (2008), 281-290.

[4] G. J. Butler, H. I. Freedman and P. Waltman, Uniformly persistent systems. Proc. Amer. Math. Soc. 96 (1986), 425-430 .

[5] M. Dicke, Evolution of induced indirect defense of plants, In Tollrian R, Harvell C. D. eds. The ecology and evolution of inducible defenses. Princeton, NJ, USA : Princeton University Press, 1999, 62-88.

[6] M. Dicke, M. W. Sabelis, How plants obtain predatory mites as bodyguards, Neth. J. Zool. 38 (2) (1987), 148-165. (1988), 148-165.

[7] N. Dudareva, F. Negre, DA Nagegowda, I. Orlova, Plant volatiles : recent advances and future perspectives, Crit. Rev. Plant. Sci. 25 (2006), 417-440.

[8] P. Fergola , W. Wang, On the influences of defensive volatile of plants in tritrophic interactions, J. Biol. Syst. 19 (2011), 345-363.

[9] M. Fiedler, Additive compound matrices and inequality for eigenvalues of stochastic matricess. Czech. Math. J.99 (1974), 392-402.

[10] H. I. Freedman and P. Waltman, Persistence in models of three interacting predator-prey populations. Math. Biosci. 68 (1984), 213-231.

[11] Y. H. Liu, D. L. Liu, M. An, Y. L. Fu, R. S. Zeng, S. M. Luo, H. Wu, J.Pratley, Modelling tritrophic interactions mediated by induced defence volatiles, Eco. Mod. 220 (2009), 3241-3247.

[12] M. Y. Li and J. Muldowney, On Bendixson's criterion. J. Differ. Equ. 106 (1994), 27-39.

[13] A. Mithöfer , W. Boland, Recognition of herbivory-associated molecular patterns, Plant Phsiology, 146 (2008), 825-831.

[14] J. S. Muldowney, Compound matricess and ordinary differential equations. Rocky Mountain J. Math. 20 (1990), 857-871.

[15] P. W. Price, Insect Ecology : Behavior, Populations and Communities([4.ed]).ed.) Cambridge University Press, 2011.

[16] P. W. Price, C. E. Bouton, P. Gross, B. A. Mcpheron, J. N. Thompson, A. E. Weiss, Interaction among three trophic levels : Influence of plants on interactions between insect herbivores and natural enemies, Annu. Rev. Ecol. Syst. 11 (1980), 41-65.

[17] L. Schoonhoven, J. Van Loon, M. Dicke, Insect-Plant Biology, Oxford University Press. New York, 2005.

[18] M. J. Stout, J. S. Thaler, B.P.H.J. Thomma, Plant mediated interactions between pathogenic microorganisms and herbivorous arthropods, Annu. Rev. Entomol. 51 (2006), 663-689.

[19] R. N. Strange, P. R. Scott, Plant disease : a threat to global food security, Annual Review of Phytopathology. 43 (2005), 83-116.

[20] J. Takabayashi, M. Dicke, Plant-carnivore mutualism through herbivore-induced carnivore attractants, Trends Plant Sci. 1 (1996), 109-113.

[21] J. H. Tumilson, P. W. Pare, T. C. J. Turlings, Plant production of volatile semiochemicals in response to insect-derived elicitors, In Chadwick D. J, Goode J. A, eds. Insect-plant interactions and induced plant defence. Chichester, U.K : Wiley, 1999, 95-109.