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Delay induced oscillation in a nutrient-plant-herbivore system with plant toxicity*

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Abstract. In this paper, a delayed nutrient-plant-herbivore system with plant toxicity is investigated. In absence of delay, local stability of boundary and interior equilibrium points are discussed. Persistence criteria is derived. By considering the delay as bifurcation parameter, local stability and Hopf bifurcation of periodic solution are shown. Further, we also study the direction of Hopf bifurcations and stability of bifurcated periodic solutions by applying the normal form theory and center manifold theorem. From our numerical simulations, we observe that delay plays an important role on the dynamic behaviour of our system.

Keywords: plant toxicity, time delay, stability, Hopf bifurcation

1 Introduction

Plant-herbivore interactions have been investigated by many researchers using ordinary differential equations. Dynamical behaviour of such interaction is complex in nature. Mathematical models play a vital role to understand the complex dynamics of ecological systems. Herbivore's functional response has major impact on the dynamics. Holling type II functional response for mammalian herbivory did not include plant toxicity[4, 16, 18]. It is seen that herbivore growth rate is controlled by plant toxins[17]. To study the effect of toxicity in feeding rate, Feng et al.[7, 8], Li et al.[14] and Liu et al.[15] developed a toxin-determined functional response model (acronym TDFRM) by modifying traditional Holling type II response model (acronym H2FRM). The modified model includes the negative effect of toxin on herbivore growth.

The modified Holling type II response function is

$$C(X) = f(X)(1 - \frac{f(X)}{4G}), \tag{1}$$

where

$$f(X) = \frac{e\sigma X}{1 + he\sigma X}. \tag{2}$$

The term $f(X)$ is the conventional Holling type II functional response in which X is plant biomass density, e is the encounter rate of herbivores and plant biomass, h is the handling time per unit biomass, which incorporates the time required for the digestive tract to handle the item and σ is the fraction of encountered food items that are ingested, which control herbivore intake rate. The second factor in $C(X)$, which accounts the negative effect of toxin. The parameter G represents for the ratio M/T where M is the maximum amount of toxicant per unit time that the herbivore can tolerate and T is the amount of toxicant per unit of plant biomass. The factor 4 simplifies the peak value of $C(X)$ as a function of X.

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The difference in dynamical behaviour of using two different functional response is discussed in [15]. Traditional Holling type II response function in plant-herbivore system can generate Hopf bifurcation while toxin induced functional response function exhibit homoclinic bifurcation. A comparative study between TDFRM and H2FRM with field data from the Alaska Bonanza Creek Long-Term Ecological Research Project showed that TDFRM explains much better agreements than H2FRM [8].

Time delays are taken into population models for gestation period, maturing times or regeneration times[6, 10]. Discussion on importance and usefulness of time delays in realistic models may be found in [3, 5, 19–23]. In general, time delays are inevitable in population interactions and tend to destabilize the system. From our previous discussion it appears that the form of functional response is important for generating Hopf bifurcation. But other factor like delay can give rise to oscillation. So in this paper, our main attempt is to investigate the effect of delay in nutrient-plant-herbivore interaction in presence of plant toxin. The role of discrete time delay is not studied in [7, 8, 14, 15]. Further we have incorporated nutrient into the TDFRM to make it more realistic.

We now consider a system modelling of nutrient (N)-plant (X)-herbivore (Y) interactions. We take delay $\tau(>0)$ due to gestation. The model is described by

$$\begin{aligned}\frac{dN}{dt} =& I_n - r_n N - \frac{NX}{k_1+N},\\ \frac{dX}{dt} =& \frac{r_1 NX}{k_1+N} - C(X)Y - d_1 X,\\ \frac{dY}{dt} =& Y[-d_2 + mC(X(t-\tau))],\end{aligned} \tag{3}$$

with initial conditions given by $N(0) = N_0 \geq 0$, $Y(0) = Y_0 \geq 0$, $X(t) = X_0(t) \geq 0$ where $X_0(t)$ is a given continuous, non-negative function on $-\tau \leq t \leq 0$. $C(X)$ is defined by (1). Here I_n denotes input rate of nutrient. r_n is the output rate of nutrient. $d_i, i = 1, 2$ represent mortality rate of plant and herbivore respectively. k_1 is the half saturation constant. r_1 and m are the intake rate of plant and herbivore respectively. All the parameters are assumed to be positive.

The paper is structured as follows. In Section 2, we present dynamical behaviour of the system without delay. In presence of delay, stability of the positive equilibrium and the existence of Hopf bifurcation are derived in Section 3. The direction of Hopf bifurcation and the stability of bifurcated periodic solution are developed in Section 4. Numerical simulations are carried out to illustrate the analytical results obtained in Section 5.

2 Boundedness and dynamical behaviour when $\tau = 0$

In this section, we shall show that, all the solutions of system (3) are bounded in a positive orthant R^3_+. The boundedness of system (3) is given by the following lemma.

Lemma 1. *The set* $B = \{N, X, Y\} \in R^3_+ : 0 < W = r_1 N(t) + X(t) + \frac{1}{m}Y(t) \leq \frac{r_1 I_n}{\eta}\}$ *is a region of the attraction for all solutions initiating in the interior of the positive orthant, where* $0 < \eta < d$ *and* $d = \min(d_1, d_2, r_n)$.

Proof. Let $W(t) = r_1 N(t) + X(t) + \frac{1}{m}Y(t)$ and $\eta > 0$ be a constant. Then

$$\begin{aligned}\frac{dW}{dt} + \eta W =& r_1\frac{dN}{dt} + \frac{dX}{dt} + \frac{1}{m}\frac{dY}{dt} + \eta r_1 N + \eta X + \frac{\eta}{m}Y\\ =& r_1 I_n - (d_1-\eta)X - \frac{1}{m}(d_2-\eta)Y - r_1 N(r_n - \eta).\end{aligned} \tag{4}$$

Now choose η such that $0 < \eta < d$. Then (4) implies that $\frac{dW}{dt} + \eta W \leq r_1 I_n$. By using the differential inequality[1] we obtain

$$0 < W(N(t), X(t), y(t)) \leq \frac{r_1 I_n(1-e^{-\eta t})}{\eta} + (N(0), X(0), Y(0))e^{-\eta t}.$$

Taking limit when $t \to \infty$, we have, $0 < W(t) \leq \frac{r_1 I_n}{\eta}$, proving the lemma.

Evidently, system (3) has non-negative equilibrium $E_0 = (\frac{I_n}{r_n}, 0, 0)$ which exists for all parametric values, and we can show that if $\frac{r_1}{d_1} > \frac{I_n + r_n k_1}{I_n}$ then there exists a unique non-negative rest point, $E_1 = (\hat{N}, \hat{X}, 0)$ where $\hat{N} = \frac{d_1 k_1}{r_1 - d_1}$, $\hat{X} = \frac{r_1[I_n(r_1-d_1) - r_n d_1 k_1]}{d_1(r_1-d_1)}$. Now we first give stability result.

Theorem 1. *i) E_0 is unstable if E_1 is feasible. ii) E_1 is unstable or stable according as $mC(\hat{X}) >$ or $< d_2$.*

We state condition which guarantees the persistence of system (3).

Theorem 2. *If E_1 exists and $mC(\hat{X}) > d_2$ then system (3) 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 claim that $E_0 \notin \Omega(x)$.If $E_0 \in \Omega(x)$, then by Butler-McGehee lemma[9], 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 $N - Y$ plane, and hence orbits in the plane emanate from either E_0 or an unbounded orbits lies in $\Omega(x)$, which is a contradiction.

Next $E_1 \notin \Omega(x)$, for otherwise, since E_1 is a saddle point follows from the condition $mC(\hat{X}) > d_2$, by Butler-McGehee lemma, there exists a point p in $\Omega(x) \cap W^s(E_1)$ where $W^s(E_1)$ denotes the strong stable manifold of E_1. Since $o(p)$ lies in $\Omega(x)$ and $W^s(E_1)$is $N - X$ plane hence orbits in the plane emanate from E_0 or unbounded orbits lies in $\Omega(x)$ a contradiction.

There does not exist any equilibrium point in the $X - Y$ and $N - Y$ plane. The orbits in this plane are unbounded so $W^s(\Omega(X-Y)) \cap \Omega(x) = \phi$ and $W^s(\Omega(N-Y)) \cap \Omega(x) = \phi$. Thus, $\Omega(x)$ does not intersect any of the coordinate planes and hence system (3) is persistent. Since (3) is bounded, by main theorem in [2], this implies that the system is uniformly persistent.

In this section, we proved that system (3) exhibits uniform persistence provided that the conditions in Theorem 2 are satisfied. Further, it is proved in uniform persistence implies the existence of an interior equilibrium point [13]. Hence $E_2 = (N^*, X^*, Y^*)$ exists; that is, in effect Theorem 2 implies that E_2 exists.

Theorem 3. *Suppose all the conditions of Theorem 2 be satisfied. Then E_2 is locally asymptotically stable provided the following conditions are satisfied :*
$a_i > 0, i = 1, 2, 3$ and $a_1 a_2 - a_3 > 0$ where

$$\begin{aligned}
a_1 &= r_n + \frac{k_1 X^*}{(k_1+N^*)^2} + (C'(X^*) - \frac{C(X^*)}{X^*})Y^*, \\
a_2 &= \{r_n + \frac{k_1 X^*}{(k_1+N^*)^2}\}\{(C'(X^*) - \frac{C(X^*)}{X^*})Y^*\} + mY^*C(X^*)C'(X^*) + \frac{X^* r_1 k_1}{(k_1+N^*)^3}, \\
a_3 &= \{r_n + \frac{k_1 X^*}{(k_1+N^*)^2}\} mY^*C(X^*)C'(X^*).
\end{aligned}$$

Proof. The characteristic equation about E_2 is given by $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$. The result follows by the application of Routh-Hurwitz criterion.

3 Stability of positive equilibrium and Hopf bifurcation when $\tau \neq 0$

In presence of delay, we discuss stability of positive equilibrium point E_2 and Hopf bifurcation. The linearization of Eq. (3) around E_2 is

$$\frac{dW}{dt} = -(r_n + \frac{k_1 X^*}{(k_1+N^*)^2})U(t) - \frac{N^*}{k_1+N^*}V(t),$$
$$\frac{dV}{dt} = \frac{k_1 X^* r_1}{(k_1+N^*)^2}U(t) - (C'(X^*) - \frac{C(X^*)}{X^*})Y^*V(t) - C(X^*)W(t), \tag{5}$$
$$\frac{dW}{dt} = mY^*C'(X^*)W(t).$$

The characteristic equation about E_2 is given by

$$\begin{vmatrix} -a_{11}-\lambda & -a_{12} & -0 \\ a_{21} & -a_{22}-\lambda & -a_{23} \\ 0 & a_{32}e^{-\lambda\tau} & -\lambda \end{vmatrix} = 0, \tag{6}$$

where
$a_{11} = r_n + \frac{k_1 X^*}{(k_1+N^*)^2}$, $a_{22} = (C^{'}(X^*) - \frac{C(X^*)}{X^*})Y^*$, $a_{12} = \frac{N^*}{k_1+N^*}$, $a_{21} = \frac{k_1X^*r_1}{(k_1+N^*)^2}$, $a_{23} = C(X^*)$, $a_{32} = mY^*C'(X^*)$. Eq. (6) can be written in the form

$$\lambda^3 + p_1\lambda^2 + p_2\lambda + (q_1\lambda + q_2)e^{-\lambda\tau} = 0, \tag{7}$$

where
$p_1 = a_{11} + a_{22}, p_2 = a_{12}a_{21} + a_{11}a_{22}, q_1 = a_{23}a_{32}, q_2 = a_{11}a_{23}a_{32}$. When $\tau = 0$, Eq. (7) reduces to

$$\lambda^3 + p_1\lambda^2 + (p_2 + q_1)\lambda + q_2 = 0. \tag{8}$$

By Routh-Hurwitz criterion, we know that all the roots of Eq. (8) have negative real parts, i.e., the positive equilibrium E_2 is locally asymptotically stable provided that the conditions:
$(H_1) : p_1 > 0$,
$(H_2) : p_2 + q_1 > 0$;
$(H_3) : p_1(p_2 + q_1) - q_2 > 0$ hold.
We now turn to investigation of the type of stability for system (3) at the positive equilibrium E_2. We shall state two lemmas.

Lemma 2. *For the polynomial equation* $z^3 + r_1z^2 + r_2z + r_3 = 0$*:*
(1) If $r_3 < 0$*,the equation has at least one positive root;*
(2) If $r_3 \geq 0$ *and* $\triangle = r_1^2 - 3r_2 \leq 0$*, the equation has no positive roots;*
(3) If $r_3 \geq 0$ *and* $\triangle = r_1^2 - 3r_2 > 0$*, the equation has positive roots if and only if* $z_1^* = \frac{-r_1+\sqrt{\triangle}}{3}$ *and* $h(z_1^*) \leq 0$ *where* $h(z) = z^3 + r_1z^2 + r_2z + r_3$

Lemma 3. *(i) The positive equilibrium* E_2 *of system (3) is absolutely stable if and only if the equilibrium* E_2 *of the corresponding ordinary differential equation (ODE) system is asymptotically and the characteristic Eq. (7) has no purely imaginary roots for any* $\tau > 0$*; (ii)The positive equilibrium* E_2 *of system (3) is conditionally stable if and only if all the roots of the characteristic Eq. (7) have negative real parts at* $\tau = 0$ *and there exist some positive values* τ *such that the characteristic Eq. (7) has a pair of purely imaginary roots* $\pm i\omega_0$*.*

Theorem 4. *For system (3), if the conditions* $(H_1), (H_2)$ *and* (H_3) *hold,the positive equilibrium* E_2 *of system (3) is conditionally stable.*

Proof. Assume that for some $\tau > 0, i\omega(\omega > 0)$ is a root of characteristic Eq. (7). Now substituting $i\omega(\omega > 0)$ in (7) and separating the real and imaginary parts, we obtain the system of transcendental equations

$$p_1\omega^2 = q_1\omega sin\omega\tau + q_2 cos\omega\tau, \tag{9}$$
$$\omega^3 - p_2\omega = q_1\omega cos\omega\tau - q_2 sin\omega\tau. \tag{10}$$

Squaring and adding we have

$$\omega^6 + P_1\omega^4 + P_2\omega^2 + P_3 = 0, \tag{11}$$

where $P_1 = p_1^2 - 2p_2, P_2 = p_2^2 - q_1^2$ and $P_3 = -q_2^2$. Clearly, $P_3 < 0$. By Lemma 2, there is at least one positive ω_0 satisfying (11) i.e. the characteristic Eq. (7) has a pair of of imaginary roots of the form $\pm i\omega_0$. From Eqs. (9) and (10), we can get the corresponding $\tau_k > 0$ such that the characteristic Eq. (7) has a pair of purely imaginary roots

$$\tau_k = \frac{1}{\omega_0} arccos[\frac{\omega_0^2(q_1(\omega_0^2 - p_2) + p_1q_2)}{q_2^2 + q_1^2\omega_0^2}] + \frac{2k\pi}{\omega_0}, k = 0, 1, 2, \cdots \tag{12}$$

We know that under conditions of $(H_1), (H_2)$ and (H_3) all the roots of the characteristic Eq. (7) have negative real parts when $\tau = 0$. By Lemma 3,positive equilibrium E_2 of system (3) is conditionally stable. This completes the proof.

Theorem 5. *Assume that $2p_2 < p_1^2$. If E_2 exists then system (3) undergoes Hopf bifurcation at the positive equilibrium E_2 when $\tau = \tau_k$.*

Proof. Let $\lambda(\tau) = u + i\omega(\tau)$ be a root of the characteristic Eq. (7). Separating the real and imaginary parts of transcendental Eq. (7) we have

$$\begin{aligned} H_1(u, \omega, \tau) = 0, \\ H_2(u, \omega, \tau) = 0, \end{aligned} \tag{13}$$

where

$$\begin{aligned} H_1(u, \omega, \tau) =& u^3 - 3u\omega^2 + p_1(u^2 - \omega^2) + p_2u + (q_1u + q_2)e^{-u\tau}cos\omega\tau + q_1\omega e^{-u\tau}sin\omega\tau, \\ H_2(u, \omega, \tau) =& -\omega^3 + 3u^2\omega + 2p_1\omega u + p_2\omega + q_1\omega e^{-u\tau}cos\omega\tau - (q_1u + q_2)e^{-u\tau}sin\omega\tau. \end{aligned}$$

By Theorem 4, we have $H_1(0, \omega, \tau) = H_2(0, \omega, \tau) = 0$. To check that the Jacobian matrix

$$J = \begin{pmatrix} \frac{\partial H_1}{\partial u} & \frac{\partial H_1}{\partial \omega} \\ \frac{\partial H_2}{\partial u} & \frac{\partial H_2}{\partial \omega} \end{pmatrix}$$

satisfies $|J|_{(0,\omega_0,\tau_k)} > 0$. By means of the implicit function theorem, we deduce that Eq. (13) define u, ω as functions of τ in a neighbourhood of $(0, \omega_0, \tau_k)$ such that $u(\tau_k) = 0$ and $\omega(\tau_k) = 0$. We now investigate how the real part of the root of characteristic Eq. (7) varies as τ varies in a small neighbourhood of τ_k. Next, we turn to show

$$\frac{d(Re\lambda)}{d\tau}|_{\tau=\tau_k} \neq 0.$$

This will ensure that there exists at least one eigenvalue with positive real part for $\tau > \tau_k$. Differentiating the transcendental Eq. (7) with respect to τ, we get

$$(3\lambda^2 + 2p_1\lambda + p_2 + q_1e^{-\lambda\tau})\frac{d\lambda}{d\tau} + (q_1\lambda + q_2)(-\tau e^{-\lambda\tau}\frac{d\lambda}{d\tau} - \lambda e^{-\lambda\tau}).$$

Thus

$$\begin{aligned} (\frac{d\lambda}{d\tau})^{-1} =& \frac{3\lambda^2 + 2p_1\lambda + p_2}{\lambda e^{-\lambda\tau}(q_1\lambda + q_2)} + \frac{q_1}{\lambda(q_1\lambda + q_2)} - \frac{\tau}{\lambda} \\ =& \frac{3\lambda^2 + 2p_1\lambda + p_2}{-\lambda(\lambda^3 + p_1\lambda^2 + p_2\lambda)} + \frac{q_1}{\lambda(q_1\lambda + q_2)} - \frac{\tau}{\lambda}. \end{aligned}$$

Then

$$\begin{aligned} sgn\Big[\frac{d(Re\lambda)}{d\tau}\Big]_{\tau=\tau_k} &= sgn\Big[Re(\frac{d\lambda}{d\tau})^{-1}\Big]_{\lambda=i\omega_0} \\ &= sgnRe\Big[\frac{(p_2-3\omega_0^2)+2p_1\omega_0 i}{\omega_0^4-p_2\omega_0^2-p_1\omega_0^3 i}+\frac{q_1}{(-q_1\omega_0^2+q_2\omega_0 i)}-\frac{\tau}{i\omega_0}\Big]. \\ &= sgn\Big[\frac{(p_2-3\omega_0^2)(\omega_0^4-p_2\omega_0^2)-2p_1^2\omega_0^4}{(\omega_0^4-p_2\omega_0^2)^2+p_1^2\omega_0^6}-\frac{q_1^2\omega_0^2}{q_1^2\omega_0^4+q_2^2\omega_0^2}\Big] \\ &= sgn\Big[\frac{-3\omega_0^4+2(2p_2-p_1^2)-p_2^2}{\omega_0^2(\omega_0^2-a_2)^2+p_1^2\omega_0^4}-\frac{q_1^2}{q_1^2\omega_0^2+q_2^2}\Big]. \end{aligned}$$

As $2p_2 < p_1^2$, we have

$$\frac{d(Re\lambda)}{d\tau}|_{\tau=\tau_k} \neq 0$$

4 Stability of bifurcated periodic solutions

In the previous section, we have obtained the conditions under which a family of periodic solutions bifurcate from the positive equilibrium of system (3) when delay crosses through the critical value τ_k.

In this section, we shall study the direction of Hopf bifurcations and stability of bifurcated periodic solutions arising through Hopf bifurcation by applying the normal form theory and center manifold theorem introduced by [11].

Let $u_1 = U(\tau t), u_2 = V(\tau t), u_3 = W(\tau t), \tau = \tau_k + \mu$. where τ_k is defined by (12),$\mu \in R$, then system (3) can be transformed as in FDE in $C = C([-1, 0], \Re^3)$

$$u'(t) = L_\mu(u_t) + H(\mu, u_t), \tag{14}$$

where $u(t) = (u_1, u_2, u_3)^T \in \Re^3$ and $L_\mu : C \to \Re, H : \Re \times C \to \Re$ are given by

$$L_\mu(\phi) = (\tau_k+\mu)\begin{pmatrix} -a_{11} & -a_{12} & 0 \\ a_{21} & -a_{22} & -a_{23} \\ 0 & 0 & 0 \end{pmatrix}\begin{pmatrix} \phi_1(0) \\ \phi_2(0) \\ \phi_3(0) \end{pmatrix} + (\tau_k+\mu)\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & a_{32} & 0 \end{pmatrix}\begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \\ \phi_3(-1) \end{pmatrix} \tag{15}$$

and

$$H(\mu, \phi) = (\tau_k+\mu)\begin{pmatrix} -\frac{\phi_1(0)\phi_2(0)}{k_1+\phi_1(0)} \\ -\frac{r_1\phi_1(0)\phi_2(0)}{k_1+\phi_1(0)} - C(\phi_2(0))\phi_3(0) \\ mC(\phi_2(-1))\phi_3(0) \end{pmatrix}.$$

By the Riesz representation theorem,there exists a matrix whose components are bounded variation functions $\eta(\theta, \mu)$ in [-1,0] such that

$$L_\mu\phi = \int_{-1}^{0} d\eta(\theta, \mu)\phi(\theta), \phi \in C([-1, 0], \Re^3). \tag{16}$$

In fact, we choose

$$\eta(0, \mu) = (\tau_k+\mu)\begin{pmatrix} -a_{11} & -a_{12} & 0 \\ a_{21} & -a_{22} & -a_{23} \\ 0 & 0 & 0 \end{pmatrix}\delta(\theta) - (\tau_k+\mu)\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & a_{32} & 0 \end{pmatrix}\delta(\theta+1), \tag{17}$$

where δ is the Dirac delta function defined by

$$\delta(\theta) = \begin{cases} 0 & ,\theta = 0 \\ 1 & ,\theta \neq 0 \end{cases}. \tag{18}$$

For $\phi \in C^1([-1,0], \Re^3)$, define

$$A(\mu)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta} & , -1 \le \theta < 0 \\ \int_{-1}^{0} d\eta(\mu, s)\phi(s) & , \theta = 0 \end{cases} \tag{19}$$

and

$$R(\mu)\phi = \begin{cases} 0 & , -1 \le \theta < 0 \\ H(\mu, \phi) & , \theta = 0 \end{cases} . \tag{20}$$

Then system (14) can be transformed into a operator differential equation of the form

$$u'(t) = A(\mu)u_t + R(\mu)u_t, \tag{21}$$

where $u(t) = u(t+\theta), \theta \in [-1, 0]$. The adjoint operator A^* of A is defined by

$$A^*(\mu)\psi = \begin{cases} -\frac{d\psi(s)}{ds}, & 0 < s \le 1 \\ \int_{-1}^{0} \psi(-t)d\eta(0,t), & s = 0 \end{cases}$$

associated with a bilinear form

$$< \psi(s), \phi(s) >= \overline{\psi(0)}\phi(0) - \int_{\theta=1}^{0}\int_{\xi=0}^{\theta} \bar{\psi}^T(\xi-\theta)d\eta(\theta)\phi(\xi)d\xi, \tag{22}$$

where $\eta(\theta) = \eta(\theta, 0)$, we know that $\pm i\tau_k\omega_0$ are eigenvalues of $A(0)$. Thus they are also eigenvalues of $A*$ belonging to the eigenvalue $-i\omega_0$.

Suppose that $q(\theta) = (1, \alpha, \beta)^T e^{i\theta\omega_0\tau_k}$ is the eigenvector of $A(0)$ corresponding to $i\tau_k\omega_0$.Then $A(0)q(\theta) = i\omega_0\tau_k q(\theta)$.It follows from the definition of $A(0)$ and (14),(16) and (17) that

$$\tau_k \begin{pmatrix} i\omega_0 + a_{11} & a_{12} & 0 \\ -a_{21} & i\omega_0 + a_{22} & a_{23} \\ 0 & -a_{32}e^{-i\omega_0\tau_k} & i\omega_0 \end{pmatrix} \begin{pmatrix} 1 \\ \alpha \\ \beta \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}.$$

So we have

$$\alpha = -\frac{i\omega_0 + a_{11}}{a_{12}}, \beta = \frac{a_{32}e^{-i\omega_0\tau_k}}{i\omega_0}.$$

Similarly, assume that the eigenvector $q*$ of $A*$ is

$$q*(s) = D(1, \alpha^*, \beta^*)e^{is\omega_0\tau_k}, 0 \le s < 1.$$

Then we obtain

$$A * q * (0) = -i\tau_k\omega_0 q * (0),$$

i.e.

$$\tau_k \begin{pmatrix} -i\omega_0 + a_{11} & -a_{21} & 0 \\ a_{12} & -i\omega_0 + a_{22} & -a_{32}e^{i\omega_0\tau_k} \\ 0 & a_{23} & -i\omega_0 \end{pmatrix} \begin{pmatrix} 1 \\ \alpha^* \\ \beta^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}.$$

Hence, we obtain $\alpha* = \frac{-i\omega_0 + a_{11}}{a_{21}}$, $\beta* = \frac{(-i\omega_0 + a_{11})a_{23}}{i\omega_0}$. By $< q^*, q >= 1$, we can get D, that is

$$\begin{aligned} < q*, q > &= \bar{D}(1, \bar{\alpha}^*, \bar{\beta}^*)(1, \alpha, \beta)^T - \int_{\theta=-1}^{0}\int_{\xi=0}^{\theta} \bar{D}(1, \bar{\alpha}*, \bar{\beta}*)e^{-i\omega_0\tau_k(\xi-\theta)}d\eta(\theta)(1, \alpha, \beta)^T e^{-i\omega_0\tau_k}d\xi \\ &= \bar{D}[1 + \alpha\bar{\alpha}^* + \beta\bar{\beta}^* - \int_{-1}^{0}(1, \bar{\alpha}*, \bar{\beta}*)\theta e^{i\omega_0\theta\tau_k}d\eta(\theta)(1, \alpha, \beta)^T] \\ &= \bar{D}[1 + \alpha\bar{\alpha}^* + \beta\bar{\beta}^* + a_{32}\tau_k\bar{\beta} * \alpha e^{-i\omega_0\tau_k}]. \end{aligned}$$

Hence, we have

$$\bar{D} = \frac{1}{1 + \alpha\bar{\alpha}^* + \beta\bar{\beta}^* + a_{32}\tau_k\bar{\beta} * \alpha e^{-i\omega_0\tau_k}}$$
$$D = \frac{1}{1 + \bar{\alpha}^*\alpha + \bar{\beta}^*\beta + a_{32}\tau_k\bar{\beta} * \alpha e^{i\omega_0\tau_k}}$$

Let u_t be the solution of Eq. (14) when $\mu = 0$ and define $z(t) =< q*, u_t >$,

$$W(t,\theta) = u_t(\theta) - z(t)q(\theta) - \overline{z(t)}q*(\theta) = u_t(\theta) - 2Re\{z(t)q(\theta)\} \tag{23}$$

On the center manifold C_0 we have

$$W(t,\theta) = W(z(t), \overline{z(t)}, \theta),$$

where

$$W(t,\theta) = W(z(t), \overline{z(t)}, \theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}\frac{\bar{z}^2}{2} + \cdots. \tag{24}$$

In fact, $z(t), \overline{z(t)}$ are local coordinates of center manifold C_0 in the direction of q and $q*$, respectively. For the solution $u_t \in C_0$ of (21), since $\mu = 0$, we know that $< \psi, A\phi >=< A * \psi, \phi >$ for $(\phi, \psi) \in D(A) \times D(A)$, then $z'(t) =< q*, u'(t) >=< q^*, Au_t + Ru_t >=< q^*, Au_t > + < q^*, Ru_t >= \tau_k\omega_0 zi + \bar{q} * (0)H_0$. So

$$z'(t) = \tau_k\omega_0 zi + \bar{q} * (0)H_0, \tag{25}$$

that is

$$z'(t) = \tau_k\omega_0 zi + g(z,\bar{z}) + \cdots, \tag{26}$$

where

$$g(z,\bar{z}) = \frac{1}{2}g_{20}z^2 + g_{11}z\bar{z} + \frac{1}{2}g_{02}\bar{z}^2 + \frac{1}{2}g_{21}z^2\bar{z} + \cdots. \tag{27}$$

From (21), we have

$$W' = u_t - z'q - \bar{z}'\bar{q} = \begin{cases} AW - 2Re[\overline{q} * (0)H_0 q(\theta)], & -1 \le \theta < 0 \\ AW - 2Re[\overline{q} * (0)H_0 q(\theta)] + H_0, & \theta = 0. \end{cases} \tag{28}$$

Let $W' = AW + G(z, \overline{z}, \theta)$, where

$$G(z,\overline{z},\theta) = G_{20}\frac{z^2}{2} + G_{11}z\overline{z} + G_{02}\frac{\overline{z}^2}{2} + \cdots. \tag{29}$$

Differentiating both sides of (24) with respect to t, we have

$$W' = W_z z' + W_{\overline{z}}\overline{z}'.$$

Then, together with (28) and (29), we get

$$(A - 2i\tau_k\omega_0)W_{20}(\theta) = -G_{20}(\theta), \tag{30}$$
$$AW_{11}(\theta) = -G_{11}(\theta). \tag{31}$$

According to (25) and (27), we have

$$g(z,\bar{z}) = \overline{q} * (0)H_0(z,\overline{z}) = \frac{1}{2}g_{20}z^2 + g_{11}z\bar{z} + \frac{1}{2}g_{02}\bar{z}^2 + \frac{1}{2}g_{21}z^2\bar{z} + \cdots, \tag{32}$$

and so

$$u_t(\theta) = (u_{1t}(\theta), u_{2t}(\theta), u_{3t}(\theta)) = W(t,\theta) + zq + \bar{z}\bar{q},$$

where

$$u_t(t+\theta) = W^{(i)}(t,\theta) + zq^{(i)} + \bar{z}\bar{q}^{(i)} \ (i=1,2,3).$$

We have $u_t(\theta) = (u_{1t}(\theta), u_{2t}(\theta), u_{3t}(\theta))$ and $q(\theta) = (1,\alpha,\beta)^T e^{i\theta\omega_0\tau_k}$, so from (23) and (24) it follows that

$$\begin{aligned} u_t(\theta) =& W(t,\theta) + 2Re\{z(t)q(t)\} \\ =& W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + (1,\alpha,\beta)^T e^{i\omega_0\tau_k} z \\ &+ (1,\bar{\alpha},\bar{\beta})^T e^{-i\omega_0\tau_k}\bar{z} + \cdots, \end{aligned} \tag{33}$$

and then we have

$$\begin{aligned} u_{1t}(0) =& z + \bar{z} + W_{20}^{(1)}(0)\frac{z^2}{2} + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2} + \cdots, \\ u_{2t}(0) =& \alpha z + \bar{\alpha}\bar{z} + W_{20}^{(2)}(0)\frac{z^2}{2} + W_{11}^{(2)}(0)z\bar{z} + W_{02}^{(2)}(0)\frac{\bar{z}^2}{2} + \cdots, \\ u_{3t}(0) =& \beta z + \bar{\beta}\bar{z} + W_{20}^{(3)}(0)\frac{z^2}{3} + W_{11}^{(3)}(0)z\bar{z} + W_{02}^{(3)}(0)\frac{\bar{z}^2}{2} + \cdots, \\ u_{1t}(-1) =& ze^{-\omega_0\tau_k} + \bar{z}e^{i\omega_0\tau_k} + W_{20}^{(1)}(-1)\frac{z^2}{2} + W_{11}^{(1)}(-1)z\bar{z} + W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2} + \cdots, \\ u_{2t}(-1) =& \alpha ze^{-i\omega_0\tau_k} + \bar{\alpha}\bar{z}e^{i\omega_0\tau_k} + W_{20}^{(2)}(-1)\frac{z^2}{2} + W_{11}^{(2)}(-1)z\bar{z} + W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2} + \cdots, \\ u_{3t}(-1) =& \beta ze^{-i\omega_0\tau_k} + \bar{\beta}\bar{z}e^{i\omega_0\tau_k} + W_{20}^{(3)}(-1)\frac{z^2}{3} + W_{11}^{(3)}(-1)z\bar{z} + W_{02}^{(3)}(-1)\frac{\bar{z}^2}{2} + \cdots, \end{aligned} \tag{34}$$

According to (15), we have

$$\begin{aligned} g(z,\bar{z}) =& \bar{q}*(0)H_0(z,\bar{z}) = \bar{q}*(0)H_0(0,u_t) \\ =& \tau_k\bar{D}(1,\bar{\alpha}*,\bar{\beta}*)\begin{pmatrix} -\frac{u_{1t}(0)u_{2t}(0)}{k_1+u_{1t}(0)} \\ -\frac{r_1u_{1t}(0)u_{2t}(0)}{k_1+u_{1t}(0)} - C(u_{2t}(0))u_{3t}(0) \\ mC(u_{2t}(-1))u_{3t}(0) \end{pmatrix} \\ =& \frac{z^2}{2}[2\tau_k\bar{D}\{\frac{\alpha}{k_1}(\bar{\alpha}*r_1-1) - \bar{\alpha}*C'(0)\alpha\beta + \bar{\beta}*mC'(0)\alpha\beta e^{-i\omega_0\tau_k}\}] \\ &+ z\bar{z}[2\tau_k\bar{D}\{(\bar{\alpha}*r_1-1)\frac{(\alpha+\bar{\alpha})}{k_1} - \bar{\alpha}*C'(0)(\alpha\bar{\beta}+\bar{\alpha}\beta) + \bar{\beta}*mC'(0)(\alpha\bar{\beta}e^{-i\omega_0\tau_k} + \beta\bar{\alpha}e^{i\omega_0\tau_k}\}] \\ &+ \frac{\bar{z}^2}{2}[2\tau_k\bar{D}\{(\bar{\alpha}*r_1-1)\frac{\bar{\alpha}}{k_1} - \alpha*C'(0)\bar{\alpha}\bar{\beta} + \bar{\beta}*mC'(0)\bar{\alpha}\bar{\beta}e^{i\omega_0\tau_k}\}] \\ &+ \frac{z^2\bar{z}}{2}[2\tau_k\bar{D}\{\frac{1}{k_1}(\bar{\alpha}*r_1-1)(\frac{\bar{\alpha}W_{20}^{(1)}(0)}{2} + \alpha W_{11}^{(1)}(0) + \frac{W_{20}^2(0)}{2} + W_{11}^2(0)) \\ &- \bar{\alpha}*C'(0)(\bar{\beta}W_{20}^{(2)}(0) + \beta W_{11}^{(2)}(0)) + \frac{\bar{\alpha}W_{20}^{(3)}(0)}{2} + \alpha W_{11}^3(0)) + \bar{\beta}*mC'(0)(\bar{\alpha}W_{20}^3(0)e^{i\omega_0\tau_k} \\ &+ \alpha W_{11}^{(3)}(0)e^{-i\omega_0\tau_k} + \frac{\bar{\beta}W_{20}^{(2)}(-1)}{2} + \beta W_{11}^{(2)}(-1)\}] \end{aligned}$$

Comparing the coefficients with (32), we have

$g_{20} = 2\tau_k\bar{D}\{\frac{\alpha}{k_1}(\bar{\alpha}^*r_1-1) - \bar{\alpha}^*C'(0)\alpha\beta + \bar{\beta}^*mC'(0)\alpha\beta e^{-i\omega_0\tau_k}\}$

$g_{11} = 2\tau_k\bar{D}\{(\bar{\alpha}^*r_1-1)\frac{(\alpha+\bar{\alpha})}{k_1} - \bar{\alpha}^*C'(0)(\alpha\bar{\beta}+\bar{\alpha}\beta) + \bar{\beta}^*mC'(0)(\alpha\bar{\beta}e^{-i\omega_0\tau_k} + \beta\bar{\alpha}e^{i\omega_0\tau_k}\}$

$g_{02} = 2\tau_k\bar{D}\{(\bar{\alpha}^*r_1-1)\frac{\bar{\alpha}}{k_1} - \alpha^*C'(0)\bar{\alpha}\bar{\beta} + \bar{\beta}^*mC'(0)\bar{\alpha}\bar{\beta}e^{i\omega_0\tau_k}\}$

$g_{21} = 2\tau_k\bar{D}\{\frac{1}{k_1}(\bar{\alpha}^*r_1-1)(\frac{\bar{\alpha}W_{20}^{(1)}(0)}{2} + \alpha W_{11}^{(1)}(0) + \frac{W_{20}^2(0)}{2} + W_{11}^2(0)) - \bar{\alpha}^*C'(0)(\bar{\beta}W_{20}^{(2)}(0) + \beta W_{11}^{(2)}(0))$
$+ \frac{\bar{\alpha}W_{20}^{(3)}(0)}{2} + \alpha W_{11}^3(0)) + \bar{\beta}^*mC'(0)(\bar{\alpha}W_{20}^3(0)e^{i\omega_0\tau_k}) + \alpha W_{11}^{(3)}(0)e^{-i\omega_0\tau_k} + \frac{\bar{\beta}W_{20}^{(2)}(-1)}{2} + \beta W_{11}^{(2)}(-1)\}.$

Since there are $W_{20}(\theta)$ and $W_{11}(\theta)$ in g_{21}, we still require to compute them. From (28), we can get

$$G(z,\bar{z},\theta) = -\bar{q}^*(0)H_0q(\theta) - q^*(0)\bar{H}_0\bar{Q}(\theta) = -g(z,\bar{z})q(\theta) - \bar{g}(z,\bar{z})\bar{q}(\theta), -1 \le \theta < 0.$$

Comparing the coefficients with (27), we can obtain that

$$G_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta), \tag{35}$$
$$G_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta). \tag{36}$$

Substituting (30) into 35), it follows that

$$W'_{20}(\theta) = 2i\tau_k\omega_0 W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta) \tag{37}$$

It is easy to see that the solution of (37) is

$$W_{20}(\theta) = \frac{ig_{20}q(0)e^{i\tau_k\omega_0\theta}}{\tau_k\omega_0} - \frac{i\bar{g}_{02}\bar{q}(0)e^{-i\tau_k\omega_0\theta}}{3i\tau_k\omega_0} + E_1e^{2i\tau_k\omega_0\theta}.$$

Similarly, we have

$$W_{11}(\theta) = \frac{ig_{11}q(0)e^{i\tau_k\omega_0\theta}}{\tau_k\omega_0} - \frac{i\bar{g}_{11}\bar{q}(0)e^{-i\tau_k\omega_0\theta}}{i\tau_k\omega_0} + E_2e^{2i\tau_k\omega_0\theta},$$

where

$$E_1 = (E_1^{(1)}, E_1^{(2)}, E_1^{(3)}), E_2 = (E_2^{(1)}, E_2^{(2)}, E_2^{(3)}).$$

Next we focus on the computation of E_1, E_2. From (30) and (31) we have

$$\int_{-1}^{0} d\eta(\theta)W_{20}(\theta) = 2i\tau_k\omega_0 W_{20}(\theta) - G_{20}(\theta), \tag{38}$$
$$\int_{-1}^{0} d\eta(\theta)W_{11}(\theta) = -G_{11}(\theta). \tag{39}$$

and

$$G_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + 2\tau_k \begin{pmatrix} \frac{1}{k_1}(\bar{\alpha}^*r_1 - 1) \\ -C'(0)\alpha\beta \\ mC'(0)\alpha\beta e^{-i\omega_0\tau_k} \end{pmatrix}, \tag{40}$$

$$G_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + 2\tau_k \begin{pmatrix} \frac{1}{k_1}(\bar{\alpha}r_1 - 1)(\alpha+\bar{\alpha}) \\ -C'(0)(\alpha\bar{\beta}+\bar{\alpha}\beta) \\ mC'(0)(\alpha\bar{\beta}e^{-i\omega_0\tau_k} + \beta\bar{\alpha}e^{-i\omega_0\tau_k}) \end{pmatrix}, \tag{41}$$

Substituting (40) and (41) into (38), then

$$(i\tau_k\omega_0 I - \int_{-1}^{0} e^{i\tau_k\omega_0\theta}d\eta(\theta))q(0) = 0, (-i\tau_k\omega_0 I - \int_{-1}^{0} e^{-i\tau_k\omega_0\theta}d\eta(\theta))\bar{q}(0) = 0.$$

We obtain

$$(2i\tau_k\omega_0 I - \textstyle\int_{-1}^{0} e^{i\tau_k\omega_0\theta}d\eta(\theta))E_1 = 2\tau_k \begin{pmatrix} \frac{1}{k_1}(\bar{\alpha}^*r_1 - 1) \\ -C'(0)\alpha\beta \\ mC'(0)\alpha\beta e^{-i\omega_0\tau_k} \end{pmatrix},$$

namely, $\begin{pmatrix} 2i\omega_0 + a_{11} & a_{12} & 0 \\ a_{21} & 2i\omega_0 + a_{22} & a_{23} \\ 0 & -a_{32}e^{-i\omega_0\tau_k} & 2i\omega_0 \end{pmatrix} E_1 = 2 \begin{pmatrix} \frac{1}{k_1}(\bar{\alpha}^*r_1 - 1) \\ -C'(0)\alpha\beta \\ mC'(0)\alpha\beta e^{-i\omega_0\tau_k} \end{pmatrix}$

So we obtain

$$E_1^{(1)} = \frac{2}{A}\begin{vmatrix} \frac{1}{k_1}(\bar{\alpha}^* r_1 - 1) & a_{12} & 0 \\ -C'(0)\alpha\beta & 2i\omega_0 + a_{22} & a_{23} \\ mC'(0)\alpha\beta e^{-i\omega_0\tau_k} & a_{32}e^{-i\omega_0\tau_k} & 2i\omega_0 \end{vmatrix},$$

$$E_1^{(2)} = \frac{2}{A}\begin{vmatrix} 2i\omega_0 + a_{11} & \frac{1}{k_1}(\bar{\alpha}^* r_1 - 1) & 0 \\ -a_{21} & -C'(0)\alpha\beta & a_{23} \\ 0 & mC'(0)\alpha\beta e^{-i\omega_0\tau_k} & 2i\omega_0 \end{vmatrix},$$

$$E_1^{(3)} = \frac{2}{A}\begin{vmatrix} 2i\omega_0 + a_{11} & a_{12} & \frac{1}{k_1}(\bar{\alpha}^* r_1 - 1) \\ -a_{21} & 2i\omega_0 + a_{22} & -C'(0)\alpha\beta \\ 0 & -a_{32}e^{-i\omega_0\tau_k} & mC'(0)\alpha\beta e^{-i\omega_0\tau_k} \end{vmatrix},$$

where

$$A = \begin{vmatrix} 2i\omega_0 + a_{11} & a_{12} & 0 \\ -a_{21} & 2i\omega_0 + a_{22} & a_{23} \\ 0 & -a_{32}e^{-i\omega_0\tau_k} & 2i\omega_0 \end{vmatrix},$$

Similarly

$$E_2^{(1)} = \frac{2}{B}\begin{vmatrix} \frac{1}{k_1}(\bar{\alpha} r_1 - 1)(\alpha + \bar{\alpha}) & a_{12} & 0 \\ -C'(0)(\alpha\bar{\beta}) + \bar{\alpha}\beta) & a_{22} & a_{23} \\ mC'(0)(\alpha\bar{\beta}e^{-i\omega_0\tau_k} + \bar{\alpha}\beta e^{i\omega_0\tau_k}) & -a_{32} & 0 \end{vmatrix},$$

$$E_2^{(2)} = \frac{2}{B}\begin{vmatrix} a_{11} & \frac{1}{k_1}(\bar{\alpha} r_1 - 1)(\alpha + \bar{\alpha}) & 0 \\ -a_{21} & -C'(0)(\alpha\bar{\beta} + \bar{\alpha}\beta) & a_{23} \\ 0 & mC'(0)(\alpha\bar{\beta}e^{-i\omega_0\tau_k} + \bar{\alpha}\beta e^{-i\omega_0\tau_k}) & 0 \end{vmatrix},$$

$$E_2^{(3)} = \frac{2}{B}\begin{vmatrix} a_{11} & a_{12} & \frac{1}{k_1}(\bar{\alpha} r_1 - 1)(\alpha + \bar{\alpha}) \\ -a_{21} & a_{22} & -C'(0)(\alpha\bar{\beta} + \bar{\alpha}\beta) \\ 0 & -a_{32} & mC'(0)(\alpha\bar{\beta}e^{-i\omega_0\tau_k} + \bar{\alpha}\beta e^{i\omega_0\tau_k}) \end{vmatrix},$$

where

$$B = \begin{vmatrix} a_{11} & a_{12} & 0 \\ -a_{21} & a_{22} & a_{23} \\ 0 & -a_{32} & 0 \end{vmatrix}.$$

Then, g_{21} can be determined by the parameters and delay. Therefore we can calculate the following quantities :
$C_1(0) = \frac{i}{2\tau_k\omega_0}(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}) + \frac{g_{21}}{2}$,
$\mu_2 = -\frac{Re\{C_1(0)\}}{Re\{\lambda'(\tau_k)\}}$ and $\beta_2 = 2Re\{C_1(0)\}$.

Theorem 6. *(i) μ_2 determines the directions of Hopf bifurcation.If $\mu_2 > 0 (< 0)$, then the Hopf bifurcation is supercritical (subcritical).*
(ii)β_2 determines the stability of bifurcated periodic solutions. If $\beta_2 < 0 (> 0)$, the bifurcated periodic solutions are stable (unstable).

5 Numerical simulations

We now illustrate our results through numerical simulations. The particular coefficients chosen do not necessarily have biological meaning or apply to specific populations. Numerical simulations are performed with the help of Matlab 7.0.1 software package for a hypothetical set of data. In toxin mediated nutrient-plant-herbivore system, predator response function generates Hopf bifurcation. Sometimes delay can give oscillation in a system. Keeping this mind,we have varied delay parameter to observe the dynamics of system (3). We select $I_n = 1.25, r_n = .75, k_1 = 1, r_1 = 1, d_1 = 1/6, m = 3/4, d_2 = 1/4, G = 4, h = 1, e = 1, \sigma = 1$. Our numerical results show that when $\tau = 0$, the system (3) converges to the point $E_2(1.661, .01021, .09492)$ (see Fig.1). After introduction of delay, the system (3) enter into an oscillatory steady state at $\tau = .01$, in Fig.2.

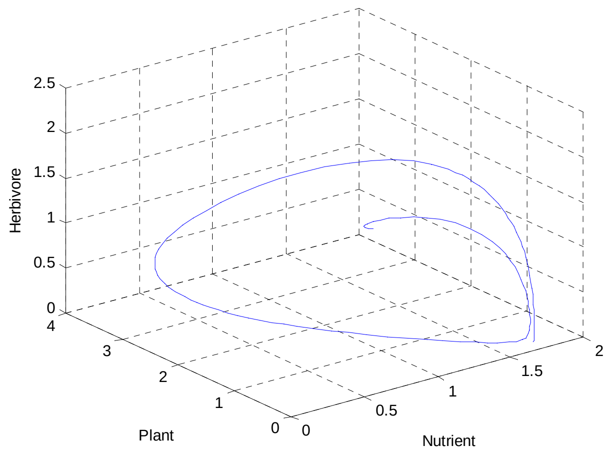

Fig. 1: Stable behaviour is observed in absence of delay

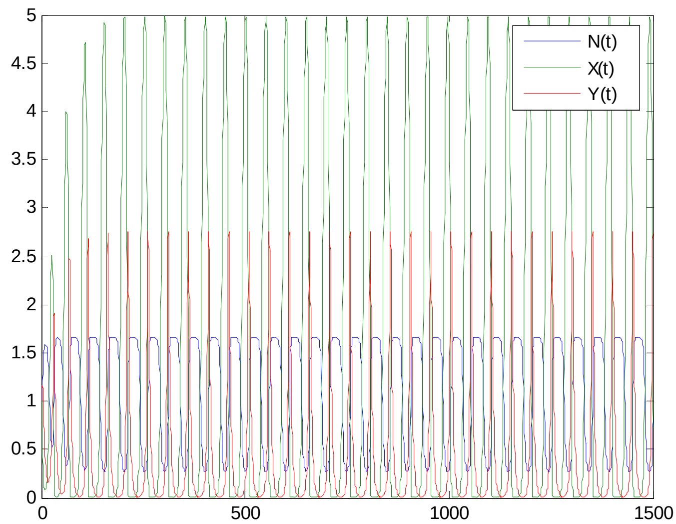

Fig. 2: Oscillatory behavior is observed when $\tau = .01$.

6 Discussion

In this paper, we investigate the dynamics of system (3), which models nutrient-plant-herbivore interactions with a functional response mediated by plant toxicity. This type of model is regarded as TDFRM. In this model ,Holling type II response is modified and the modification can be interpreted biologically[7, 14]. Delay is incorporated in the model for gestation period. The DDE system (3) is more general than those presented in Feng et al. articles. The main difference is that a nutrient is considered in the model and growth of the plant (in absence of herbivore) is described by a chemostat type system.

We first analyze the model in absence of delay. Conditions have been found that system (3) is persistent. Conditions stated in Theorem 2 for system persistence are the invasion conditions of the herbivore in (nutrient-plant) system at equilibrium. Invasion condition showed that herbivore growth rate must exceed its death rate.

We have derived sufficient conditions on the parameters for which the delay induced system maintains stability. By applying the normal form theory and the center manifold theorem, the explicit algorithm which guarantees the stability and the direction of the Hopf bifurcating periodic solutions have been developed.We observed from analytical and numerical simulation results that small amount of delay can change the stability of the positive equilibrium point. Presence of toxin in the functional response makes the model highly nonlinear with rich dynamics. In absence of delay, Liu et al.[15] conducted bifurcation analysis to explore the impact of plant toxicity and toxin-determined herbivore browsing on the plant-herbivore dynamics. But our study indicates that delay can destablize the system which was not addressed in earlier works.

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