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Hopf bifurcation analysis for a model of plant virus propagation with two delays

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Abstract

In this paper, we consider a model of plant virus propagation with two delays and Holling type II functional response. The stability of the positive equilibrium and the existence of Hopf bifurcation are analyzed by choosing τ_1 and τ_2 as bifurcation parameters, respectively. Using the center manifold theory and normal form method, we discuss conditions for determining the stability and the bifurcation direction of the bifurcating periodic solution. Finally, we carry out numerical simulations to illustrate the theoretical analysis.

Keywords: Delay differential equation; Virus propagation; Hopf bifurcation; Holling type II

1 Introduction

As we know, plants play a vital role in the everyday life of all organisms on earth. Sometimes, however, plants become infected with a virus, which can have a devastating effect on the ecosystem that depends on it. An insect-vector can cause the transmission of the virus from plant to plant. The propagation characteristics and epidemiology of plant viruses were studied in [1, 2]. In [3], the transmission pathways of plant viruses were analyzed in detail from the perspective of plants and media; the authors established a model of plant infections disease and analyzed the dynamics of the model.

Although there are many models that describe the interaction between vectors and humans, there are not as many that describe the relationship between plants and vectors. Recently, Jackson and Chen-Charpentier [4] have proposed a plant virus propagation model with the functional response Holling type II of the following form:

$$\begin{cases} \frac{dS}{dt} = \mu K + dI - \mu S - \frac{\beta Y}{1+\alpha Y}S, \\ \frac{dI}{dt} = \frac{\beta Y}{1+\alpha Y}S - (d+\mu+\gamma)I, \\ \frac{dR}{dt} = \gamma I - \mu R, \\ \frac{dX}{dt} = \Lambda - \frac{\beta_1 IX}{1+\alpha_1 I} - mX, \\ \frac{dY}{dt} = \frac{\beta_1 IX}{1+\alpha_1 I} - mY, \end{cases} \tag{1.1}$$

where $S(t), I(t), R(t), X(t)$, and $Y(t)$ denote the susceptible plants, infected plants, recovered plants, susceptible insect vectors, and infected insect vectors, respectively. The total number of plants will be denoted by the fixed positive constant K, $K = S + I + R$, and the total number of insects will be denoted by $N = X + Y$. The parameters $\beta, \beta_1, \alpha, \alpha_1, \mu, m, \gamma, \Lambda$, and d are positive real numbers; β is the infection rate of plants due to vectors, β_1 is the infection rate of vectors due to plants, α is the saturation constant of plants due to vectors, α_1 is the saturation constant of vectors due to plants, μ is the natural death rate of plants, m is the natural death rate of vectors, γ is the recovery rate of plants, Λ is the replenishing rate of vectors (birth and/or immigration), and d is the death rate of infected plants due to the disease.

In the model (1.1) the authors make the following assumptions [4]:

(1) The susceptible plants can be infected only by the infected insect vectors. This model does not consider that infection can be transmitted from plant to plant. The interaction between the insects and the plants is modeled using Holing type II since insects can only bite a limited number of plants.

(2) The total number of plants is denoted by the fixed positive constant K, because in one area, one can always keep the total number fixed by adding a new plant when a plant has died. The new plant shares the same characteristics of the plant it replaced before it was infected.

(3) The replenishment rate of insect vectors is a positive constant Λ, and all of the new born vectors are susceptible.

(4) A susceptible vector can be infected only by an infected plant host, and after it is infected, it will hold the virus for the rest of its life. Further, there is no vertical transmission of the virus, and vectors cannot transmit the virus to another vector.

Notice that adding $\frac{dX}{dt}$ and $\frac{dY}{dt}$ yields $\frac{dN}{dt} = \Lambda - mN$, where $N = X + Y$, and $N \longrightarrow \frac{\Lambda}{m}$ as $t \longrightarrow \infty$.

So equation (1.1) can be reduced to the following equations:

$$\begin{cases} \frac{dS}{dt} = \mu(K - S) - \frac{\beta Y}{1+\alpha Y} S + dI, \\ \frac{dI}{dt} = \frac{\beta Y}{1+\alpha Y} S - \omega I, \\ \frac{dY}{dt} = \frac{\beta_1 I}{1+\alpha_1 I}(\frac{\Lambda}{m} - Y) - mY, \end{cases} \tag{1.2}$$

where $\omega = d + \mu + \gamma$.

In [4], the authors analyzed the stability of equilibria with the basic reproduction number using the generation matrix approach. Considering time for the virus to enter the plant cells and to spread in the plant and time for the virus to infect the insect, the authors proposed the model with two discrete delays:

$$\begin{cases} \frac{dS}{dt} = \mu(K - S) - \frac{\beta Y(t-\tau_1)}{1+\alpha Y(t-\tau_1)} S(t - \tau_1) + dI, \\ \frac{dI}{dt} = \frac{\beta Y(t-\tau_1)}{1+\alpha Y(t-\tau_1)} S(t - \tau_1) - \omega I, \\ \frac{dY}{dt} = \frac{\beta_1 I(t-\tau_2)}{1+\alpha_1 I(t-\tau_2)}(\frac{\Lambda}{m} - Y(t - \tau_2)) - mY, \end{cases} \tag{1.3}$$

where τ_1 is the time it takes a plant to become infected after contagion, and τ_2 is the time it takes a vector to become infected after contagion.

Since the delay differential equations are extensively used in the practical life, it is very important to study the stability of differential equations with delays. Recently, a great deal of scholars have achieved very good research results in terms of multidelay differential equations [5–15].

In our paper, we continue the work of Jackson and Chen-Charpentier [4]. Viewing delays as bifurcation parameters, we discuss the stability of equilibrium and the existence of Hopf bifurcation of system (1.3) in four cases: (1) $\tau_1 = 0, \tau_2 = 0$; (2) $\tau_1 > 0, \tau_2 = 0$; (3) $\tau_1 = \tau_2 = \tau > 0$; (4) $\tau_1 \in (0, \tau_{10}), \tau_2 > 0, \tau_1 \neq \tau_2$. When $\tau_1 \neq \tau_2$, we study the properties of Hopf bifurcation by using the normal form theory and center manifold theorem.

This paper is organized as follows. In Sect. 2, we study the stability of positive equilibrium and the existence of local Hopf bifurcation of system (1.3). In Sect. 3, the direction and stability of Hopf bifurcation are determined by using normal form theory and central manifold theorem. Some numerical simulations are carried out to support our results in Sect. 4. Finally, a conclusion is given in Sect. 5.

2 Stability and existence of Hopf bifurcation

System (1.3) has a unique positive equilibrium $E(S^*, I^*, Y^*)$, provided that the following conditions are satisfied:

(H_1) $m\omega + K\mu(\beta_1 + \alpha_1 m) > dm$, $\alpha\beta_1 K\Lambda\mu + m(m\omega + K\mu(\beta_1 + \alpha_1 m) - dm) > 0$, $\beta_1\beta K\Lambda\mu > m^2\mu\omega$, $\alpha m\mu\omega + \beta(m\omega + K\mu(\beta_1 + \alpha_1 m) - dm) > 0$,

where

$$
\begin{aligned}
S^* &= \frac{\omega(\alpha\beta_1 K\Lambda\mu + m(m\omega + K\mu(\beta_1 + \alpha_1 m) - dm))}{\beta_1\beta\Lambda(\omega - d) + \alpha\beta_1\Lambda\mu\omega + \beta_1 m\mu\omega + \alpha_1 m^2\mu\omega}, \\
I^* &= \frac{\beta_1\beta K\Lambda\mu - m^2\mu\omega}{\beta_1\beta\Lambda(\omega - d) + \alpha\beta_1\Lambda\mu\omega + \beta_1 m\mu\omega + \alpha_1 m^2\mu\omega}, \\
Y^* &= \frac{\mu(\beta\beta_1 K\Lambda - \omega m^2)}{m(\alpha m\mu\omega + \beta(m\omega + K\mu(\beta_1 + \alpha_1 m) - dm))}.
\end{aligned}
$$

The linearized system of system (1.3) at $E(S^*, I^*, Y^*)$ is

$$
\begin{cases}
\frac{du_1(t)}{dt} = -\mu u_1(t) - A_0 u_1(t - \tau_1) + du_2(t) - B_0 u_3(t - \tau_1), \\
\frac{du_2(t)}{dt} = A_0 u_1(t - \tau_1) - \omega u_2(t) + B_0 u_3(t - \tau_1), \\
\frac{du_3(t)}{dt} = C_0 u_2(t - \tau_2) + D_0 u_3(t - \tau_2) - m u_3(t),
\end{cases}
\tag{2.1}
$$

where $A_0 = \frac{\beta Y^*}{1+\alpha Y^*}$, $B_0 = \frac{\beta S^*}{(1+\alpha Y^*)^2}$, $C_0 = \frac{\beta_1}{(1+\alpha_1 I^*)^2}(\frac{\Lambda}{m} - Y^*)$, and $D_0 = \frac{-\beta_1 I^*}{1+\alpha_1 I^*}$.

The characteristic equation of system (2.1) is

$$
\begin{aligned}
&\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 + \left(B_1\lambda^2 + B_2\lambda + B_3\right)e^{-\lambda\tau_1} \\
&\quad + \left(C_1\lambda^2 + C_2\lambda + C_3\right)e^{-\lambda\tau_2} + (D_1\lambda + D_2)e^{-\lambda(\tau_1+\tau_2)} = 0,
\end{aligned}
\tag{2.2}
$$

where

$$
\begin{aligned}
&A_1 = \mu + \omega + m, \qquad A_2 = \mu\omega + \mu m + m\omega, \qquad A_3 = \mu m\omega, \\
&B_1 = A_0, \qquad B_2 = A_0(\omega + m - d), \qquad B_3 = A_0 m(\omega - d), \\
&C_1 = -D_0, \qquad C_2 = D_0(-\mu - \omega), \qquad C_3 = -D_0\mu\omega, \\
&D_1 = -A_0 D_0 - B_0 C_0, \qquad D_2 = A_0 D_0 d - B_0 C_0\mu - A_0 D_0\omega.
\end{aligned}
$$

Next, we consider the following four cases.

Case (1): $\tau_1 = 0, \tau_2 = 0$.

The characteristic equation (2.2) becomes

$$\lambda^3 + (A_1 + B_1 + C_1)\lambda^2 + (A_2 + B_2 + C_2 + D_1)\lambda + (A_3 + B_3 + C_3 + D_2) = 0. \tag{2.3}$$

Let

(H_2) $A_1 + B_1 + C_1 > 0$, $A_3 + B_3 + C_3 + D_2 > 0$, $(A_1 + B_1 + C_1)(A_2 + B_2 + C_2 + D_1) - (A_3 + B_3 + C_3 + D_2) > 0$.

According to the Routh–Hurwitz criteria, if conditions (H_1) and (H_2) hold, then all the roots of (2.3) must have negative real parts. We have the following results.

Theorem 2.1 *Assume that* (H_1) *and* (H_2) *hold. If* $\tau_1 = \tau_2 = 0$, *then the positive equilibrium* $E(S^*, I^*, Y^*)$ *of system* (1.3) *is locally asymptotically stable.*

Case (2): $\tau_1 > 0, \tau_2 = 0$.

The characteristic equation (2.2) reduces to

$$\lambda^3 + (A_1 + C_1)\lambda^2 + (A_2 + C_2)\lambda + (A_3 + C_3) + \left[B_1\lambda^2 + (B_2 + D_1)\lambda + (B_3 + D_2)\right]e^{-\lambda\tau_1} = 0. \tag{2.4}$$

Let $\lambda = i\omega_1$ ($\omega_1 > 0$) be the root of equation (2.4). Then we have:

$$\begin{cases} (B_2 + D_1)\omega_1 \cos\omega_1\tau_1 + [B_1\omega_1^2 - (B_3 + D_2)] \sin\omega_1\tau_1 = \omega_1^3 - (A_2 + C_2)\omega_1, \\ (B_2 + D_1)\omega_1 \sin\omega_1\tau_1 - [B_1\omega_1^2 - (B_3 + D_2)] \cos\omega_1\tau_1 \\ \quad = (A_1 + C_1)\omega_1^2 - (A_3 + C_3). \end{cases} \tag{2.5}$$

It follows that

$$\omega_1^6 + E_{21}\omega_1^4 + E_{22}\omega_1^2 + E_{23} = 0, \tag{2.6}$$

where

$$\begin{aligned} E_{21} &= (A_1 + C_1)^2 - 2(A_2 + C_2) - B_1^2, \\ E_{22} &= (A_2 + C_2)^2 - 2(A_1 + C_1)(A_3 + C_3) + 2B_1(B_3 + D_2) - (B_2 + D_1)^2, \\ E_{23} &= (A_3 + C_3)^2 - (B_3 + D_2)^2. \end{aligned}$$

Let $r_1 = \omega_1^2$. Then equation (2.6) becomes

$$r_1^3 + E_{21}r_1^2 + E_{22}r_1 + E_{23} = 0. \tag{2.7}$$

Denote

$$h_1(r_1) = r_1^3 + E_{21}r_1^2 + E_{22}r_1 + E_{23}. \tag{2.8}$$

Thus

$$\frac{dh_1(r_1)}{dr_1} = 3r_1^2 + 2E_{21}r_1 + E_{22}.$$

If $E_{23} = (A_3 + C_3)^2 - (B_3 + D_2)^2 < 0$, then $h_1(0) < 0$ and $\lim_{r_1 \longrightarrow +\infty} h_1(r_1) = +\infty$. Equation (2.7) has at least one positive root.

If $E_{23} = (A_3 + C_3)^2 - (B_3 + D_2)^2 \geq 0$ and $\triangle_1 = E_{21}^2 - 3E_{22} \leq 0$, then equation (2.7) has no positive root for $r_1 \in [0, +\infty)$.

If $E_{23} = (A_3 + C_3)^2 - (B_3 + D_2)^2 \geq 0$ and $\triangle_1 = E_{21}^2 - 3E_{22} > 0$, then the equation

$$3r_1^2 + 2E_{21}r_1 + E_{22} = 0$$

has two real roots, $r_{11}^* = \frac{-E_{21}+\sqrt{\triangle_1}}{3}$ and $r_{12}^* = \frac{-E_{21}-\sqrt{\triangle_1}}{3}$. Because $h_1''(r_{11}^*) = 2\sqrt{\triangle_1} > 0$ and $h_1''(r_{12}^*) = -2\sqrt{\triangle_1} < 0$, equation (2.7) has at least one positive root if and only if $r_{11}^* = \frac{-E_{21}+\sqrt{\triangle_1}}{3} > 0$ and $h_1(r_{11}^*) \leq 0$, where r_{11}^* and r_{12}^* are the local minimum and maximum of $h_1(r_1)$, respectively.

Without loss of generality, we assume that (2.7) has three positive roots, defined by r_{11}, r_{12}, and r_{13}, respectively. Then (2.6) has three positive roots $\omega_{1k} = \sqrt{r_{1k}}, k = 1, 2, 3$. From (2.5) we get

$$\begin{aligned}
\cos\omega_{1k}\tau_{1k} = {} & \frac{[(B_2 + D_1) - B_1(A_1 + C_1)]\omega_{1k}^4}{[B_1\omega_{1k}^2 - (B_3 + D_2)]^2 + (B_2 + D_1)^2\omega_{1k}^2} \\
& - \frac{(A_3 + C_3)(B_3 + D_2)}{[B_1\omega_{1k}^2 - (B_3 + D_2)]^2 + (B_2 + D_1)^2\omega_{1k}^2} \\
& + \frac{[(A_1 + C_1)(B_3 + D_2) + B_1(A_3 + C_3) - (A_2 + C_2)(B_2 + D_1)]\omega_{1k}^2}{[B_1\omega_{1k}^2 - (B_3 + D_2)]^2 + (B_2 + D_1)^2\omega_{1k}^2}
\end{aligned}$$

and

$$\begin{aligned}
\tau_{1k}^{(j)} = {} & \frac{1}{\omega_{1k}}\Biggl\{\arccos\biggl(\frac{[(B_2 + D_1) - B_1(A_1 + C_1)]\omega_{1k}^4}{[B_1\omega_{1k}^2 - (B_3 + D_2)]^2 + (B_2 + D_1)^2\omega_{1k}^2} \\
& - \frac{(A_3 + C_3)(B_3 + D_2)}{[B_1\omega_{1k}^2 - (B_3 + D_2)]^2 + (B_2 + D_1)^2\omega_{1k}^2} \\
& + \frac{[(A_1 + C_1)(B_3 + D_2) + B_1(A_3 + C_3) - (A_2 + C_2)(B_2 + D_1)]\omega_{1k}^2}{[B_1\omega_{1k}^2 - (B_3 + D_2)]^2 + (B_2 + D_1)^2\omega_{1k}^2}\biggr) + 2j\pi\Biggr\},
\end{aligned}$$

where $k = 1, 2, 3, j = 0, 1, 2, \ldots$.

Denote

$$\tau_{10} = \tau_{1k_0}^{(0)} = \min_{k\in\{1,2,3\}}\bigl\{\tau_{1k}^{(0)}\bigr\}, \qquad \omega_{10} = \omega_{1k_0}.$$

Next, we verify the transversality condition. Let $\lambda(\tau_1) = \alpha_1(\tau_1) + i\omega_1(\tau_1)$ be the root of equation (2.4) near $\tau_1 = \tau_{1k}^{(j)}$ satisfying

$$\alpha_1\bigl(\tau_{1k}^{(j)}\bigr) = 0, \qquad \omega_1\bigl(\tau_{1k}^{(j)}\bigr) = \omega_{1k}.$$

Substituting $\lambda(\tau_1)$ into (2.4) and taking the derivative with respect to τ_1, we have

$$\left[\frac{d\lambda}{d\tau_1}\right]^{-1} = \frac{[3\lambda^2 + 2(A_1 + C_1)\lambda + (A_2 + C_2)]e^{\lambda\tau_1}}{\lambda[B_1\lambda^2 + (B_2 + D_1)\lambda + (B_3 + D_2)]}$$

$$+\frac{2B_1\lambda+(B_2+D_1)}{\lambda[B_1\lambda^2+(B_2+D_1)\lambda+(B_3+D_2)]}-\frac{\tau_1}{\lambda}. \tag{2.9}$$

By (2.9) we have

$$\begin{aligned}
&\left[\frac{\operatorname{Re}d(\lambda(\tau_1))}{d\tau_1}\right]^{-1}_{\tau_1=\tau_{1k}^{(j)}}\\
&=\operatorname{Re}\left[\frac{[3\lambda^2+2(A_1+C_1)\lambda+(A_2+C_2)]e^{\lambda\tau_1}}{\lambda[B_1\lambda^2+(B_2+D_1)\lambda+(B_3+D_2)]}\right]_{\tau_1=\tau_{1k}^{(j)}}\\
&\quad+\operatorname{Re}\left[\frac{2B_1\lambda+(B_2+D_1)}{\lambda[B_1\lambda^2+(B_2+D_1)\lambda+(B_3+D_2)]}\right]_{\tau_1=\tau_{1k}^{(j)}}\\
&=\frac{1}{\Lambda_1}\Big\{-\big[-3\omega_{2k}^2+(A_2+C_2)\big]\omega_{1k}\big[\big[B_1\omega_{1k}^2-(B_3+D_2)\big]\sin\big(\omega_{1k}\tau_{1k}^{(j)}\big)\\
&\quad+(B_2+D_1)\omega_{1k}\cos\big(\omega_{1k}\tau_{1k}^{(j)}\big)\big]\\
&\quad-2(A_1+C_1)\omega_{1k}^2\big[\big[B_1\omega_{1k}^2-(B_3+D_2)\big]\cos\big(\omega_{1k}\tau_{1k}^{(j)}\big)-(B_2+D_1)\omega_{1k}\sin\big(\omega_{1k}\tau_{1k}^{(j)}\big)\big]\\
&\quad-(B_2+D_1)^2\omega_{1k}^2+2B_1\omega_{1k}^2\big[(B_3+D_2)\omega_{1k}-B_1\omega_{1k}^3\big]\Big\}\\
&=\frac{1}{\Lambda_1}\Big\{3\omega_{1k}^6+2\big[(A_1+C_1)^2-2(A_2+C_2)-B_1^2\big]\omega_{1k}^4\\
&\quad+\big[(A_2+C_2)^2-2(A_1+C_1)(A_3+C_3)+2B_1(B_3+D_2)-(B_2+D_1)^2\big]\omega_{1k}^2\Big\}\\
&=\frac{1}{\Lambda_1}\big\{r_{1k}\big(3r_{1k}^2+2E_{31}r_{1k}+E_{32}\big)\big\}\\
&=\frac{1}{\Lambda_1}r_{1k}h_1''(r_{1k}),
\end{aligned}$$

where $\Lambda_1=(B_2+D_1)^2\omega_{1k}^4+[(B_3+D_2)\omega_{1k}-B_1\omega_{1k}^3]^2>0$. Notice that $\Lambda_1>0, r_{1k}>0$,

$$\operatorname{sign}\left\{\left[\frac{\operatorname{Re}d(\lambda(\tau_1))}{d\tau_1}\right]_{\tau_1=\tau_{1k}^{(j)}}\right\}=\operatorname{sign}\left\{\left[\frac{\operatorname{Re}d(\lambda(\tau_1))}{d\tau_1}\right]^{-1}_{\tau_1=\tau_{1k}^{(j)}}\right\},$$

and thus $\frac{d(\operatorname{Re}\lambda(\tau_{1k}^{(j)}))}{d\tau_1}$ has the same sign as $h_1'(r_{1k})$.

To investigate the root distribution of the transcendental equation (2.4), we introduce the result of Ruan and Wei [16].

Lemma 2.1 *Consider the exponential polynomial*

$$\begin{aligned}
&P\big(\lambda,e^{-\lambda\tau_1},\dots,e^{-\lambda\tau_m}\big)\\
&=\lambda^n+p_1^{(0)}\lambda^{n-1}+\cdots+p_{n-1}^{(0)}\lambda+p_n^{(0)}+\big[p_1^{(1)}\lambda^{n-1}+\cdots+p_{n-1}^{(1)}\lambda+p_n^{(1)}\big]e^{-\lambda\tau_1}\\
&\quad+\cdots+\big[p_1^{(m)}\lambda^{n-1}+\cdots+p_{n-1}^{(m)}\lambda+p_n^{(m)}\big]e^{-\lambda\tau_m},
\end{aligned}$$

where $\tau_i\ge 0$ $(i=1,2,\dots,m)$ and $p_j^{(i)}$ $(i=0,1,\dots,m; j=1,2,\dots,n)$ are constants. As $(\tau_1,\tau_2,\dots,\tau_m)$ vary, the sum of the order of the zeros of $P(\lambda,e^{-\lambda\tau_1},\dots,e^{-\lambda\tau_m})$ on the open right half-plane can change only if a zero appears on or crosses the imaginary axis.

According to this analysis, we have the following results.

Theorem 2.2 *For $\tau_1 > 0$ and $\tau_2 = 0$, suppose that (H_1) and (H_2) hold. Then:*

(i) *If $E_{23} \geq 0$ and $\triangle_1 = E_{21}^2 - 3E_{22} \leq 0$, then all roots of equation (2.4) have negative real parts for all $\tau_1 \geq 0$, and the positive equilibrium $E(S^*, I^*, Y^*)$ is locally asymptotically stable for all $\tau_1 \geq 0$.*

(ii) *If either $E_{23} < 0$ or $E_{23} \geq 0$, $\triangle_1 = E_{21}^2 - 3E_{22} > 0$, $r_{11}^* > 0$, and $h_1(r_{11}^*) \leq 0$, then $h_1(r_1)$ has at least one positive root, and all roots of equation (2.4) have negative real parts for $\tau_1 \in [0, \tau_{10})$, and the positive equilibrium $E(S^*, I^*, Y^*)$ is locally asymptotically stable for all $\tau_1 \in [0, \tau_{10})$.*

(iii) *If (ii) holds and $h_1'(r_{1k}) \neq 0$, then system (1.3) undergoes Hopf bifurcations at the positive equilibrium $E(S^*, I^*, Y^*)$ for $\tau_1 = \tau_{1k}^{(j)}$ ($k = 1, 2, 3; j = 0, 1, 2, \dots$).*

When $\tau_1 = 0$ and $\tau_2 > 0$, the stability of the equilibrium $E(S^*, I^*, Y^*)$ and the existence of Hopf bifurcation can be obtained based on a similar discussion, which we omit in this paper.

Case (3): $\tau_1 = \tau_2 = \tau > 0$.

When $\tau_1 = \tau_2 = \tau > 0$, the characteristic equation (2.2) becomes

$$\lambda^3 + A_{31}\lambda^2 + A_{32}\lambda + A_{33} + \left(B_{31}\lambda^2 + B_{32}\lambda + B_{33}\right)e^{-\lambda\tau} + (C_{31}\lambda + C_{32})e^{-2\lambda\tau} = 0, \tag{2.10}$$

where

$$\begin{aligned}
&A_{31} = A_1, \qquad A_{32} = A_2, \qquad A_{33} = A_3, \\
&B_{31} = B_1 + C_1, \qquad B_{32} = B_2 + C_2, \qquad B_{33} = B_3 + C_3, \\
&C_{31} = D_1, \qquad C_{32} = D_2.
\end{aligned}$$

Both sides of equation (2.10) are multiple $e^{\lambda\tau}$, and we obviously get

$$\left(\lambda^3 + A_{31}\lambda^2 + A_{32}\lambda + A_{33}\right)e^{\lambda\tau} + \left(B_{31}\lambda^2 + B_{32}\lambda + B_{33}\right) + (C_{31}\lambda + C_{32})e^{-\lambda\tau} = 0. \tag{2.11}$$

Let $\lambda = i\omega_3$ ($\omega_3 > 0$) be the root of equation (2.11). Separating the real and imaginary parts, we obtain:

$$\begin{cases}
(\omega_3^3 - (C_{31} + A_{32})\omega_3)\cos\omega_3\tau + (A_{31}\omega_3^2 - A_{33} + C_{32})\sin\omega_3\tau = B_{32}\omega_3, \\
(\omega_3^3 + (C_{31} - A_{32})\omega_3)\sin\omega_3\tau + (-A_{31}\omega_3^2 + A_{33} + C_{32})\cos\omega_3\tau \\
\quad = B_{31}\omega_3^2 - B_{33},
\end{cases} \tag{2.12}$$

from which it follows that

$$\begin{cases}
\cos\omega_3\tau = \frac{l_{34}\omega_3^4 + l_{32}\omega_3^2 + l_{30}}{\omega_3^6 + k_{34}\omega_3^4 + k_{32}\omega_3^2 + k_{30}}, \\
\sin\omega_3\tau = \frac{l_{35}\omega_3^5 + l_{33}\omega_3^3 + l_{31}\omega_3}{\omega_3^6 + k_{34}\omega_3^4 + k_{32}\omega_3^2 + k_{30}},
\end{cases} \tag{2.13}$$

where

$$l_{30} = -A_{33}B_{33} + C_{32}B_{33}, \qquad l_{31} = A_{32}B_{33} + B_{33}C_{31} - A_{33}B_{32} - A_{32}B_{32},$$

$$l_{32} = -A_{32}B_{32} + A_{31}B_{33} + A_{33}B_{31} - B_{31}C_{32} + B_{32}C_{31},$$
$$l_{33} = A_{31}B_{32} - B_{31}C_{31} - A_{32}B_{31} - B_{33}, \qquad l_{34} = B_{32} - A_{31}B_{31}, \qquad l_{35} = B_{31},$$
$$k_{30} = A_{33}^2 - C_{32}^2, \qquad k_{32} = -2A_{31}A_{33} + A_{32}^2 - C_{31}^2, \qquad k_{34} = A_{31}^2 - 2A_{32}.$$

Since $\sin^2\omega_3\tau + \cos^2\omega_3\tau = 1$, we have

$$\omega_3^{12} + E_{31}\omega_3^{10} + E_{32}\omega_3^8 + E_{33}\omega_3^6 + E_{34}\omega_3^4 + E_{35}\omega_3^2 + E_{36} = 0, \tag{2.14}$$

where

$$E_{31} = 2k_{34} - l_{35}^2, \qquad E_{32} = 2k_{32} + k_{34}^2 - 2l_{33}l_{35} - l_{34}^2,$$
$$E_{33} = 2k_{30} + 2k_{32}k_{34} - 2l_{31}l_{35} - l_{33}^2 - 2l_{32}l_{34},$$
$$E_{34} = 2k_{30}k_{34} + k_{32}^2 - 2l_{31}l_{33} - 2l_{30}l_{34} - l_{32}^2,$$
$$E_{35} = 2k_{30}k_{32} - l_{31}^2 - 2l_{30}l_{32}, \qquad E_{36} = k_{30}^2 - l_{30}^2.$$

Letting $r_3 = \omega_3^2$, equation (2.14) is transformed into

$$r_3^6 + E_{31}r_3^5 + E_{32}r_3^4 + E_{33}r_3^3 + E_{34}r_3^2 + E_{35}r_3 + E_{36} = 0. \tag{2.15}$$

If all the parameters of system (1.3) are given, then it is easy to get the roots of equation (2.15) by using the Matlab software package. To give the main results in this paper, we make the following assumption.

(H_3) equation (2.15) has at least one positive real root.

Suppose that condition (H_3) holds. Without loss of generality, we assume that (2.14) has six positive real roots, say $r_{31}, r_{32}, \dots, r_{36}$. Then (2.13) has six positive real roots

$$\omega_{31} = \sqrt{r_{31}}, \qquad \omega_{32} = \sqrt{r_2}, \qquad \dots, \qquad \omega_{3i} = \sqrt{r_{3i}} \quad (i = 1, 2, \dots, 6).$$

Thus, if we denote

$$\tau_{3k}^{(j)} = \frac{1}{\omega_{3k}}\left\{\arccos\left(\frac{l_{34}\omega_{3k}^4 + l_{32}\omega_{3k}^2 + l_{30}}{\omega_{3k}^6 + k_{34}\omega_{3k}^4 + k_{32}\omega_{3k}^2 + k_{30}}\right) + 2j\pi\right\} \tag{2.16}$$

for $k = 1, 2, \dots, 6, j = 0, 1, 2, \dots$, then $\pm i\omega_{3k}$ is a pair of purely imaginary roots of (2.11) corresponding to $\tau_{3k}^{(j)}$. Define

$$\tau_{30} = \tau_{3k_0} = \min_{k\in\{1,2,\dots,6\}}\left\{\tau_{3k}^{(0)}\right\}, \qquad \omega_{30} = \omega_{3k_0}.$$

Let $\lambda(\tau) = \alpha_3(\tau) + i\omega_3(\tau)$ be the root of equation (2.11) near $\tau = \tau_{3k}^{(j)}$ satisfying

$$\alpha_2\left(\tau_{3k}^{(j)}\right) = 0, \qquad \omega_3\left(\tau_{3k}^{(j)}\right) = \omega_{3k}.$$

Substituting $\lambda(\tau)$ into (2.11) and taking the derivative with respect to τ, we have

$$\left[\frac{d\lambda}{d\tau}\right]^{-1} = -\frac{(3\lambda^2 + 2A_{31}\lambda + A_{32})e^{\lambda\tau} + 2B_{31}\lambda + B_{32} + C_{31}e^{-\lambda\tau}}{\lambda[(\lambda^3 + A_{31}\lambda^2 + A_{32}\lambda + A_{33})e^{\lambda\tau} - (C_{31}\lambda + C_{32})e^{-\lambda\tau}]} - \frac{\tau}{\lambda}. \tag{2.17}$$

Letting $\lambda = \pm i\omega_{3k}$ at the roots of equation (2.11) at $\tau = \tau_{3k}^{(j)}$, we should compute $\frac{d\,\mathrm{Re}(\lambda((\tau_{3k}^{(j)}))}{d\tau}$. By calculation we get

$$\mathrm{Re}\left[\frac{d\lambda}{d\tau}\right]_{\tau=\tau_{3k}^{(j)}}^{-1} = \frac{P_{33} + iP_{34}}{P_{31} + iP_{32}} - \frac{\tau}{\lambda},$$

where

$$\begin{aligned}
P_{31} &= \left(-\omega_{3k}^4 + A_{32}\omega_{3k}^2 - C_{31}\omega_{3k}^2\right)\cos\left(\omega_{3k}\tau_{3k}^{(j)}\right) \\
&\quad + \left(-A_{31}\omega_{3k}^3 + A_{33}\omega_{3k} + C_{32}\omega_{3k}\right)\sin\left(\omega_{3k}\tau_{3k}^{(j)}\right), \\
P_{32} &= \left(A_{31}\omega_{3k}^3 - A_{33}\omega_{3k} + C_{32}\omega_{3k}\right)\cos\left(\omega_{3k}\tau_{3k}^{(j)}\right) \\
&\quad + \left(-\omega_{3k}^4 + A_{32}\omega_{3k}^2 + C_{31}\omega_{3k}^2\right)\sin\left(\omega_{3k}\tau_{3k}^{(j)}\right), \\
P_{33} &= \left(-3\omega_{3k}^2 + A_{32} + C_{31}\right)\cos\left(\omega_{3k}\tau_{3k}^{(j)}\right) - 2A_{31}\omega_{3k}\sin\left(\omega_{3k}\tau_{3k}^{(j)}\right) + B_{32}, \\
P_{34} &= 2A_{31}\omega_{3k}\cos\left(\omega_{3k}\tau_{3k}^{(j)}\right) + \left(-3\omega_{3k}^2 + A_{32} - C_{31}\right)\sin\left(\omega_{3k}\tau_{3k}^{(j)}\right) + 2B_{31}\omega_{3k}.
\end{aligned}$$

So, we have

$$\mathrm{Re}\left[\frac{d\lambda}{d\tau}\right]_{\tau=\tau_{3k}^{(j)}}^{-1} = \frac{P_{33}P_{31} + P_{34}P_{32}}{P_{31}^2 + P_{32}^2}.$$

Obviously, if condition

(H_4) $P_{31}P_{33} + P_{32}P_{34} \neq 0$

holds, then $\frac{d\,\mathrm{Re}\,\lambda(\tau)}{d\tau}|_{\lambda=i\omega_{3k}} = \mathrm{Re}[\frac{d\lambda(\tau)}{d\tau}]_{\lambda=i\omega_{3k}}^{-1} \neq 0$. Thus, we have the following results.

Theorem 2.3 *For system (1.3) with $\tau_1 = \tau_2 = \tau > 0$, let (H_1)–(H_4) hold. The equilibrium point $E(S^*, I^*, Y^*)$ is asymptotically stable for $\tau \in [0, \tau_{3k}^{(j)})$ and unstable for $\tau > \tau_{3k}^{(j)}$; Hopf bifurcation occurs when $\tau = \tau_{3k}^{(j)}$.*

Case (4): $\tau_1 \in (0, \tau_{10})$, $\tau_2 > 0$, $\tau_1 \neq \tau_2$.

We consider (2.2) with τ_1 in its stable interval $[0, \tau_{10})$ and τ_2 considered as a parameter. Let $\lambda = i\omega_2^*(\omega_2^* > 0)$ be a root of equation (2.2). Separating real and imaginary parts leads to

$$\begin{cases}
(C_2\omega_2^* + D_1\omega_2^*\cos(\omega_2^*\tau_1^*) - D_2\sin(\omega_2^*\tau_1))\cos(\omega_2^*\tau_2) \\
\qquad + (C_1\omega_2^{*2} - C_3 - D_1\omega_2^*\sin(\omega_2^*\tau_1) - D_2(\cos\omega_2^*\tau_1))\sin(\omega_2^*\tau_2) \\
\quad = \omega_2^{*3} - A_2\omega_2^* - B_2\omega_2^*\cos(\omega_2^*\tau_1) - B_1\omega_2^{*2}\sin(\omega_2^*\tau_1) + B_3\sin(\omega_2^*\tau_1), \\
(C_2\omega_2^* + D_1\omega_2^*\cos(\omega_2^*\tau_1) - D_2\sin(\omega_2^*\tau_1))\sin(\omega_2^*\tau_2) \\
\qquad - (C_1\omega_2^{*2} - C_3 - D_1\omega_2^*\sin(\omega_2^*\tau_1) - D_2(\cos\omega_2^*\tau_1))\cos(\omega_2^*\tau_2) \\
\quad = A_1\omega_2^{*2} - A_3 - B_2\omega_2^*\sin(\omega_2^*\tau_1) + B_1\omega_2^{*2}\cos(\omega_2^*\tau_1) - B_3\cos(\omega_2^*\tau_1).
\end{cases} \tag{2.18}$$

From equation (2.18) we can obtain

$$\cos\left(\omega_2^*\tau_2^*\right) = \frac{h_{41}\omega_2^{*4} + h_{42}\omega_2^{*3} + h_{43}\omega_2^{*2} + h_{44}\omega_2^* + h_{45}}{f_{41}\omega_2^{*4} + f_{42}\omega_2^{*3} + f_{43}\omega_2^{*2} + f_{44}\omega_2^* + f_{45}}, \tag{2.19}$$

where

$$\begin{aligned}
h_{41} &= C_2 - C_1A_1 - B_1C_1\cos(\omega_2^*\tau_1) + D_1\cos(\omega_2^*\tau_1),\\
h_{42} &= -B_1C_2\sin(\omega_2^*\tau_1) - D_2\sin(\omega_2^*\tau_1) + B_2C_1\sin(\omega_2^*\tau_1) + A_1D_1\sin(\omega_2^*\tau_1),\\
h_{43} &= -A_2C_2 - B_2C_2\cos(\omega_2^*\tau_1) - A_2D_1\cos(\omega_2^*\tau_1) - B_2D_1 + B_1D_2\\
&\quad + A_3C_1 + B_3C_1\cos(\omega_2^*\tau_1) + A_1C_3 + B_1C_3\cos(\omega_2^*\tau_1) + A_1D_2\cos(\omega_2^*\tau_1),\\
h_{44} &= B_3C_2\sin(\omega_2^*\tau_1) + A_2D_2\sin(\omega_2^*\tau_1) - B_2C_3\sin(\omega_2^*\tau_1) - A_3D_1\sin(\omega_2^*\tau_1),\\
h_{45} &= -B_3D_2 - A_3C_3 - B_3C_3(\cos\omega_2^*\tau_1) - A_3D_2\cos(\omega_2^*\tau_1),\\
f_{41} &= C_1^2,\\
f_{42} &= -2C_1D_1\sin(\omega_2^*\tau_1),\\
f_{43} &= C_2^2 + 2C_2D_1\cos(\omega_2^*\tau_1) + D_1^2 - 2C_1C_3 - 2C_1C_3\cos(\omega_2^*\tau_1),\\
f_{44} &= 2C_3D_1\sin(\omega_2^*\tau_1) - 2C_2D_2\sin(\omega_2^*\tau_1),\\
f_{45} &= C_3^2 + D_2^2 + 2C_3D_2\cos(\omega_2^*\tau_1).
\end{aligned}$$

From equation (2.18) we obtain:

$$\omega_2^{*6} + E_{41}\omega_2^{*4} + E_{42}\omega_2^{*2} + E_{43} + E_{44}\sin(\omega_2^*\tau_1) + E_{45}\cos(\omega_2^*\tau_1) = 0, \tag{2.20}$$

where

$$\begin{aligned}
E_{41} &= B_1^2 - 2A_2 - C_1^2 + A_1^2,\\
E_{42} &= A_2^2 + 2C_1C_3 - 2A_1A_3 + B_2^2 - 2B_1B_2 - C_2^2 - D_1^2,\\
E_{43} &= B_3^2 - D_2^2 - C_3^2 + A_3^2,\\
E_{44} &= -2B_1\omega_2^{*5} + 2(B_3 - A_1B_2 + A_2B_1 + C_1D_1)\omega_2^{*3} + 2(C_2D_2 + A_3B_2 - C_3D_1 - A_2B_3)\omega_2^*,\\
E_{45} &= 2(A_1B_1 - B_2)\omega_2^{*4} + 2(A_2B_2 - A_3B_1 - C_2D_1 + C_1D_2 - A_1B_3)\omega_2^{*2}\\
&\quad + 2(A_3B_3 - C_3D_2).
\end{aligned}$$

Denote $F_1(\omega_2^*) = \omega_2^{*6} + E_{41}\omega_2^{*4} + E_{42}\omega_2^{*2} + E_{43} + E_{44}\sin(\omega_2^*\tau_1) + E_{45}\cos(\omega_2^*\tau_1)$. If $E_{43} = B_3^2 - D_2^2 - C_3^2 + A_3^2 < 0$, then

$$F_1(0) < 0, \qquad \lim_{\omega_2^*\longrightarrow+\infty} F_1(\omega_2^*) = +\infty.$$

We can see that (2.20) has at most six positive roots $\omega_{21}^*, \omega_{22}^*, \ldots, \omega_{26}^*$. For every fixed ω_{2k}^* ($k = 1, 2, \ldots, 6$), for (2.19), the critical value

$$\tau_{2k}^{*\,(j)} = \frac{1}{\omega_{2k}^*}\left\{\arccos\left(\frac{h_{41}\omega_{2k}^{*\,4} + h_{42}\omega_{2k}^{*\,3} + h_{43}\omega_{2k}^{*\,2} + h_{44}\omega_{2k}^* + h_{45}}{f_{41}\omega_{2k}^{*\,4} + f_{42}\omega_{2k}^{*\,3} + f_{43}\omega_{2k}^{*\,2} + f_{44}\omega_{2k}^* + f_{45}}\right) + 2j\pi\right\}$$
$$(k = 1, 2, \ldots, 6; j = 0, 1, 2, \ldots). \tag{2.21}$$

There exists a sequence $\{\tau_{2k}^{*\,(j)} | j = 0, 1, 2, \ldots\}$ such that (2.18) holds.

Let

$$\tau_{20}^{*}=\tau_{2k_0}^{*}{}^{(0)}=\min_{k\in\{1,2,\ldots,6\}}\bigl\{\tau_{2k}^{*}{}^{(0)}\bigr\},\qquad \omega_{20}^{*}=\omega_{2k_0}^{*}. \tag{2.22}$$

Substituting τ_2 into (2.2) and taking the derivative with respect to τ_2, we have

$$\left[\frac{d\lambda}{d\tau_2}\right]^{-1}=\frac{1}{\lambda}\frac{Q_{11}+Q_{12}e^{-\lambda\tau_1}+Q_{13}e^{-\lambda\tau_2}+Q_{14}e^{-\lambda(\tau_1+\tau_2)}}{Q_{15}e^{-\lambda(\tau_1+\tau_2)}+Q_{16}e^{-\lambda\tau_2}}, \tag{2.23}$$

where

$$\begin{aligned}
&Q_{11}=3\lambda^2+2A_1\lambda+A_2,\qquad Q_{12}=-B_1\tau_1\lambda^2+(2B_1-\tau_1B_2)\lambda+B_2-\tau_1B_3,\\
&Q_{13}=2C_1\lambda+C_2,\qquad Q_{14}=-\tau_1D_1\lambda+(D_1-\tau_1D_2),\\
&Q_{15}=D_1\lambda+D_2,\qquad Q_{16}=C_1\lambda^2+C_2\lambda+C_3.
\end{aligned}$$

By (2.23) we have

$$\operatorname{Re}\left[\frac{d\lambda(\tau_{2k}^{*}{}^{(j)})}{d\tau_2}\right]^{-1}_{\lambda=i\omega_{2k}^{*}}=\frac{Q_{31}Q_{33}+Q_{32}Q_{34}}{Q_{31}^2+Q_{32}^2},$$

where

$$\begin{aligned}
Q_{31}={}&D_2\omega_{2k}^{*}\sin\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr)-D_1\omega_{2k}^{*}{}^2\cos\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr)\\
&-C_1\omega_{2k}^{*}{}^3\sin\bigl(\omega_{2k}^{*}\tau_{2k}^{*}\bigr)+C_3\omega_{2k}^{*}\sin\bigl(\omega_{2k}^{*}\tau_{2k}^{*}{}^{(j)}\bigr)-C_2\omega_{2k}^{*}{}^2\cos\bigl(\omega_{2k}^{*}\tau_{2k}^{*}{}^{(j)}\bigr),\\
Q_{32}={}&D_2\omega_{2k}^{*}\cos\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr)+D_1\omega_{2k}^{*}{}^2\sin\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr)\\
&-C_1\omega_{2k}^{*}{}^3\cos\bigl(\omega_{2k}^{*}\tau_{2k}^{*}{}^{(j)}\bigr)+C_3\omega_{2k}^{*}\cos\bigl(\omega_{2k}^{*}\tau_{2k}^{*}{}^{(j)}\bigr)+C_2\omega_{2k}^{*}{}^2\sin\bigl(\omega_{2k}^{*}\tau_{2k}^{*}{}^{(j)}\bigr),\\
Q_{33}={}&-3\omega_{2k}^{*}{}^2+A_2+2B_1\omega_{2k}^{*}\sin\bigl(\omega_{2k}^{*}\tau_1\bigr)-\tau_1B_2\omega_{2k}^{*}\sin\bigl(\omega_{2k}^{*}\tau_1\bigr)\\
&+B_2\cos\bigl(\omega_{2k}^{*}\tau_1\bigr)+\tau_1B_1\omega_{2k}^{*}{}^2\cos\bigl(\omega_{2k}^{*}\tau_1\bigr)-\tau_1B_3\cos\bigl(\omega_{2k}^{*}\tau_1\bigr)\\
&+2C_1\omega_{2k}^{*}\sin\bigl(\omega_{2k}^{*}\tau_{2k}^{*}{}^{(j)}\bigr)+C_2\cos\bigl(\omega_{2k}^{*}\tau_{2k}^{*}{}^{(j)}\bigr)-\tau_1D_1\omega_{2k}^{*}\sin\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr)\\
&+D_1\cos\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr)-\tau_1D_2\cos\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr),\\
Q_{34}={}&2A_1\omega_{2k}^{*}+2B_1\omega_{2k}^{*}\cos\bigl(\omega_{2k}^{*}\tau_1\bigr)-\tau_1B_2\omega_{2k}^{*}\cos\bigl(\omega_{2k}^{*}\tau_1\bigr)-B_2\sin\bigl(\omega_{2k}^{*}\tau_1\bigr)\\
&-\tau_1B_1\omega_{2k}^{*}{}^2\sin\bigl(\omega_{2k}^{*}\tau_1\bigr)+\tau_1B_3\sin\bigl(\omega_{2k}^{*}\tau_1\bigr)+2C_1\omega_{2k}^{*}\cos\bigl(\omega_{2k}^{*}\tau_{2k}^{*}\bigr)\\
&-C_2\sin\bigl(\omega_{2k}^{*}\tau_{2k}^{*}{}^{(j)}\bigr)-\tau_1D_1\omega_{2k}^{*}\cos\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr)\\
&-D_1\sin\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr)+\tau_1D_2\sin\bigl(\omega_{2k}^{*}\bigl(\tau_1+\tau_{2k}^{*}{}^{(j)}\bigr)\bigr).
\end{aligned}$$

We suppose that

(H_5) $Q_{31}Q_{33}+Q_{32}Q_{34}\neq 0$.

Then $\operatorname{Re}(\frac{d\lambda}{d\tau_2})_{\lambda=i\omega_{2k}^{*}}\neq 0$, and we have the following result on the stability and Hopf bifurcation in system (1.3).

Theorem 2.4 *For system (1.3) with $\tau_1\in[0,\tau_{10})$, suppose that (H_1), (H_2), and (H_5) hold. If $E_{43}=B_3^2-D_2^2-C_3^2+A_3^2<0$, then the positive equilibrium point $E(S^*,I^*,Y^*)$ is locally* *asymptotically stable for* $\tau_2 \in [0, \tau_{20}^*)$ *and unstable for* $\tau_2 > \tau_{20}^*$. *Hopf bifurcation occurs when* $\tau_2 = \tau_{2k}^{*\,(j)}$ $(k = 1, 2, \dots, 6; j = 0, 1, 2, \dots)$.

When $\tau_1 > 0, \tau_2 \in (0, \tau_{20}), \tau_1 \neq \tau_2$, the stability of the equilibrium $E(S^*, I^*, Y^*)$ and the existence of Hopf bifurcation can be obtained based on a similar discussion, which we omit in this paper.

3 Direction and stability of the Hopf bifurcation

In this section, we employ the normal form method and center manifold theorem [17–19] to determine the direction of Hopf bifurcation and stability of the bifurcated periodic solutions of system (1.3) with respect to τ_2 for $\tau_1 \in (0, \tau_{10})$. Without loss of generality, we denote any of the critical values $\tau_2 = \tau_{2k}^{*\,(j)}$ $(k = 1, 2, \dots, 6; j = 0, 1, 2, \dots)$ by τ_{20}^*.

Let $u_1 = x - S^*$, $u_2 = y - I^*$, $u_3 = z - Y^*$, $t = t/\tau_2$, and $\tau_2 = \tau_{20}^* + \mu$, $\mu \in R^3$. Then $\mu = 0$ is the Hopf bifurcation value of system (1.3), which may be written as a functional differential equation in $C = C([-1, 0], R^3)$,

$$\dot{u}(t) = L_\mu(u_t) + f(\mu, u_t), \tag{3.1}$$

where $u(t) = (x(t), y(t), z(t))^T \in R^3$, and $L_\mu(\phi) : C \to R^3$ and $f(\mu, u_t)$ are given by

$$L_\mu(\phi) = (\tau_{20}^* + \mu)A' \begin{bmatrix} \phi_1(0) \\ \phi_2(0) \\ \phi_3(0) \end{bmatrix} + (\tau_{20}^* + \mu)B' \begin{bmatrix} \phi_1(-\frac{\tau_1}{\tau_{20}^*}) \\ \phi_2(-\frac{\tau_1}{\tau_{20}^*}) \\ \phi_3(-\frac{\tau_1}{\tau_{20}^*}) \end{bmatrix} + (\tau_{20}^* + \mu)C' \begin{bmatrix} \phi_1(-1) \\ \phi_2(-1) \\ \phi_3(-1) \end{bmatrix}, \tag{3.2}$$

where $\phi = (\phi_1, \phi_2, \phi_3)^T \in C([-1, 0], R^3)$, and

$$A' = \begin{pmatrix} -\mu & d & 0 \\ 0 & \omega & 0 \\ 0 & 0 & -m \end{pmatrix}, \qquad B' = \begin{pmatrix} -A_0 & 0 & -B_0 \\ A_0 & 0 & B_0 \\ 0 & 0 & 0 \end{pmatrix}, \qquad C' = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & C_0 & D_0 \end{pmatrix}.$$

$$f(\mu, \phi) = (\tau_{20}^* + \mu) \begin{pmatrix} f_1 \\ f_2 \\ f_3 \end{pmatrix}, \tag{3.3}$$

where

$$\begin{aligned} f_1 &= k_{11}\phi_1\left(-\frac{\tau_1}{\tau_{20}^*}\right)\phi_3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{12}\phi_3^2\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{13}\phi_1\left(-\frac{\tau_1}{\tau_{20}^*}\right)\phi_3^2\left(-\frac{\tau_1}{\tau_{20}^*}\right) \\ &\quad + k_{14}\phi_3^3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{15}\phi_1\left(-\frac{\tau_1}{\tau_{20}^*}\right)\phi_3^3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + \cdots, \\ f_2 &= k_{21}\phi_1\left(-\frac{\tau_1}{\tau_{20}^*}\right)\phi_3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{22}\phi_3^2\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{23}\phi_1\left(-\frac{\tau_1}{\tau_{20}^*}\right)\phi_3^2\left(-\frac{\tau_1}{\tau_{20}^*}\right) \\ &\quad + k_{24}\phi_3^3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{25}\phi_1\left(-\frac{\tau_1}{\tau_{20}^*}\right)\phi_3^3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + \cdots, \\ f_3 &= k_{31}\phi_2(-1)\phi_3(-1) + k_{32}\phi_2^2(-1) + k_{33}\phi_2^2(-1)\phi_3(-1) + k_{34}\phi_2^3(-1) \\ &\quad + k_{35}\phi_2^3(-1)\phi_3(-1), \end{aligned}$$

$$
\begin{aligned}
&k_{11} = -\frac{\beta}{(1+\alpha Y^*)^2}, \qquad k_{12} = \frac{\alpha\beta S^*}{(1+\alpha Y^*)^3}, \qquad k_{13} = \frac{\alpha\beta}{(1+\alpha Y^*)^3},\\
&k_{14} = -\frac{\alpha^2\beta S^*}{(1+\alpha Y^*)^4}, \qquad k_{15} = -\frac{\alpha^2\beta}{(1+\alpha Y^*)^4},\\
&k_{21} = \frac{\beta}{(1+\alpha Y^*)^2}, \qquad k_{22} = -\frac{\alpha\beta S^*}{(1+\alpha Y^*)^3}, \qquad k_{23} = -\frac{\alpha\beta}{(1+\alpha Y^*)^3},\\
&k_{24} = \frac{\alpha^2\beta S^*}{(1+\alpha Y^*)^4}, \qquad k_{25} = \frac{\alpha^2\beta}{(1+\alpha Y^*)^4},\\
&k_{31} = -\frac{\beta_1}{(1+\alpha_1 I^*)^2}, \qquad k_{32} = -\frac{\alpha_1\beta_1}{(1+\alpha_1 I^*)^3}\left(\frac{\Lambda}{m} - Y^*\right), \qquad k_{33} = \frac{\alpha_1\beta_1}{(1+\alpha_1 I^*)^3},\\
&k_{34} = \frac{\alpha_1^2\beta_1}{(1+\alpha_1 I^*)^4}\left(\frac{\Lambda}{m} - Y^*\right), \qquad k_{35} = -\frac{\alpha_1^2\beta_1}{(1+\alpha_1 I^*)^4}.
\end{aligned}
$$

Obviously, $L_\mu(\phi)$ is a continuous linear mapping from $C([-1,0],R^3)$ into R^3. By the Riesz representation theorem there exists a 3×3 matrix function $\eta(\theta,\mu)$ $(-1\le\theta\le 0)$, whose elements are of bounded variation such that

$$
L_\mu(\phi) = \int_{-1}^{0} d\eta(\theta,\mu)\phi(\theta), \quad \phi\in C\bigl([-1,0],R^3\bigr). \tag{3.4}
$$

In fact, we can choose $\eta(\theta,\mu) = (\tau_{20}^*+\mu)[A'\delta(\theta) + C'\delta(\theta+1) + B'\delta(\theta+\frac{\tau_1}{\tau_{20}^*})]$, where δ is the Dirac delta function. For $\phi\in C^1([-1,0],R^3)$, we define

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

and

$$
R(\mu)\phi = \begin{cases} 0, & \theta\in[-1,0),\\ f(\mu,\phi), & \theta = 0.\end{cases}
$$

Then, for $\theta = 0$, system (3.1) is equivalent to

$$
\dot{u_t} = A(\mu)u_t + R(\mu)u_t, \tag{3.5}
$$

where $u_t = u(t+\theta) = (u_1(t+\theta), u_2(t+\theta), u_3(t+\theta))$ for $\theta\in[-1,0]$.

The adjoint operator A^* of A is defined by

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

associated with the bilinear form

$$
\bigl\langle\psi(s),\phi(\theta)\bigr\rangle = \bar{\psi}(0)\phi(0) - \int_{-1}^{0}\int_{\xi=0}^{\theta}\bar{\psi}(\xi-\theta)\,d\eta(\theta)\phi(\xi)\,d\xi, \tag{3.6}
$$

where $\eta(\theta) = \eta(\theta,0)$, Denote $A = A(0)$. Then A and A^* are adjoint operators. From our discussion we see that $\pm i\omega_{20}^*\tau_{20}^*$ are eigenvalues of A, and they also are eigenvalues of A^*.

Suppose that $q(\theta) = (1, q_2, q_3)^T e^{i\omega_{20}^*\tau_{20}^*\theta}$ is the eigenvector of A corresponding to $i\omega_{20}^*\tau_{20}^*$ and $q^*(s) = D(1, q_2^*, q_3^*)e^{i\omega_{20}^*\tau_{20}^* s}$ is the eigenvector of A^* corresponding to $-i\omega_{20}^*\tau_{20}^*$. Then by a simple computation we obtain

$$q_2 = \frac{i\omega_{20}^* + \mu}{d - i\omega_{20}^* + \omega}, \qquad q_3 = \frac{(i\omega_{20}^* + \mu)(i\omega_{20}^* - \omega) - A_0 e^{-i\omega_{20}^*\tau_1}(d - i\omega_{20}^* + w)}{B_0 e^{-i\omega_{20}^*\tau_1}(d - i\omega_{20}^* + w)}.$$

$$q_2^* = \frac{-i\omega_{20}^* + \mu + A_0 e^{i\omega_{20}^*\tau_1}}{A_0 e^{i\omega_{20}^*\tau_1}}, \qquad q_3^* = \frac{-dA_0 e^{i\omega_{20}^*\tau_1} - (i\omega_{20}^* + \omega)(-i\omega_{20}^* + \mu + A_0 e^{i\omega_{20}^*\tau_1})}{A_0 C_0 e^{i\omega_{20}^*(\tau_1 + \tau_{20}^*)}}.$$

From (3.6) we have

$$\begin{aligned}
\langle q^*(s), q(\theta)\rangle &= \bar{D}(1, \bar{q}_2^*, \bar{q}_3^*)(1, q_2, q_3)^T \\
&\quad - \int_{-1}^{0}\int_{\xi=0}^{\theta} \bar{D}(1, \bar{q}_2^*, \bar{q}_3^*)e^{-i(\xi-\theta)\omega_{20}^*\tau_1}\, d\eta(\theta)(1, q_2, q_3)^T e^{i\xi\omega_{20}^*\tau_1}\, d\xi \\
&\quad - \int_{-1}^{0}\int_{\xi=0}^{\theta} \bar{D}(1, \bar{q}_2^*, \bar{q}_3^*)e^{-i(\xi-\theta)\omega_{20}^*\tau_{20}^*}\, d\eta(\theta)(1, q_2, q_3)^T e^{i\xi\omega_{20}^*\tau_{20}^*}\, d\xi \\
&= \bar{D}\bigl\{1 + q_2\bar{q}_2^* + q_3\bar{q}_3^* + \tau_1 e^{i\omega_{20}^*\tau_1}\bigl(1, \bar{q}_2^*, \bar{q}_3^*\bigr)\cdot B'(1, q_2, q_3)^T \\
&\quad + \tau_{20}^* e^{i\omega_{20}^*\tau_{20}^*}\bigl(1, \bar{q}_2^*, \bar{q}_3^*\bigr)\cdot C'(1, q_2, q_3)^T\bigr\} \\
&= \bar{D}\bigl\{1 + q_2\bar{q}_2^* + q_3\bar{q}_3^* + \tau_1 e^{-i\omega_{20}^*\tau_1}\bigl[A_0\bar{q}_2^* - A_0 + q_3\bigl(B_0\bar{q}_2^* - B_0\bigr)\bigr] \\
&\quad + \tau_{20}^* e^{-i\omega_{20}^*\tau_{20}^*}\bigl[\bar{q}_3^*(C_0 q_2 + D_0 q_3)\bigr]\bigr\}.
\end{aligned}$$

Thus we can choose

$$\begin{aligned}
\bar{D} &= \bigl\{1 + q_2\bar{q}_2^* + q_3\bar{q}_3^* + \tau_1 e^{-i\omega_{20}^*\tau_1}\bigl[A_0\bar{q}_2^* - A_0 + q_3\bigl(B_0\bar{q}_2^* - B_0\bigr)\bigr] \\
&\quad + \tau_{20}^* e^{-i\omega_{20}^*\tau_{20}^*}\bigl[\bar{q}_3^*(C_0 q_2 + D_0 q_3)\bigr]\bigr\}^{-1}
\end{aligned} \tag{3.7}$$

such that $\langle q^*(s), q(\theta)\rangle = 1$ and $\langle q^*(s), \bar{q}(\theta)\rangle = 0$.

Next, we use the same notations as those in Hassard [19] and firstly compute the coordinates to describe the center manifold C_0 at $\mu = 0$. Let u_t be the solution of equation (3.1) with $\mu = 0$. Define

$$z(t) = \langle q^*, u_t\rangle, \qquad W(t,\theta) = u_t(\theta) - 2\,\mathrm{Re}\bigl\{z(t)q(\theta)\bigr\}. \tag{3.8}$$

On the center manifold C_0, we have

$$W(t,\theta) = W\bigl(z(t), \bar{z}(t), \theta\bigr) = W_{20}(0)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + W_{30}(\theta)\frac{z^3}{6} + \cdots,$$

where z and $\bar{z}$ are the local coordinates for center manifold C_0 in the directions of q and $\bar{q}$. Note that W is real if u_t is real. For the solution $u_t \in C_0$ of (3.1), since $\mu = 0$, we have

$$\begin{aligned}
\dot{z} &= i\omega_{20}^*\tau_{20}^* z + \bigl\langle q^*(\theta), f\bigl(0, W\bigl(z(t), \bar{z}(t), \theta\bigr) + 2\,\mathrm{Re}\bigl\{z(t)q(\theta)\bigr\}\bigr\rangle \\
&= i\omega_{20}^*\tau_{20}^* z + \bar{q}^*(0) f\bigl(0, W\bigl(z(t), \bar{z}(t), 0\bigr) + 2\,\mathrm{Re}\bigl\{z(t)q(0)\bigr\}
\end{aligned}$$

$$= i\omega_{20}^*\tau_{20}^* z + \bar{q}^*(0) f_0(z,\bar{z}) \triangleq i\omega_{20}^*\tau_{20}^* z + g(z,\bar{z}), \tag{3.9}$$

where

$$g(z,\bar{z}) = \bar{q^*}(0) f_0(z,\bar{z}) = g_{20}\frac{z^2}{2} + g_{11} z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{\bar{z}z^2}{2} + \cdots. \tag{3.10}$$

Then

$$\begin{aligned}
g(z,\bar{z}) &= \bar{q^*}(0) f_0(z,\bar{z}) \\
&= \bar{D}\tau_{20}^*\big(1, \bar{q_2^*}, \bar{q_3^*}\big)\big(f_1^{(0)} f_2^{(0)} f_3^{(0)}\big)^T \\
&= \bar{D}\tau_{20}^*\Bigg\{\Bigg[k_{11}u_{1t}\left(-\frac{\tau_1}{\tau_{20}^*}\right)u_{3t}\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{12}u_{3t}^2\left(-\frac{\tau_1}{\tau_{20}^*}\right) \\
&\quad + k_{13}u_{1t}\left(-\frac{\tau_1}{\tau_{20}^*}\right)u_{3t}^2\left(-\frac{\tau_1}{\tau_{20}^*}\right) \\
&\quad + k_{14}u_{3t}^3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{15}u_{1t}\left(-\frac{\tau_1}{\tau_{20}^*}\right)u_{3t}^3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + \cdots\Bigg] \\
&\quad + \bar{q_2^*}\Bigg[k_{21}u_{1t}\left(-\frac{\tau_1}{\tau_{20}^*}\right)u_{3t}\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{22}u_{3t}^2\left(-\frac{\tau_1}{\tau_{20}^*}\right) \\
&\quad + k_{23}u_{1t}\left(-\frac{\tau_1}{\tau_{20}^*}\right)u_{3t}^2\left(-\frac{\tau_1}{\tau_{20}^*}\right) \\
&\quad + k_{24}u_{3t}^3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + k_{25}u_{1t}\left(-\frac{\tau_1}{\tau_{20}^*}\right)u_{3t}^3\left(-\frac{\tau_1}{\tau_{20}^*}\right) + \cdots\Bigg] \\
&\quad + \bar{q_3^*}\big[k_{31}u_{2t}(-1)u_{3t}(-1) + k_{32}u_{2t}^2(-1) + k_{33}u_{2t}^2(-1)u_{3t}(-1) + k_{34}u_{2t}^3(-1) \\
&\quad + k_{35}u_{2t}^3(-1)u_{3t}(-1)\big]\Bigg\}.
\end{aligned}$$

Since $u_t(\theta) = (u_{1t}(\theta), u_{2t}(\theta), u_{3t}(\theta))^T = W(t,\theta) + zq(\theta) + \bar{z}\bar{q}(\theta)$ and $q(\theta) = (1, q_2, q_3)^T e^{i\omega_{20}^*\tau_{20}^*\theta}$, we have

$$\begin{aligned}
u_{1t}\left(-\frac{\tau_1}{\tau_{20}^*}\right) &= ze^{-i\omega_{20}^*\tau_1} + \bar{z}e^{i\omega_{20}^*\tau_1} + W_{20}^{(1)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)\frac{z^2}{2} + W_{11}^{(1)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)z\bar{z} \\
&\quad + W_{02}^{(1)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)\frac{\bar{z}^2}{2} + O\big(|(z,\bar{z})|^3\big), \\
u_{2t}\left(-\frac{\tau_1}{\tau_{20}^*}\right) &= q_2 ze^{-i\omega_{20}^*\tau_1} + \bar{q}_2\bar{z}e^{i\omega_{20}^*\tau_1} + W_{20}^{(2)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)\frac{z^2}{2} \\
&\quad + W_{11}^{(2)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)z\bar{z} + W_{02}^{(2)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)\frac{\bar{z}^2}{2} + O\big(|(z,\bar{z})|^3\big), \\
u_{3t}\left(-\frac{\tau_1}{\tau_{20}^*}\right) &= q_3 ze^{-i\omega_{20}^*\tau_1} + \bar{q}_3\bar{z}e^{i\omega_{20}^*\tau_1} + W_{20}^{(3)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)\frac{z^2}{2} + W_{11}^{(3)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)z\bar{z} \\
&\quad + W_{02}^{(3)}\left(-\frac{\tau_1}{\tau_{20}^*}\right)\frac{\bar{z}^2}{2} + O\big(|(z,\bar{z})|^3\big), \\
u_{1t}(-1) &= ze^{-i\omega_{20}^*\tau_{20}^*} + \bar{z}e^{i\omega_{20}^*\tau_{20}^*} + W_{20}^{(1)}(-1)\frac{z^2}{2} + W_{11}^{(1)}(-1)z\bar{z}
\end{aligned}$$

$$
\begin{aligned}
&+ W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2} + O\big(\big|(z,\bar{z})\big|^3\big),\\
u_{2t}(-1) &= q_2 z e^{-i\omega_{20}^*\tau_{20}^*} + \bar{q}_2\bar{z}e^{i\omega_{20}^*\tau_{20}^*} + W_{20}^{(2)}(-1)\frac{z^2}{2} + W_{11}^{(2)}(-1)z\bar{z}\\
&+ W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2} + O\big(\big|(z,\bar{z})\big|^3\big),\\
u_{3t}(-1) &= q_3 z e^{-i\omega_{20}^*\tau_{20}^*} + \bar{q}_3\bar{z}e^{i\omega_{20}^*\tau_{20}^*} + W_{20}^{(3)}(-1)\frac{z^2}{2} + W_{11}^{(3)}(-1)z\bar{z}\\
&+ W_{02}^{(3)}(-1)\frac{\bar{z}^2}{2} + O\big(\big|(z,\bar{z})\big|^3\big).
\end{aligned}
$$

Comparing the coefficients with (3.10), we have

$$
\begin{aligned}
g_{20} &= 2\bar{D}\tau_{20}^*\big\{\big[k_{11}q_3e^{-2i\omega_{20}^*\tau_1} + k_{12}q_3^2e^{-2i\omega_{20}^*\tau_1}\big] + \bar{q}_2^*\big[k_{21}q_3e^{-2i\omega_{20}^*\tau_1} + k_{22}q_3^2e^{-2i\omega_{20}^*\tau_1}\big]\\
&+ \bar{q}_3^*\big[k_{31}q_2q_3e^{-2i\omega_{20}^*\tau_{20}^*} + k_{32}q_2^2e^{-2i\omega_{20}^*\tau_{20}^*}\big]\big\},\\
g_{11} &= \bar{D}\tau_{20}^*\big\{\big[k_{11}(q_3+\bar{q}_3) + 2k_{12}q_3\bar{q}_3\big] + \bar{q}_2^*\big[k_{21}(q_3+\bar{q}_3) + 2k_{22}q_3\bar{q}_3\big]\\
&+ \bar{q}_3^*\big[k_{31}(q_2\bar{q}_3 + \bar{q}_2q_3) + 2k_{32}q_2\bar{q}_2\big]\big\},\\
g_{02} &= 2\bar{D}\tau_{20}^*\big\{\big[k_{11}\bar{q}_3e^{2i\omega_{20}^*\tau_1} + k_{12}\bar{q}_3{}^2e^{2i\omega_{20}^*\tau_1}\big] + \bar{q}_2^*\big[k_{21}\bar{q}_3e^{2i\omega_{20}^*\tau_1} + k_{22}\bar{q}_3{}^2e^{2i\omega_{20}^*\tau_1}\big]\\
&+ \bar{q}_3^*\big[k_{31}\bar{q}_2\bar{q}_3e^{2i\omega_{20}^*\tau_{20}^*} + k_{32}\bar{q}_2{}^2e^{2i\omega_{20}^*\tau_{20}^*}\big]\big\},\\
g_{21} &= \bar{D}\tau_{20}^*\Bigg\{\Bigg[k_{11}\Bigg(2e^{-i\omega_{20}^*\tau_1}W_{11}^{(3)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg) + e^{i\omega_{20}^*\tau_1}W_{20}^{(3)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg) + \bar{q}_3e^{i\omega_{20}^*\tau_1}W_{20}^{(1)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg)\\
&+ 2q_3e^{-i\omega_{20}^*\tau_1}W_{11}^{(1)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg)\Bigg)\\
&+ k_{12}\Bigg(2\bar{q}_3e^{i\omega_{20}^*\tau_1}W_{20}^{(3)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg) + 4q_3e^{-i\omega_{20}^*\tau_1}W_{11}^{(3)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg)\Bigg)\\
&+ k_{13}\big(4\bar{q}_3q_3e^{-i\omega_{20}^*\tau_1} + 2q_3^2e^{-i\omega_{20}^*\tau_1}\big) + 6k_{14}q_3^2\bar{q}_3{}^2e^{-i\omega_{20}^*\tau_1}\Bigg]\\
&+ \bar{q}_2^*\Bigg[k_{21}\Bigg(2e^{-i\omega_{20}^*\tau_1}W_{11}^{(3)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg) + e^{i\omega_{20}^*\tau_1}W_{20}^{(3)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg)\\
&+ \bar{q}_3e^{i\omega_{20}^*\tau_1}W_{20}^{(1)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg) + 2q_3e^{-i\omega_{20}^*\tau_1}W_{11}^{(1)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg)\Bigg)\\
&+ k_{22}\Bigg(2\bar{q}_3e^{i\omega_{20}^*\tau_1}W_{20}^{(3)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg) + 4q_3e^{-i\omega_{20}^*\tau_1}W_{11}^{(3)}\Bigg(-\frac{\tau_1}{\tau_{20}^*}\Bigg)\Bigg)\\
&+ k_{23}\big(4\bar{q}_3q_3e^{-i\omega_{20}^*\tau_1} + 2q_3^2e^{-i\omega_{20}^*\tau_1}\big) + 6k_{24}q_3^2\bar{q}_3{}^2e^{-i\omega_{20}^*\tau_1}\Bigg]\\
&+ \bar{q}_3^*\big[k_{31}\big(2q_2e^{-i\omega_{20}^*\tau_{20}^*}W_{11}^{(3)}(-1) + \bar{q}_2e^{i\omega_{20}^*\tau_{20}^*}W_{20}^{(3)}(-1)\\
&+ \bar{q}_3e^{i\omega_{20}^*\tau_{20}^*}W_{20}^{(2)}(-1) + 2q_3e^{-i\omega_{20}^*\tau_{20}^*}W_{11}^{(2)}(-1)\big)\\
&+ k_{32}\big(4q_2e^{-i\omega_{20}^*\tau_{20}^*}W_{11}^{(2)}(-1) + 2\bar{q}_2e^{i\omega_{20}^*\tau_{20}^*}W_{20}^{(2)}(-1)\big)\\
&+ k_{33}\big(4q_2\bar{q}_2q_3e^{-i\omega_{20}^*\tau_{20}^*} + 2q_2^2\bar{q}_3e^{-i\omega_{20}^*\tau_{20}^*}\big)\\
&+ 6k_{34}q_2^2\bar{q}_2e^{-i\omega_{20}^*\tau_{20}^*}\big]\Bigg\},
\end{aligned}
$$

where

$$W_{20}(\theta) = \frac{ig_{20}}{\omega_{20}^*\tau_{20}^*} q(0) e^{i\omega_{20}^*\tau_{20}^*\theta} + \frac{i\bar{g}_{02}}{3\omega_{20}^*\tau_{20}^*} \bar{q}(0) e^{-i\theta\omega_{20}^*\tau_{20}^*} + E_1 e^{2i\theta\omega_{20}^*\tau_{20}^*},$$

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega_{20}^*\tau_{20}^*} q(0) e^{i\theta\omega_{20}^*\tau_{20}^*} + \frac{i\bar{g}_{11}}{\omega_{20}^*\tau_{20}^*} \bar{q}(0) e^{-i\theta\omega_{20}^*\tau_{20}^*} + E_2,$$

and

$$E_1 = 2 \begin{bmatrix} 2i\omega_{20}^* + \mu + A_0 e^{-2i\omega_{20}^*\tau_1} & -d & B_0 e^{-2i\omega_{20}^*\tau_1} \\ -A_0 e^{-2i\omega_{20}^*\tau_1} & 2i\omega_{20}^* - \omega & -B_0 e^{-2i\omega_{20}^*\tau_1} \\ 0 & -C_0 e^{-2i\omega_{20}^*\tau_{20}^*} & 2i\omega_{20}^* - D_0 e^{-2i\omega_{20}^*\tau_{20}^*} + m \end{bmatrix}^{-1} \cdot \begin{bmatrix} M_1 \\ M_2 \\ M_3 \end{bmatrix},$$

$$E_2 = 2 \begin{bmatrix} -\mu - A_0 & d & -B_0 \\ A_0 & \omega & B_0 \\ 0 & C_0 & D_0 - m \end{bmatrix}^{-1} \cdot \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix},$$

where

$$M_1 = k_{11} q_3 e^{-2i\omega_{20}^*\tau_1} + k_{12} q_3^2 e^{-2i\omega_{20}^*\tau_1}, \qquad M_2 = k_{21} q_3 e^{-2i\omega_{20}^*\tau_1} + k_{22} q_3^2 e^{-2i\omega_{20}^*\tau_1},$$

$$M_3 = k_{31} q_2 q_3 e^{-2i\omega_{20}^*\tau_{20}^*} + k_{32} q_2^2 e^{-2i\omega_{20}^*\tau_{20}^*}, \qquad N_1 = k_{11}(q_3 + \bar{q}_3) + 2k_{12} q_3 \bar{q}_3,$$

$$N_2 = k_{21}(q_3 + \bar{q}_3) + 2k_{22} q_3 \bar{q}_3, \qquad N_3 = k_{31}(q_2 \bar{q}_3 + \bar{q}_2 q_3) + 2k_{32} q_2 \bar{q}_2.$$

Thus we can calculate the following values:

$$C_1(0) = \frac{i}{2\omega_{20}^*\tau_{20}^*}\left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \qquad \mu_2 = -\frac{\operatorname{Re}(C_1(0))}{\operatorname{Re}(\lambda'(\tau_{20}^*))},$$

$$T_2 = -\frac{\operatorname{Im} C_1(0) + \mu_2 \operatorname{Im} \lambda'(\tau_{20}^*)}{\omega_{20}^*\tau_{20}^*}, \qquad \beta_2 = 2\operatorname{Re}\bigl(C_1(0)\bigr).$$

Based on this discussion, we obtain the following results.

Theorem 3.1

(i) *μ_2 determines the direction of the Hopf bifurcation. If $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical* (*subcritical*).

(ii) *β_2 determines the stability of the bifurcating periodic solutions. If $\beta_2 < 0$ ($\beta_2 > 0$), then the bifurcating periodic solutions are stable* (*unstable*).

(iii) *T_2 determines the period of the bifurcating periodic solutions. If $T_2 > 0$ ($T_2 < 0$), then the period of the bifurcating periodic solutions increases* (*decreases*).

4 Numerical simulation

In this section, we give some numerical simulations supporting our theoretical predictions. The selection of parameter values refers to [4] and references therein. The same parameters as in [4] are adopted: $\mu = 0.1, k = 63, \beta = 0.01, \beta_1 = 0.01, \gamma = 0.01$. According to [4] and references therein, the other parameters $\alpha, \alpha_1, \Lambda, d, m$ are appropriately chosen to system (1.3). As an example, we consider the following system:

$$\begin{cases} \frac{dS}{dt} = 0.01(63 - S) - \frac{0.01Y(t-\tau_1)}{1+0.02Y(t-\tau_1)} S(t-\tau_1) + 0.02I, \\ \frac{dI}{dt} = \frac{0.01Y(t-\tau_1)}{1+0.02Y(t-\tau_1)} S(t-\tau_1) - 0.04I, \\ \frac{dY}{dt} = \frac{0.01I(t-\tau_2)}{1+0.01I(t-\tau_2)} (\frac{10}{0.1} - Y(t-\tau_2)) - 0.1Y. \end{cases} \tag{4.1}$$

Obviously, hypotheses (H_1) and (H_2) hold:

(H_1) $m\omega + K\mu(\beta_1 + \alpha_1 m) - dm = 0.0089$, $\alpha\beta_1 K\Lambda\mu + m(m\omega + K\mu(\beta_1 + \alpha_1 m) - dm) = 0.0022 > 0$, $\beta_1\beta K\Lambda\mu - m^2\mu\omega = 6.26e{-}04$, $\alpha m\mu\omega + \beta(m\omega + K\mu(\beta_1 + \alpha_1 m) - dm) = 9.01e{-}05 > 0$;

(H_2) $A_1 + B_1 + C_1 = 0.6684 > 0$, $A_3 + B_3 + C_3 + D_2 = 0.002 > 0$, $(A_1 + B_1 + C_1)(A_2 + B_2 + C_2 + D_1) - (A_3 + B_3 + C_3 + D_2) = 0.0759 > 0$.

Then $E = (4.0546, 29.4727, 69.4784)$ is a unique positive equilibrium of system (4.1).

(1) When $\tau_1 = \tau_2 = 0$, the positive equilibrium $E = (4.0546, 29.4727, 69.4784)$ of system (4.1) is locally asymptotically stable.

(2) When $\tau_2 = 0$ and $\tau_1 \neq 0$, the characteristic equation is

$$\lambda^3 + 0.3776\lambda^2 + 0.0168\lambda + 1.3105e{-}04 + \left(0.29076\lambda^2 + 0.0998\lambda + 0.0019\right)e^{-\lambda\tau_1} = 0.$$

By a simple computation we can easily get $E_{23} = -3.5637e{-}06 < 0$, $\omega_{10} = 0.2862$, $\tau_{10} = 5.8744$. By Theorem 2.2, if $\tau_1 = 3 < \tau_{10} = 5.8744$ or $\tau_1 = 5.79 < \tau_{10} = 5.8744$, then the positive equilibrium E is asymptotically stable. If $\tau_1 = 5.88 > \tau_{10} = 5.8744$, then the positive equilibrium E is unstable, and system (4.1) undergoes a Hopf bifurcation at E, and a family of periodic solutions bifurcate from the positive equilibrium E. This property can be illustrated by in Figs. 1–3. Further, we can compute the values

$$c_1(0) = -0.6538 - 0.005i, \qquad \mu_2 = 0.1314, \qquad T_2 = -1.3628, \qquad \beta_2 = -0.3076.$$

Since $\mu_2 > 0$ and $\beta_2 < 0$, the bifurcating periodic solution from E is supercritical and asymptotically stable at $\tau = \tau_1$.

(3) When $\tau_1 > 0$ and $\tau_2 > 0$, let $\tau_1 = 5.79 \in (0, 5.8744)$ and chose τ_2 as a parameter. Then the characteristic equation is

$$\begin{aligned} &\lambda^3 + 0.15\lambda^2 + 0.0054\lambda + 4.0e{-}05 + \left(0.2906\lambda^2 + 0.349\lambda + 5.8151e{-}04\right)e^{-5.79\lambda} \\ &\quad + \left(0.2276\lambda^2 + 0.0114\lambda + 9.1054e{-}05\right)e^{-\lambda\tau_2} + (0.0649\lambda + 0.0013)e^{-\lambda(5.79+\tau_2)} \\ &\quad = 0. \end{aligned}$$

We obtain $E_{43} = -1.3868e{-}06 < 0$, $\omega_{20}^* = 0.4438$, $\tau_{20}^* = 4.5647$, and condition

(H_5) $Q_{31}Q_{33} + Q_{32}Q_{34} = 0.0079 \neq 0$

is satisfied. From Theorem 2.4 we know that the positive equilibrium E is asymptotically stable for $\tau_2 \in [0, \tau_{20}^*)$. As τ_2 continues to increase, the positive equilibrium E will lose stability, and a Hopf bifurcation occurs once $\tau_2 > \tau_{20}^*$. The corresponding numerical simulation results are shown Figs. 4–5.

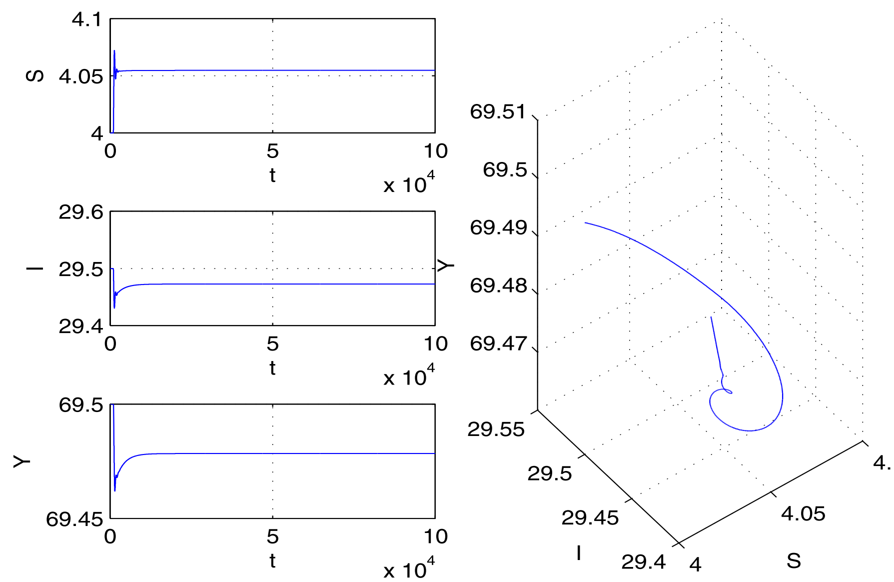

Figure 1 The trajectories of system (4.1) with $\tau_1 = 3 < \tau_{10} = 5.8744$, $\tau_2 = 0$. The positive equilibrium E is asymptotically stable. The initial value is $(4, 29.5, 69.5)$

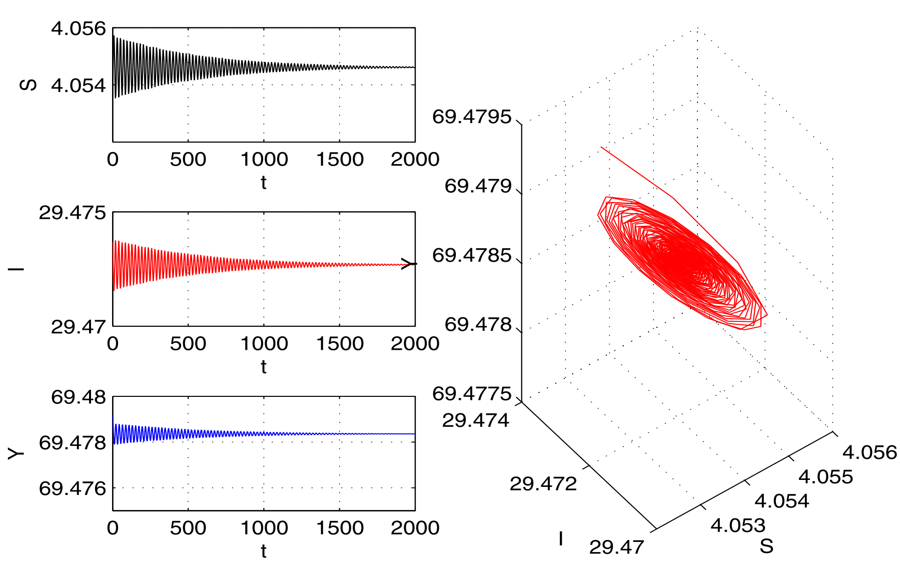

Figure 2 The trajectories of system (4.1) with $\tau_1 = 5.79 < \tau_{10} = 5.8744$, $\tau_2 = 0$. The positive equilibrium E is asymptotically stable. The initial value is $(4, 29.5, 69.5)$

Further, we get $c_1(0) = -0.0055 - 0.005i$, $\mu_2 = 0.2471$, $T_2 = 0.0044$, $\beta_2 = -0.0111$. Therefore, from Theorem 3.1, we know that the Hopf bifurcation is supercritical and the bifurcating periodic solutions are stable.

5 Conclusion

In this paper, we study the dynamics of plant virus propagation model with two delays. First, we obtain sufficient conditions for the stability of positive equilibrium E and the ex-

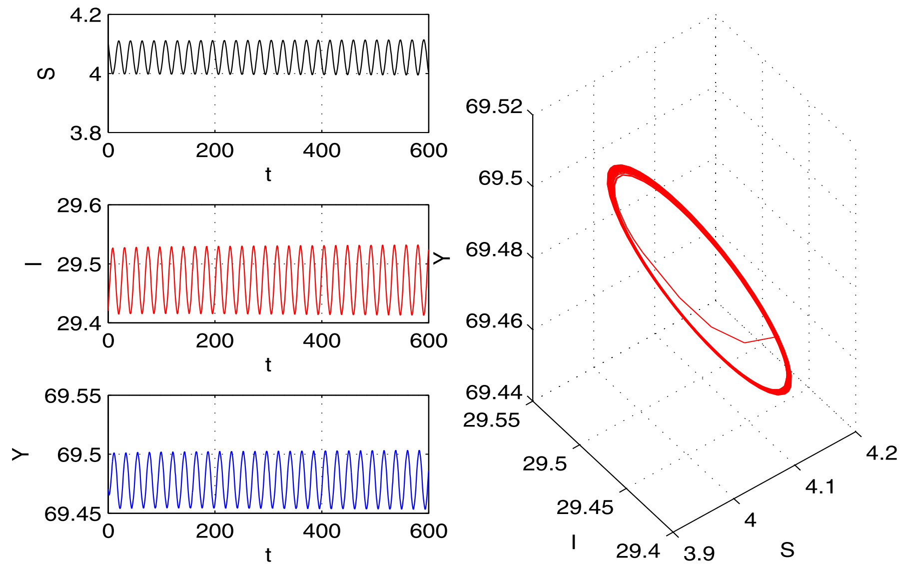

Figure 3 The trajectories of system (4.1) with $\tau_1 = 5.88 > \tau_{10} = 5.8744, \tau_2 = 0$. A Hopf bifurcation occurs from the positive equilibrium E. The initial value is $(4, 29.5, 69.5)$

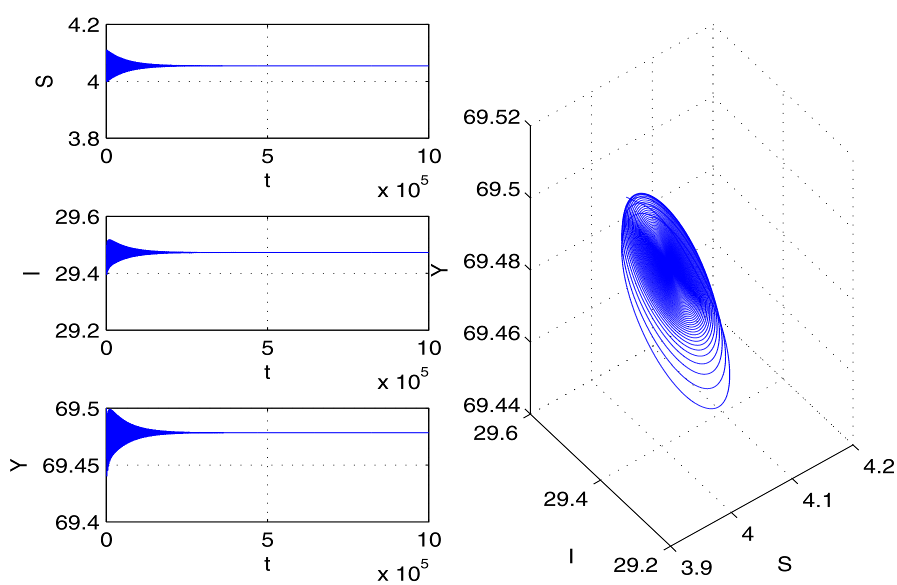

Figure 4 The trajectories of system (4.1) with $\tau_1 = 5.79, \tau_2 = 1 < \tau_{20}^* = 4.5647$. The positive equilibrium E is asymptotically stable. The initial value is $(4, 29.5, 69.5)$

istence of Hopf bifurcation when $\tau_1 > 0, \tau_2 = 0$ and $\tau_1 \in (0, \tau_{10}), \tau_2 > 0, \tau_1 \neq \tau_2$, respectively. Next, when $\tau_1 \neq \tau_2$, by using the center manifold and normal form theory, regarding τ_2 as a parameter, we investigate the direction and stability of the Hopf bifurcation. We derive an explicit algorithm for determining the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions. Finally, a numerical example supporting our theoretical predictions is given.

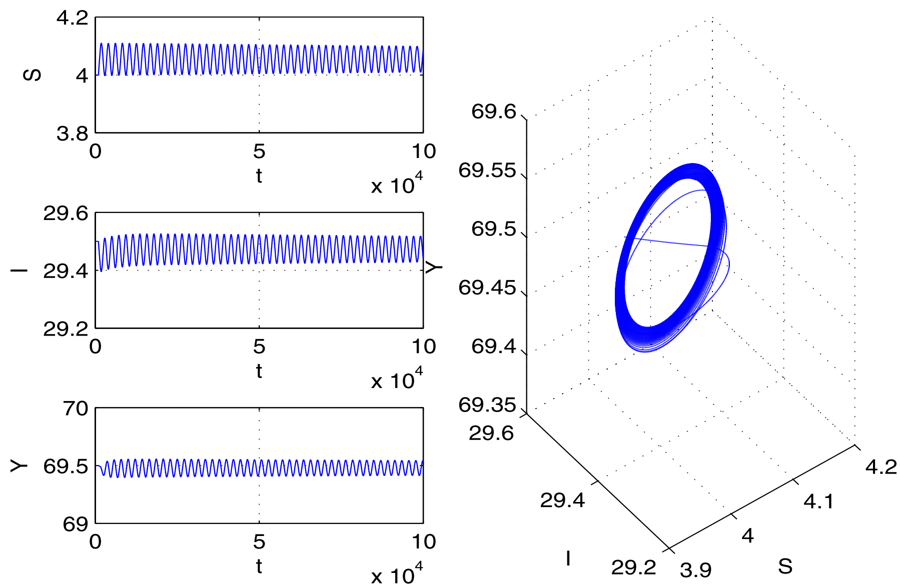

Figure 5 The trajectories of system (4.1) with $\tau_1 = 5.79, \tau_2 = 5.2 > \tau_{20}^{*} = 4.5647$. A Hopf bifurcation occurs from the positive equilibrium E. The initial value is $(4, 29.5, 69.5)$

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Competing interests
The authors declare that they have no competing interests.

Authors' contributions
All authors contributed equally to the writing of this paper. All authors read and approved the final manuscript.

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