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Research Article

Stability and Hopf Bifurcation Analysis of a Plant Virus Propagation Model with Two Delays

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To understand the interaction between the insects and the plants, a system of delay differential equations is proposed and studied. We prove that if $R_0 \leq 1$, the disease-free equilibrium is globally asymptotically stable for any length of time delays by constructing a Lyapunov functional, and the system admits a unique endemic equilibrium if $R_0 > 1$. We establish the sufficient conditions for the stability of the endemic equilibrium and existence of Hopf bifurcation. Using the normal form theory and center manifold theorem, the explicit formulae which determine the stability, direction, and other properties of bifurcating periodic solutions are derived. Some numerical simulations are given to confirm our analytic results.

1. Introduction

Plants are very important not only to man's survival but to every species on Earth; however, plants may contract a disease by many different ways. Tremendous crop losses and global threat to food security have been caused by plant diseases [1, 2]. In recent years, plant diseases have attracted the interest of many mathematical modeling researchers and epidemiologists [3–7].

Mathematical models provide powerful tools for investigating how an infection propagates within a population of plants. Shi et al. [8] have proposed an epidemic model which describes vector-borne plant diseases, and the global dynamics of the system have been analyzed in terms of the basic reproduction number. Luo et al. [9] studied a discrete plant virus disease model with roguing and replanting; they proved that the basic reproduction number serves as a threshold parameter in determining the global dynamics of the model. The plant diseases epidemic models have been extensively studied by many authors (see [10–14]).

In [15], a delay differential equations was proposed to model the interaction between plants, a plant virus, and the insect-vector that transfers the virus from one plant to another. Since insects can only bite a limited number of plants, then the interaction between vector and plant is of predator-prey Holling type II [16]. In order to consider the time it takes for the virus to spread throughout the plant or insect-vector, a couple of delays were introduced to the model (see [15] for more details). They obtained the following model:

$$\begin{aligned}
\frac{dS}{dt} &= \mu(K-S) - \frac{\beta Y(t-\tau_1)}{1+\alpha Y(t-\tau_1)} S(t-\tau_1) + dI, \\
\frac{dI}{dt} &= \frac{\beta Y(t-\tau_1)}{1+\alpha Y(t-\tau_1)} S(t-\tau_1) - (d+\mu+\gamma) I, \\
\frac{dR}{dt} &= \gamma I - \mu R, \qquad (1) \\
\frac{dX}{dt} &= \Lambda - \frac{\beta_1 I(t-\tau_2)}{1+\alpha_1 I(t-\tau_2)} X(t-\tau_2) - mX, \\
\frac{dY}{dt} &= \frac{\beta_1 I(t-\tau_2)}{1+\alpha_1 I(t-\tau_2)} X(t-\tau_2) - mY,
\end{aligned}$$

where the state variables $S(t)$, $I(t)$, and $R(t)$ represent the number of susceptible, infected, and recovered plants at time t, respectively. Because when a plant dies by the virus or natural death in farms, it is replaced with a new healthy plant. The new plant shares the same characteristics of the plant it replaced, before it was infected. Then it is supposed that the total number of plants stabilizes at K, $K = S + I + R$. μ is the natural death rate of plants; β is the infection rate of plants due to vectors; α is the saturation constant of plants due to vectors; d is the death rate of infected plants due to the disease; γ is the recovery rate of plants. The insect-vectors are divided into two populations: susceptible and infective denoted by $X(t)$ and $Y(t)$, respectively. The total number of insects is denoted by $N(t)$, and then $N(t) = X(t) + Y(t)$. Λ is the replenishing rate of vectors (birth and/or immigration); β_1 is the infection rate of vectors due to plants; α_1 is the saturation constant of vectors due to plants; m is the natural death rate of vectors. 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.

Notice that

$$\frac{dN}{dt} = \Lambda - mN, \tag{2}$$

and then $N(t) \to \Lambda/m$ as $t \to \infty$.

Thus, one can consider the following reduced system:

$$\begin{aligned} \frac{dS}{dt} &= \mu (K - S) - \frac{\beta Y(t-\tau_1)}{1+\alpha Y(t-\tau_1)} S(t-\tau_1) + dI, \\ \frac{dI}{dt} &= \frac{\beta Y(t-\tau_1)}{1+\alpha Y(t-\tau_1)} S(t-\tau_1) - aI, \\ \frac{dY}{dt} &= \frac{\beta_1 I(t-\tau_2)}{1+\alpha_1 I(t-\tau_2)} \left(\frac{\Lambda}{m} - Y(t-\tau_2)\right) - mY, \end{aligned} \tag{3}$$

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

For model (3), Jackson and Chen-Charpentier [15] gave the basic reproduction number and found the equilibria of the model, and then they studied the stability of equilibria only for particular values of the parameters using numerical methods. Therefore, in this paper, we reconsider the plant disease model (3) in theoretical aspects, and we establish the stability of equilibria, the existence of Hopf bifurcation, and the stability, direction, and other properties of bifurcating periodic solution will also be discussed.

This paper is organized as follows. In Section 2, we discuss the stability of the equilibria and the existence of the Hopf bifurcations occurring at the endemic equilibrium. In Section 3, the formulae determining the direction of the Hopf bifurcations and the stability of bifurcating periodic solutions on the center manifold are obtained by using the normal form theory and the center manifold theorem by Hassard et al. [17]. In Section 4, we perform numerical simulations to illustrate the analytical results. We conclude with a brief discussion in Section 5.

2. Stability Analysis and Hopf Bifurcation

Let $\tau = \max\{\tau_1, \tau_2\}$, and the initial conditions for (3) are

$$\begin{aligned} (\phi_1(\theta), \phi_2(\theta), \phi_3(\theta)) &\in C_+ = C\left([-\tau, 0], \mathbb{R}_+^3\right), \\ \phi_i(0) &> 0, \quad i = 1, 2, 3. \end{aligned} \tag{4}$$

By the fundamental theory of functional differential equations [18], it follows that, for any initial conditions (4), there is a unique solution $(S(t), I(t), Y(t))$ of (3) for all $t \geq 0$.

Let Ω be the following subset of $\mathbb{R}_+^3$:

$$\Omega = \left\{(S, I, Y) \in \mathbb{R}_+^3 : S + I \leq K,\ Y \leq \frac{\Lambda}{m}\right\}. \tag{5}$$

Using a proof process similar to that in [19, 20], we obtain the following lemma.

Lemma 1. *The solutions of system (3) which satisfy the initial conditions (4) are positive. The set Ω is positively invariant.*

In [15], the basic reproduction number for (3) has been identified as

$$R_0 = \sqrt{\frac{\beta\beta_1 \Lambda K}{m^2 a}}. \tag{6}$$

Equation (3) always has a disease-free equilibrium $E_0(K, 0, 0)$. If $R_0 > 1$, then (3) admits a unique endemic equilibrium $E^*(S^*, I^*, Y^*)$, where

$$\begin{aligned} S^* &= \frac{a(\alpha\beta_1 K\Lambda\mu + m(ma + K\mu(\beta_1 + \alpha_1 m) - dm))}{\beta_1\beta\Lambda(\mu+\gamma) + a\beta_1\Lambda\mu a + \beta_1 m\mu a + \alpha_1 m^2 \mu a}, \\ I^* &= \frac{\beta_1\beta K\Lambda\mu - m^2\mu a}{\beta_1\beta\Lambda(\mu+\gamma) + a\beta_1\Lambda\mu a + \beta_1 m\mu a + \alpha_1 m^2 \mu a}, \\ Y^* &= \frac{\beta_1\beta K\Lambda\mu - m^2\mu a}{m(\alpha m\mu a + \beta(ma + K\mu(\beta_1 + \alpha_1 m) - dm))}. \end{aligned} \tag{7}$$

However, Jackson and Chen-Charpentier [15] did not give detailed dynamical analysis to this model. Theoretical analysis makes the model dynamics clear and enhances our understanding to the mathematical models. In this paper, we will give some analytic results of model (3).

Linearizing system (3) at E_0 gives characteristic equation

$$\begin{aligned} (\lambda + \mu)\left[\lambda^2 + (m+a)\lambda + ma - \frac{\beta\beta_1 K\Lambda}{m} e^{-\lambda\tau}\right] &= 0, \\ \tau &= \tau_1 + \tau_2. \end{aligned} \tag{8}$$

It is clear that $-\mu$ is one root of (8). Let $G(\lambda) = \lambda^2 + (m+a)\lambda + ma - (\beta\beta_1 K\Lambda/m)e^{-\lambda\tau}$. If $R_0 > 1$, we get $G(0) = ma(1 - R_0^2) < 0$, and $\lim_{\lambda\to+\infty} G(\lambda) = +\infty$, then $G(\lambda) = 0$ has one positive real root, and, hence, E_0 is unstable.

If $R_0 < 1$, it is easy to show that E_0 is locally asymptotically stable when $\tau = 0$, and then, by Theorem 3.4.1 in Kuang [21], E_0 is locally asymptotically stable for all $\tau \geq 0$.

Theorem 2. *If $R_0 \leq 1$, then E_0 is globally asymptotically stable for all $\tau_1 \geq 0$ and $\tau_2 \geq 0$.*

Proof. Constructing the following Lyapunov functional:

$$V(t) = I(t) + \frac{\beta K}{m} Y(t) + \int_{t-\tau_1}^{t} \frac{\beta S(\rho) Y(\rho)}{1+\alpha Y(\rho)} d\rho + \frac{\beta \beta_1 K \Lambda}{m^2} \int_{t-\tau_2}^{t} \frac{I(\rho)}{1+\alpha_1 I(\rho)} d\rho, \quad (9)$$

then

$$\begin{aligned} V'(t)\Big|_{(2)} &= \frac{\beta S Y}{1+\alpha Y} - \beta K Y - \frac{\beta\beta_1 K I(t-\tau_2) Y(t-\tau_2)}{m[1+\alpha_1 I(t-\tau_2)]} + \frac{\beta\beta_1 K\Lambda}{m^2}\frac{I}{1+\alpha_1 I} - aI \\ &\leq \beta S Y - \beta K Y + \frac{\beta\beta_1 K\Lambda}{m^2}\frac{I}{1+\alpha_1 I} - aI \\ &\leq \frac{\beta\beta_1 K\Lambda}{m^2} I - aI = \left(R_0^2 - 1\right) aI \leq 0. \end{aligned} \quad (10)$$

If we set $\{(S, I, Y) \mid V'(t) = 0\}$, then the largest invariant set is the singleton $\{E_0\}$. Therefore, by LaSalle's invariance principle [22], E_0 is globally asymptotically stable for all $\tau_1 \geq 0$ and $\tau_2 \geq 0$.

We now consider the local stability of the coexistence equilibrium $E^*(S^*, I^*, Y^*)$ and the existence of Hopf bifurcation at E^*. The linearized system of (3) at E^* is given by

$$\begin{aligned} \frac{dS}{dt} &= a_{11} S(t) + b_{11} S(t-\tau_1) + a_{12} I(t) + b_{13} Y(t-\tau_1), \\ \frac{dI}{dt} &= b_{21} S(t-\tau_1) + b_{23} Y(t-\tau_1) + a_{22} I(t), \\ \frac{dY}{dt} &= b_{32} I(t-\tau_2) + a_{33} Y(t) + b_{33} Y(t-\tau_2), \end{aligned} \quad (11)$$

with

$$\begin{aligned} a_{11} &= -\mu, \\ b_{11} &= -\frac{\beta Y^*}{1+\alpha Y^*}, \\ a_{12} &= d, \\ b_{13} &= -\frac{\beta S^*}{(1+\alpha Y^*)^2}, \\ b_{21} &= \frac{\beta Y^*}{1+\alpha Y^*}, \\ b_{23} &= \frac{\beta S^*}{(1+\alpha Y^*)^2}, \\ a_{22} &= -a, \\ b_{32} &= \frac{\beta_1}{(1+\alpha_1 I^*)^2}\left(\frac{\Lambda}{m} - Y^*\right), \\ a_{33} &= -m, \\ b_{33} &= -\frac{\beta_1 I^*}{1+\alpha_1 I^*}. \end{aligned} \quad (12)$$

Therefore, we obtain the following characteristic equation:

$$\begin{aligned} &\lambda^3 + m_2\lambda^2 + m_1\lambda + m_0 + e^{-\lambda\tau_1}\left(n_2\lambda^2 + n_1\lambda + n_0\right) \\ &+ e^{-\lambda\tau_2}\left(p_2\lambda^2 + p_1\lambda + p_0\right) \\ &+ e^{-\lambda(\tau_1+\tau_2)}\left(q_1\lambda + q_0\right) = 0, \end{aligned} \quad (13)$$

where

$$\begin{aligned} m_2 &= -\left(a_{11} + a_{22} + a_{33}\right), \\ m_1 &= a_{11}a_{22} + a_{11}a_{33} + a_{22}a_{33}, \\ m_0 &= -a_{11}a_{22}a_{33}, \\ n_0 &= b_{21}a_{33}\left(a_{12} + a_{22}\right), \\ n_1 &= -b_{21}\left(a_{12} + a_{22} + a_{33}\right), \\ n_2 &= b_{21}, \\ p_2 &= -b_{33}, \\ p_1 &= b_{33}\left(a_{11} + a_{22}\right), \\ p_0 &= -b_{33}a_{11}a_{22}, \\ q_1 &= -\left(b_{21}b_{33} + b_{23}b_{32}\right), \\ q_0 &= b_{21}b_{33}\left(a_{12} + a_{22}\right) + b_{23}b_{32}a_{11}. \end{aligned} \quad (14)$$

□

Case 1 ($\tau_1 = \tau_2 = 0$). Characteristic equation (13) becomes

$$\lambda^3 + m_{12}\lambda^2 + m_{11}\lambda + m_{10} = 0, \quad (15)$$

where

$$\begin{aligned} m_{12} &= m_2 + n_2 + p_2, \\ m_{11} &= m_1 + n_1 + p_1 + q_1, \\ m_{10} &= m_0 + n_0 + p_0 + q_0. \end{aligned} \quad (16)$$

Note that

$$\begin{aligned} \left(\frac{\beta_1 I^*}{1+\alpha_1 I^*}\right)\left(\frac{\Lambda}{m} - Y^*\right) &= mY^*, \\ \frac{\beta Y^* S^*}{1+\alpha Y^*} &= aI^*, \end{aligned} \quad (17)$$

then we get $(\beta S^*/(1+\alpha Y^*))(\beta_1/(1+\alpha_1 I^*))(\Lambda/m - Y^*) = ma$, and thus

$$\begin{aligned}
m_{12} &= \mu + a + m + \frac{\beta Y^*}{1+\alpha Y^*} + \frac{\beta_1 I^*}{1+\alpha_1 I^*} > 0, \\
m_{11} &= \mu a + \mu m + ma + \frac{\beta Y^*}{1+\alpha Y^*}(m+\mu+\gamma) \\
&\quad + \frac{\beta_1 I^*}{1+\alpha_1 I^*}(a+\mu) + \frac{\beta\beta_1 Y^* I^*}{(1+\alpha Y^*)(1+\alpha_1 I^*)} \\
&\quad - \frac{\beta S^*}{(1+\alpha Y^*)^2}\frac{\beta_1}{(1+\alpha_1 I^*)^2}\left(\frac{\Lambda}{m} - Y^*\right) > 0, \\
m_{10} &= ma\mu + \left(m + \frac{\beta_1 I^*}{1+\alpha_1 I^*}\right)(\mu+\gamma)\frac{\beta Y^*}{1+\alpha Y^*} \\
&\quad + \mu a \frac{\beta_1 I^*}{1+\alpha_1 I^*} \\
&\quad - \frac{\beta S^*}{(1+\alpha Y^*)^2}\frac{\beta_1}{(1+\alpha_1 I^*)^2}\left(\frac{\Lambda}{m} - Y^*\right)\mu > 0.
\end{aligned} \tag{18}$$

Since $m_{11} > \mu m + (\beta Y^*/(1+\alpha Y^*))(\mu+\gamma) + \beta_1 I^* a/(1+\alpha_1 I^*)$ and $m_{12} > \mu + a + m + \beta_1 I^*/(1+\alpha_1 I^*)$), it is easy to show that $m_{11}m_{12} - m_{10} > 0$, and, thus, all roots of (15) have negative real parts. That is, $E^*(S^*, I^*, Y^*)$ is locally asymptotically stable. Actually, by a similar proof as in [23], we can show that $E^*(S^*, I^*, Y^*)$ is globally asymptotically stable for $\tau_1 = \tau_2 = 0$.

Case 2 ($\tau_1 > 0, \tau_2 = 0$). Characteristic equation (13) becomes

$$\begin{aligned}
&\lambda^3 + m_{22}\lambda^2 + m_{21}\lambda + m_{20} \\
&\quad + \left(n_{22}\lambda^2 + n_{21}\lambda + n_{20}\right)e^{-\lambda\tau_1} = 0,
\end{aligned} \tag{19}$$

where

$$\begin{aligned}
m_{22} &= m_2 + p_2, \\
m_{21} &= m_1 + p_1, \\
m_{20} &= m_0 + p_0, \\
n_{22} &= n_2, \\
n_{21} &= n_1 + q_1, \\
n_{20} &= n_0 + q_0.
\end{aligned} \tag{20}$$

Suppose $\lambda = i\omega$ ($\omega > 0$) is a root of (19), similar discussion as those in [24], and we have

$$g(\rho) = \rho^3 + e_{22}\rho^2 + e_{21}\rho + e_{20} = 0, \tag{21}$$

where $\rho = \omega^2$, $e_{22} = m_{22}^2 - n_{22}^2 - 2m_{21}$, $e_{21} = m_{21}^2 - n_{21}^2 - 2m_{20}m_{22} + 2n_{20}n_{22}$, and $e_{20} = m_{20}^2 - n_{20}^2$.

Note that $g(0) = e_{20}$ and $\lim_{\rho\to+\infty} g(\rho) = +\infty$, and then, by [25], we have the following lemma.

Lemma 3. *For polynomial equation (21), we have the following results:*

(1) If (H21) $e_{20} \geq 0$ and $\Delta = e_{22}^2 - 3e_{21} \leq 0$, then (21) has no positive root.

(2) If (H22) $e_{20} \geq 0$, $\Delta = e_{22}^2 - 3e_{21} > 0$, $\rho^* = (-e_{21} + \sqrt{\Delta})/3 > 0$, $g'(\rho^*) = 3(\rho^*)^2 + 2e_{22}\rho^* + e_{21} \leq 0$, or (H23) $e_{20} < 0$, then (21) has positive root.

Suppose that (21) has positive roots, and we assume that (21) has three positive roots: ρ_1, ρ_2, and ρ_3; then $\omega_k = \sqrt{\rho_k}$, $k = 1,2,3$. The corresponding critical value of time delay $\tau_{1k}^{(j)}$ is

$$\begin{aligned}
\tau_{1k}^{(j)} &= \frac{1}{\omega_k}\arccos\left\{\frac{A_{24}\omega_k^4 + A_{22}\omega_k^2 + A_{20}}{B_{24}\omega_k^4 + B_{22}\omega_k^2 + B_{20}}\right\} + \frac{2\pi j}{\omega_k}, \\
&\qquad k = 1,2,3;\ j = 0,1,2,\ldots,
\end{aligned} \tag{22}$$

where

$$\begin{aligned}
A_{24} &= n_{21} - m_{22}n_{22}, \\
A_{22} &= n_{20}(m_{22} + m_{20}) - n_{21}m_{21}, \\
A_{20} &= -n_{20}m_{20}, \\
B_{24} &= n_{22}^2, \\
B_{22} &= n_{21}^2 - 2n_{20}n_{22}, \\
B_{20} &= n_{20}^2.
\end{aligned} \tag{23}$$

$\pm i\omega_k$ is a pair of purely imaginary roots of (19) with $\tau_1 = \tau_{1k}^{(j)}$. Let $\tau_{10}^* = \min_{k\in\{1,2,3\}}\{\tau_{1k}^{(0)}\}$, when $\tau_1 = \tau_{10}^*$, and (19) has a pair of purely imaginary roots $\pm i\omega_{10}^*$.

We now verify the transversality condition, again by the analysis in [24], and we get

$$\begin{aligned}
\operatorname{sign}\left\{\frac{d(\operatorname{Re}\lambda)}{d\tau_1}\right\}_{\lambda=i\omega_{10}^*} &= \operatorname{sign}\left\{\operatorname{Re}\left(\frac{d\lambda}{d\tau_1}\right)^{-1}\right\}_{\lambda=i\omega_{10}^*} \\
&= \frac{g'\left((\omega_{10}^*)^2\right)}{\left(n_{21}\omega_{10}^*\right)^2 + \left(n_{20} - n_{22}(\omega_{10}^*)^2\right)^2},
\end{aligned} \tag{24}$$

assuming that

$$(H24)\quad g'\left((\omega_{10}^*)^2\right) \neq 0. \tag{25}$$

Therefore, we have the following result.

Theorem 4. *For system (3), if $\tau_2 = 0$,*

(1) if (H21) holds, then the endemic equilibrium $E^*(S^*, I^*, Y^*)$ is locally asymptotically stable for all $\tau_1 \geq 0$,

(2) if (H22) or (H23) and (H24) hold, then as τ_1 increases from zero, there is a value τ_{10}^* such that the endemic equilibrium $E^*(S^*, I^*, Y^*)$ is locally asymptotically stable when $\tau_1 \in [0, \tau_{10}^*)$ and unstable when $\tau_1 > \tau_{10}^*$. Furthermore, system (3) undergoes a Hopf bifurcation at E^* when $\tau_1 = \tau_{10}^*$.

Case 3 ($\tau_1 = 0, \tau_2 > 0$). With similar analysis as to Case 2, we get the following theorem.

Theorem 5. *For system (3), if $\tau_1 = 0$,*

(1) if (H31) holds, then the endemic equilibrium $E^*(S^*, I^*, Y^*)$ is locally asymptotically stable for all $\tau_2 \geq 0$,

(2) if (H32) or (H33) and (H34) hold, then as τ_2 increases from zero, there is a value τ_{20}^* such that the endemic equilibrium $E^*(S^*, I^*, Y^*)$ is locally asymptotically stable when $\tau_2 \in [0, \tau_{20}^*)$ and unstable when $\tau_2 > \tau_{20}^*$. Furthermore, system (3) undergoes a Hopf bifurcation at E^* when $\tau_2 = \tau_{20}^*$.

Assumptions ($H31$)–($H34$) are very similar to ($H21$)–($H24$), so we omit them.

Case 4 ($\tau_1 > 0, \tau_2 \in [0, \tau_{20}^*)$). We consider (3) with τ_2 in its stable interval and regard τ_1 as a parameter. Let $\lambda = i\omega_1$ ($\omega_1 > 0$) be a root of (13), separating real and imaginary parts, and we have the following:

$$\begin{aligned} A_{41} \sin \omega_1 \tau_1 + A_{42} \cos \omega_1 \tau_1 &= A_{43}, \\ A_{41} \cos \omega_1 \tau_1 - A_{42} \sin \omega_1 \tau_1 &= A_{44}, \end{aligned} \tag{26}$$

where

$$\begin{aligned} A_{41} &= -n_1\omega_1 + q_0 \sin \omega_1 \tau_2 - q_1 \omega_1 \cos \omega_1 \tau_2, \\ A_{42} &= n_2 \omega_1^2 - n_0 - q_0 \cos \omega_1 \tau_2 - q_1 \omega_1 \sin \omega_1 \tau_2, \\ A_{43} &= -\omega_1^2 \left(m_2 + p_2 \cos \omega_1 \tau_2\right) + p_1 \omega_1 \sin \omega_1 \tau_2 \\ &\quad + p_0 \cos \omega_1 \tau_2 + m_0, \\ A_{44} &= -\omega_1^3 + p_2 \omega_1^2 \sin \omega_1 \tau_2 + \omega_1 \left(m_1 + p_1 \cos \omega_1 \tau_2\right) \\ &\quad - p_0 \sin \omega_1 \tau_2. \end{aligned} \tag{27}$$

From (26), we have

$$\begin{aligned} &\omega_1^6 + e_{42}\omega_1^4 + e_{41}\omega_1^2 + e_{40} \\ &\quad + \cos \omega_1 \tau_2 \left(c_{44}\omega_1^4 + c_{42}\omega_1^2 + c_{40}\right) \\ &\quad + \sin \omega_1 \tau_2 \left(c_{45}\omega_1^5 + c_{43}\omega_1^3 + c_{41}\omega_1\right) = 0, \end{aligned} \tag{28}$$

where

$$\begin{aligned} e_{40} &= m_0^2 + p_0^2 - q_0^2 - n_0^2, \\ e_{41} &= m_1^2 - 2m_0 m_2 - 2p_0 p_2 + p_1^2 - n_1^2 + 2n_0 n_2 - q_1^2, \\ e_{42} &= m_2^2 - 2m_1 + p_2^2 - n_2^2, \\ c_{40} &= 2\left(m_0 p_0 - n_0 q_0\right), \\ c_{41} &= 2\left(m_0 p_1 - p_0 m_1 + n_1 q_0 - n_0 q_1\right), \\ c_{42} &= 2\left(m_1 p_1 - m_0 p_2 - m_2 p_0 - n_1 q_1 + q_0 n_2\right), \\ c_{43} &= 2\left(m_1 p_2 - m_2 p_1 + p_0 + n_2 q_1\right), \\ c_{44} &= 2\left(m_2 p_2 - p_1\right), \\ c_{45} &= -2p_2. \end{aligned} \tag{29}$$

We make the following assumption.

($H41$) Equation (28) has finite positive roots $\omega_1^{(1)}, \omega_1^{(2)}, \ldots, \omega_1^{(k)}$.

For every fixed $\omega_1^{(i)}$, $i = 1, 2, \ldots, k$, there exists a sequence $\tau_{1i}^{(j)}$ such that (28) holds, where

$$\begin{aligned} \tau_{1i}^{(j)} &= \frac{1}{\omega_1^{(i)}} \arccos \left\{ \frac{A_{41}A_{44} + A_{42}A_{43}}{A_{41}^2 + A_{42}^2} \right\} + \frac{2\pi j}{\omega_1^{(i)}}, \\ &\qquad i = 1, 2, \ldots, k; \;\; j = 0, 1, 2, \ldots. \end{aligned} \tag{30}$$

Let $\tau_{10} = \min\{\tau_{1i}^{(0)} \mid i = 1, 2, \ldots, k\}$, when $\tau_1 = \tau_{10}$, and (13) has a pair of purely imaginary roots $\pm i\omega_{10}$.

In addition to ($H41$), we further assume that

$$(H42) \qquad \left[\frac{d}{d\tau_1}(\operatorname{Re}\lambda)\right]_{\lambda = i\omega_{10}} \neq 0. \tag{31}$$

Therefore, by the Hopf bifurcation theorem for functional differential equations in Hale [18], the following result holds.

Theorem 6. *For system (3), suppose (H41) and (H42) are satisfied, and $\tau_1 > 0$ and $\tau_2 \in [0, \tau_{20}^*)$. Then the positive equilibrium $E^*(S^*, I^*, Y^*)$ is asymptotically stable when $\tau_1 \in (0, \tau_{10})$ and unstable when $\tau_1 > \tau_{10}$. Furthermore, system (3) undergoes a Hopf bifurcation at E^* when $\tau_1 = \tau_{10}$.*

For the cases $\tau_2 > 0$, and $\tau_1 \in [0, \tau_{10}^*)$, we can get similar results as those in Theorem 6.

3. Direction and Stability of the Hopf Bifurcation

In this section, we shall study the direction of the Hopf bifurcation and stability of bifurcating periodic solutions by using the normal form theory and the center manifold theorem due to Hassard et al. [17]. In the previous section, we have shown that system (3) undergoes the Hopf bifurcation at $\tau_1 = \tau_{10}$, without loss of generality, and we assume that $\tau_2^* < \tau_{10}$, where $\tau_2^* \in (0, \tau_{20}^*)$.

Let $x_1 = S - S^*$, $x_2 = I - I^*$, $x_3 = Y - Y^*$, $\tau_1 = \tau_{10} + \nu$, and $\overline{x}_i(t) = x_i(\tau_1 t)$ and, dropping the bars for simplification of notations, system (3) is transformed into a functional differential equation in $C = C([-1, 0], \mathbb{R}^3)$ as

$$\dot{x}(t) = L_\nu(x_t) + F(\nu, x_t), \tag{32}$$

where $x(t) = (x_1(t), x_2(t), x_3(t))^T \in \mathbb{R}^3$ and $L_\nu : C \to \mathbb{R}^3$ and $F : \mathbb{R} \times C \to \mathbb{R}^3$ are given, respectively, by

$$\begin{aligned} L_\nu(\phi) &= (\tau_{10} + \nu)\widetilde{A}\phi(0) + (\tau_{10} + \nu)\widetilde{B}\phi\left(-\frac{\tau_2^*}{\tau_1}\right) \\ &\quad + (\tau_{10} + \nu)\widetilde{C}\phi(-1), \end{aligned} \tag{33}$$

$$F(\nu, \phi) = (\tau_{10} + \nu)\left(F_1, F_2, F_3\right)^T, \tag{34}$$

where

$$
\widetilde{A} = \begin{pmatrix} a_{11} & a_{12} & 0 \\ 0 & a_{22} & 0 \\ 0 & 0 & a_{33} \end{pmatrix},
\widetilde{B} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & b_{32} & b_{33} \end{pmatrix},
\widetilde{C} = \begin{pmatrix} b_{11} & 0 & b_{13} \\ b_{21} & 0 & b_{23} \\ 0 & 0 & 0 \end{pmatrix},
$$
$$
F_1 = K_{11}\phi_1(-1)\phi_3(-1) + K_{12}\phi_3^2(-1) + K_{13}\phi_1(-1)\phi_3^2(-1) + K_{14}\phi_3^3(-1) + \cdots,
$$
$$
F_2 = K_{21}\phi_1(-1)\phi_3(-1) + K_{22}\phi_3^2(-1) + K_{23}\phi_1(-1)\phi_3^2(-1) + K_{24}\phi_3^3(-1) + \cdots,
$$
$$
F_3 = K_{31}\phi_2^2\left(-\frac{\tau_2^*}{\tau_1}\right) + K_{32}\phi_2\left(-\frac{\tau_2^*}{\tau_1}\right)\phi_3\left(-\frac{\tau_2^*}{\tau_1}\right) + K_{33}\phi_2^3\left(-\frac{\tau_2^*}{\tau_1}\right) + K_{34}\phi_2^2\left(-\frac{\tau_2^*}{\tau_1}\right)\phi_3\left(-\frac{\tau_2^*}{\tau_1}\right) + \cdots,
$$
$$
K_{11} = -\frac{\beta}{(1+\alpha Y^*)^2}, \quad K_{12} = \frac{\alpha\beta S^*}{(1+\alpha Y^*)^3}, \quad K_{13} = \frac{\alpha\beta}{(1+\alpha Y^*)^3}, \quad K_{14} = -\frac{\alpha^2\beta S^*}{(1+\alpha Y^*)^4},
$$
$$
K_{21} = \frac{\beta}{(1+\alpha Y^*)^2}, \quad K_{22} = -\frac{\alpha\beta S^*}{(1+\alpha Y^*)^3}, \quad K_{23} = -\frac{\alpha\beta}{(1+\alpha Y^*)^3}, \quad K_{24} = \frac{\alpha^2\beta S^*}{(1+\alpha Y^*)^4},
$$
$$
K_{31} = \frac{\alpha_1\beta_1(Y^* - \Lambda/m)}{(1+\alpha_1 I^*)^3}, \quad K_{32} = -\frac{\beta_1}{(1+\alpha_1 I^*)^2}, \quad K_{33} = \frac{\alpha_1^2\beta_1(\Lambda/m - Y^*)}{(1+\alpha_1 I^*)^4}, \quad K_{34} = \frac{\alpha_1\beta_1}{(1+\alpha_1 I^*)^3}. \tag{35}
$$

By the Riesz representation theorem, there exists a function $\eta(\theta, \nu)$ of bounded variation for $\theta \in [-1, 0]$, such that

$$
L_\nu(\phi) = \int_{-1}^{0} d\eta(\theta,\nu)\phi(\theta) \quad \text{for } \phi \in C. \tag{36}
$$

In fact, we can choose

$$
\eta(\theta,\nu) = \begin{cases} (\tau_{10}+\nu)\left(\widetilde{A}+\widetilde{B}+\widetilde{C}\right), & \theta = 0, \\ (\tau_{10}+\nu)\left(\widetilde{B}+\widetilde{C}\right), & \theta \in \left[-\dfrac{\tau_2^*}{\tau_1}, 0\right), \\ (\tau_{10}+\nu)\widetilde{C}, & \theta \in \left(-1, -\dfrac{\tau_2^*}{\tau_1}\right), \\ 0, & \theta = -1. \end{cases} \tag{37}
$$

For $\phi \in C^1([-1,0],\mathbb{R}^3)$, define

$$
A(\nu)\phi = \begin{cases} \dfrac{d\phi(\theta)}{d\theta}, & \theta \in [-1,0), \\ \displaystyle\int_{-1}^{0} d\eta(s,\nu)\phi(s), & \theta = 0, \end{cases}
\qquad
R(\nu)(\phi) = \begin{cases} 0, & \theta \in [-1,0), \\ F(\nu,\phi), & \theta = 0. \end{cases} \tag{38}
$$

Then system (32) is equivalent to

$$
\dot{x}_t = A(\nu)x_t + R(\nu)x_t, \tag{39}
$$

where $x_t(\theta) = x(t+\theta)$ for $\theta \in [-1, 0]$.

For $\psi \in C^1([0,1],(\mathbb{R}^3)^*)$, define

$$
A^*\psi(s) = \begin{cases} -\dfrac{d\psi(s)}{ds}, & s \in (0,1], \\ \displaystyle\int_{-1}^{0} d\eta^T(t,0)\psi(-t), & s = 0, \end{cases} \tag{40}
$$

and a bilinear inner product

$$
\langle\psi(s),\phi(\theta)\rangle = \overline{\psi}(0)\phi(0) - \int_{-1}^{0}\int_{\xi=0}^{\theta}\overline{\psi}(\xi-\theta)\,d\eta(\theta)\,\phi(\xi)\,d\xi, \tag{41}
$$

where $\eta(\theta) = \eta(\theta, 0)$. Then $A(0)$ and A^* are adjoint operators. By the discussion in Section 2, we know that $\pm i\omega_{10}\tau_{10}$ are eigenvalues of $A(0)$. Hence, they are also eigenvalues of A^*. We first need to compute the eigenvectors of $A(0)$ and A^* corresponding to $i\omega_{10}\tau_{10}$ and $-i\omega_{10}\tau_{10}$, respectively.

Suppose $q(\theta) = (1, q_2, q_3)^T e^{i\omega_{10}\tau_{10}\theta}$ is the eigenvector of $A(0)$ corresponding to $i\omega_{10}\tau_{10}$, and then $A(0)q(\theta) = i\omega_{10}\tau_{10}q(\theta)$. Then, from the definition of $A(0)$ and (33), we have

$$q_2 = \frac{a_{11} - i\omega_{10}}{i\omega_{10} - a_{22} - a_{12}},$$
$$q_3 = \frac{b_{32}e^{-i\omega_{10}\tau_2^*}\left(a_{11} - i\omega_{10}\right)}{\left(i\omega_{10} - a_{33} - b_{33}e^{-i\omega_{10}\tau_2^*}\right)\left(i\omega_{10} - a_{22} - a_{12}\right)}. \tag{42}$$

Similarly, we can obtain the eigenvector $q^*(s) = D(1, q_2^*, q_3^*)e^{i\omega_{10}\tau_{10}s}$ of A^* corresponding to $-i\omega_{10}\tau_{10}$, where

$$q_2^* = -\frac{a_{11} + i\omega_{10} + b_{11}e^{i\omega_{10}\tau_{10}}}{b_{21}e^{i\omega_{10}\tau_{10}}},$$
$$q_3^* = \frac{b_{23}\left(a_{11} + i\omega_{10}\right)}{b_{21}\left(a_{33} + b_{33}e^{i\omega_{10}\tau_2^*} + i\omega_{10}\right)}. \tag{43}$$

Choosing $\overline{D}$ as $\overline{D} = \{1 + q_2\overline{q}_2^* + q_3\overline{q}_3^* + \tau_{10}e^{-i\omega_{10}\tau_{10}}(b_{11} + \overline{q}_2^*b_{21} + q_3b_{13} + q_3\overline{q}_2^*b_{23}) + \tau_2^*\overline{q}_3^*e^{-i\omega_{10}\tau_2^*}(q_2b_{32} + q_3b_{33})\}^{-1}$, then, by (41), we see $\langle q^*(s), q(\theta)\rangle = 1$.

In the remainder of this section, we use the algorithms given in [17] and, using a computation process similar to that in [24–27], we get the coefficients used in determining the qualities of bifurcating periodic solutions:

$$g_{20} = 2\tau_{10}\overline{D}\left[q_3e^{-2i\omega_{10}\tau_{10}}\left(1 - \overline{q}_2^*\right)\left(K_{11} + q_3K_{12}\right) + \overline{q}_3^*q_2e^{-2i\omega_{10}\tau_2^*}\left(q_2K_{31} + q_3K_{32}\right)\right],$$

$$g_{11} = \tau_{10}\overline{D}\left[\left(1 - \overline{q}_2^*\right)\left(K_{11}\left(q_3 + \overline{q}_3\right) + 2K_{12}q_3\overline{q}_3\right) + \overline{q}_3^*\left(K_{32}\left(q_2\overline{q}_3 + \overline{q}_2q_3\right) + 2K_{31}q_2\overline{q}_2\right)\right],$$

$$g_{02} = 2\tau_{10}\overline{D}\left[e^{2i\omega_{10}\tau_{10}}\overline{q}_3\left(1 - \overline{q}_2^*\right)\left(K_{11} + \overline{q}_3K_{12}\right) + \overline{q}_3^*\overline{q}_2e^{2i\omega_{10}\tau_2^*}\left(\overline{q}_2K_{31} + \overline{q}_3K_{32}\right)\right],$$

$$\begin{aligned}
g_{21} = 2\tau_{10}\overline{D}\Bigg\{&\left(1 - \overline{q}_2^*\right) \cdot \Bigg[K_{11}\Bigg(\left(\frac{W_{20}^{(1)}(-1)}{2}\overline{q}_3 + \frac{W_{20}^{(3)}(-1)}{2}\right)e^{i\omega_{10}\tau_{10}} + \left(W_{11}^{(1)}(-1)\,q_3 + W_{11}^{(3)}(-1)\right)e^{-i\omega_{10}\tau_{10}}\Bigg) \\
&+ K_{12}\left(W_{20}^{(3)}(-1)\,\overline{q}_3e^{i\omega_{10}\tau_{10}} + 2W_{11}^{(3)}(-1)\,q_3e^{-i\omega_{10}\tau_{10}}\right) \\
&+ K_{13}\left(q_3^2 + 2q_3\overline{q}_3\right)e^{-i\omega_{10}\tau_{10}} + 3K_{14}q_3^2\overline{q}_3e^{-i\omega_{10}\tau_{10}}\Bigg] \\
&+ \overline{q}_3^*\Bigg[K_{31}\left(W_{20}^{(2)}\left(-\frac{\tau_2^*}{\tau_{10}}\right)\overline{q}_2e^{i\omega_{10}\tau_2^*} + 2W_{11}^{(2)}\left(-\frac{\tau_2^*}{\tau_{10}}\right)q_2e^{-i\omega_{10}\tau_2^*}\right) \\
&+ K_{32}\Bigg(e^{i\omega_{10}\tau_2^*}\left(\frac{W_{20}^{(2)}\left(-\tau_2^*/\tau_{10}\right)}{2}\overline{q}_3 + \frac{W_{20}^{(3)}\left(-\tau_2^*/\tau_{10}\right)}{2}\overline{q}_2\right) \\
&+ e^{-i\omega_{10}\tau_2^*}\left(W_{11}^{(2)}\left(-\frac{\tau_2^*}{\tau_{10}}\right)q_3 + W_{11}^{(3)}\left(-\frac{\tau_2^*}{\tau_{10}}\right)q_2\right)\Bigg) \\
&+ 3K_{33}q_2^2\overline{q}_2e^{-i\omega_{10}\tau_2^*} + K_{34}q_2\left(q_2\overline{q}_3 + 2\overline{q}_2q_3\right)e^{-i\omega_{10}\tau_2^*}\Bigg]\Bigg\},
\end{aligned} \tag{44}$$

where

$$W_{20}(\theta) = \frac{ig_{20}}{\omega_{10}\tau_{10}}q(0)\,e^{i\omega_{10}\tau_{10}\theta} + \frac{i\overline{g}_{02}}{3\omega_{10}\tau_{10}}\overline{q}(0)\,e^{-i\omega_{10}\tau_{10}\theta} + E_1e^{2i\omega_{10}\tau_{10}\theta},$$

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega_{10}\tau_{10}}q(0)\,e^{i\omega_{10}\tau_{10}\theta} + \frac{i\overline{g}_{11}}{\omega_{10}\tau_{10}}\overline{q}(0)\,e^{-i\omega_{10}\tau_{10}\theta} + E_2,$$

$$E_1^{(1)} = \frac{M_{11}}{M_1},$$

$$E_1^{(2)} = \frac{M_{12}}{M_1},$$

$$E_1^{(3)} = \frac{M_{13}}{M_1},$$

$$E_2^{(1)} = \frac{M_{21}}{M_2},$$

$$E_2^{(2)} = \frac{M_{22}}{M_2},$$

$$E_2^{(3)} = \frac{M_{23}}{M_2},$$
$$M_1 = \begin{vmatrix} 2i\omega_{10} - a_{11} - b_{11}e^{-2i\omega_{10}\tau_{10}} & -a_{12} & -b_{13}e^{-2i\omega_{10}\tau_{10}} \\ -b_{21}e^{-2i\omega_{10}\tau_{10}} & 2i\omega_{10} - a_{22} & -b_{23}e^{-2i\omega_{10}\tau_{10}} \\ 0 & -b_{32}e^{-2i\omega_{10}\tau_2^*} & 2i\omega_{10} - a_{33} - b_{33}e^{-2i\omega_{10}\tau_2^*} \end{vmatrix},$$
$$M_{11} = 2\begin{vmatrix} q_3e^{-2i\omega_{10}\tau_{10}}\left(K_{11} + q_3K_{12}\right) & -a_{12} & -b_{13}e^{-2i\omega_{10}\tau_{10}} \\ -q_3e^{-2i\omega_{10}\tau_{10}}\left(K_{11} + q_3K_{12}\right) & 2i\omega_{10} - a_{22} & -b_{23}e^{-2i\omega_{10}\tau_{10}} \\ q_2e^{-2i\omega_{10}\tau_2^*}\left(q_2K_{31} + q_3K_{32}\right) & -b_{32}e^{-2i\omega_{10}\tau_2^*} & 2i\omega_{10} - a_{33} - b_{33}e^{-2i\omega_{10}\tau_2^*} \end{vmatrix},$$
$$M_{12} = 2\begin{vmatrix} 2i\omega_{10} - a_{11} - b_{11}e^{-2i\omega_{10}\tau_{10}} & q_3e^{-2i\omega_{10}\tau_{10}}\left(K_{11} + q_3K_{12}\right) & -b_{13}e^{-2i\omega_{10}\tau_{10}} \\ -b_{21}e^{-2i\omega_{10}\tau_{10}} & -q_3e^{-2i\omega_{10}\tau_{10}}\left(K_{11} + q_3K_{12}\right) & -b_{23}e^{-2i\omega_{10}\tau_{10}} \\ 0 & q_2e^{-2i\omega_{10}\tau_2^*}\left(q_2K_{31} + q_3K_{32}\right) & 2i\omega_{10} - a_{33} - b_{33}e^{-2i\omega_{10}\tau_2^*} \end{vmatrix},$$
$$M_{13} = 2\begin{vmatrix} 2i\omega_{10} - a_{11} - b_{11}e^{-2i\omega_{10}\tau_{10}} & -a_{12} & q_3e^{-2i\omega_{10}\tau_{10}}\left(K_{11} + q_3K_{12}\right) \\ -b_{21}e^{-2i\omega_{10}\tau_{10}} & 2i\omega_{10} - a_{22} & -q_3e^{-2i\omega_{10}\tau_{10}}\left(K_{11} + q_3K_{12}\right) \\ 0 & -b_{32}e^{-2i\omega_{10}\tau_2^*} & q_2e^{-2i\omega_{10}\tau_2^*}\left(q_2K_{31} + q_3K_{32}\right) \end{vmatrix},$$
$$M_2 = \begin{vmatrix} a_{11} + b_{11} & a_{12} & b_{13} \\ b_{21} & a_{22} & b_{23} \\ 0 & b_{32} & a_{33} + b_{33} \end{vmatrix},$$
$$M_{21} = \begin{vmatrix} -K_{11}\left(q_3 + \overline{q}_3\right) - 2K_{12}q_3\overline{q}_3 & a_{12} & b_{13} \\ K_{11}\left(q_3 + \overline{q}_3\right) + 2K_{12}q_3\overline{q}_3 & a_{22} & b_{23} \\ -K_{32}\left(q_2\overline{q}_3 + \overline{q}_2q_3\right) - 2K_{31}q_2\overline{q}_2 & b_{32} & a_{33} + b_{33} \end{vmatrix},$$
$$M_{22} = \begin{vmatrix} a_{11} + b_{11} & -K_{11}\left(q_3 + \overline{q}_3\right) - 2K_{12}q_3\overline{q}_3 & b_{13} \\ b_{21} & K_{11}\left(q_3 + \overline{q}_3\right) + 2K_{12}q_3\overline{q}_3 & b_{23} \\ 0 & -K_{32}\left(q_2\overline{q}_3 + \overline{q}_2q_3\right) - 2K_{31}q_2\overline{q}_2 & a_{33} + b_{33} \end{vmatrix},$$
$$M_{23} = \begin{vmatrix} a_{11} + b_{11} & a_{12} & -K_{11}\left(q_3 + \overline{q}_3\right) - 2K_{12}q_3\overline{q}_3 \\ b_{21} & a_{22} & K_{11}\left(q_3 + \overline{q}_3\right) + 2K_{12}q_3\overline{q}_3 \\ 0 & b_{32} & -K_{32}\left(q_2\overline{q}_3 + \overline{q}_2q_3\right) - 2K_{31}q_2\overline{q}_2 \end{vmatrix}. \quad (45)$$

Thus, we can determine $W_{20}(\theta)$ and $W_{11}(\theta)$. Furthermore, we can compute g_{21} by (44). Then we can compute the following values:

$$c_1(0) = \frac{i}{2\omega_{10}\tau_{10}}\left(g_{20}g_{11} - 2\left|g_{11}\right|^2 - \frac{\left|g_{02}\right|^2}{3}\right) + \frac{g_{21}}{2},$$
$$\mu_2 = -\frac{\operatorname{Re}\{c_1(0)\}}{\operatorname{Re}\{\lambda'(\tau_{10})\}}, \quad (46)$$
$$T_2 = -\frac{\operatorname{Im}\{c_1(0)\} + \mu_2\operatorname{Im}\{\lambda'(\tau_{10})\}}{\omega_{10}\tau_{10}},$$
$$\beta_2 = 2\operatorname{Re}\left(c_1(0)\right).$$

From [17], we know that μ_2 determines the directions of the Hopf bifurcation: if $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical (subcritical); β_2 determines the stability of the bifurcating periodic solutions: the bifurcating periodic solutions are stable (unstable) if $\beta_2 < 0$ ($\beta_2 > 0$); and T_2 determines the period of the bifurcating periodic solutions: the period increases (decreases) if $T_2 > 0$ ($T_2 < 0$).

4. Numerical Simulations

From Section 3, we can determine the direction of a Hopf bifurcation and the stability of the bifurcating periodic solutions. In this section, we will give some numerical simulations of system (3) at different values of time delays.

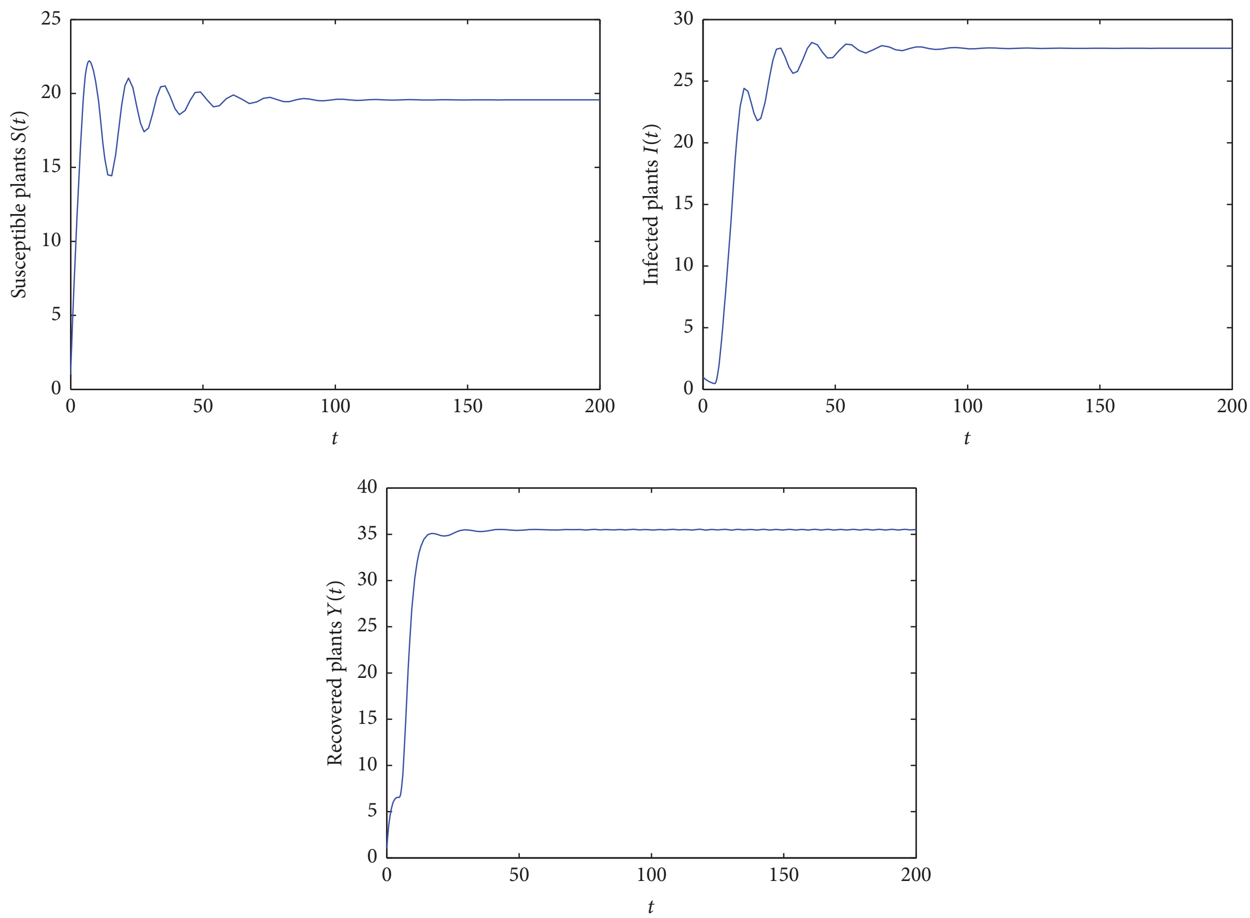

Figure 1: E^* is asymptotically stable, where $\tau_1 = 4.3 < \tau_{10}^* = 4.4686$ and $\tau_2 = 0$.

We choose the coefficients as follows: $\mu = 0.1$, $K = 50$, $\beta = 0.1$, $\alpha = 0.2$, $d = 0.2$, $\beta_1 = 0.1$, $\alpha_1 = 0.1$, $\Lambda = 15$, $\gamma = 0.01$, and $m = 0.3$. α, d, α_1, and γ are taken from [15]. Then system (3) has an endemic equilibrium $E^*(19.5683, 27.6652, 35.5003)$. When $\tau_2 = 0$, we then have $\omega_{10}^* = 0.312$ and $\tau_{10}^* = 4.4686$. From Theorem 4, we know that E^* is asymptotically stable when $\tau_1 < \tau_{10}^*$, which is illustrated in Figure 1.

When τ_1 passes through the critical value τ_{10}^*, E^* loses its stability and a Hopf bifurcation occurs; that is, a family of periodic solutions bifurcate from E^* (see Figure 2). Similarly, we get $\omega_{20}^* = 0.6679$ and $\tau_{20}^* = 2.4472$.

Regard τ_1 as a parameter, for $\tau_2 = 2 \in (0, 2.4472)$, and then we have $\omega_{10} = 0.3116$ and $\tau_{10} = 7.4719$. Theorem 6 shows that E^* is asymptotically stable when $\tau_1 < \tau_{10}$ (see Figure 3) and unstable when $\tau_1 > \tau_{10}$. From formulae (46) in Section 3, it follows that $c_1(0) = -5.3591 \times 10^{-5} + 2.2474 \times 10^{-5} i$, $\mu_2 = 0.0086$, $\beta_2 = -1.0718 \times 10^{-4}$, and $T_2 = 1.1427 \times 10^{-4}$. Since $\mu_2 > 0$ and $\beta_2 < 0$, the Hopf bifurcation is supercritical, and these bifurcating periodic solutions from E^* at τ_{10} are stable, which are depicted in Figure 4.

5. Discussion

In this paper, we have studied the dynamics of a plant virus propagation model with two delays (3) proposed by Jackson and Chen-Charpentier [15]. The model describes the disease transmission dynamics between the insects and the plants.

Jackson and Chen-Charpentier [15] studied model (3) using numerical methods. However, the problem of the theoretical analysis of this model remained unsolved and was an open problem.

For this problem, first, by analyzing the characteristic equation, constructing a Lyapunov functional, and using LaSalle's invariance principle, we prove that the disease-free equilibrium E_0 is globally asymptotically stable if $R_0 \leq 1$ (Theorem 2), regardless of the length of the time delays, the sufficient conditions for the stability of the endemic equilibrium, and existence of Hopf bifurcation if $R_0 > 1$ have been given, respectively. Then, by using normal form theory and center manifold theorem introduced by Hassard et al. [17], regarding τ_1 as a parameter, we investigate the direction and stability of the Hopf bifurcation, and the explicit formulae which determine the direction and stability of the bifurcating periodic solutions are derived. Finally, the numerical simulation results in Figures 1–4 have verified the obtained analytic results.

Our simulation results show that, for the parameter values considered, the disease will persist and exhibit oscillatory bahavior, and this manifests that the densities of the plants and insect-vectors will remain in an oscillatory case, and then

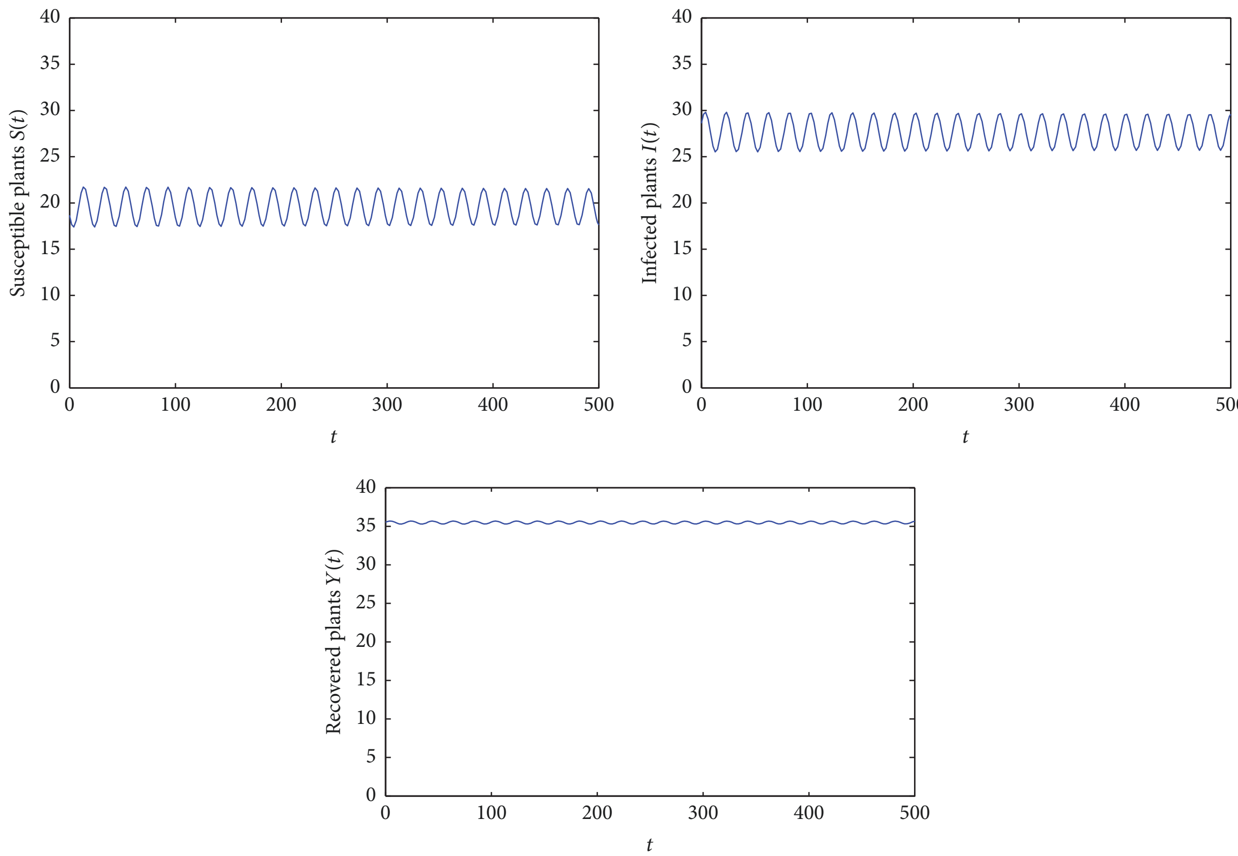

Figure 2: System (3) undergoes a Hopf bifurcation at the endemic equilibrium E^*, where $\tau_1 = 7.3 > \tau_{10}^* = 4.4686$ and $\tau_2 = 0$.

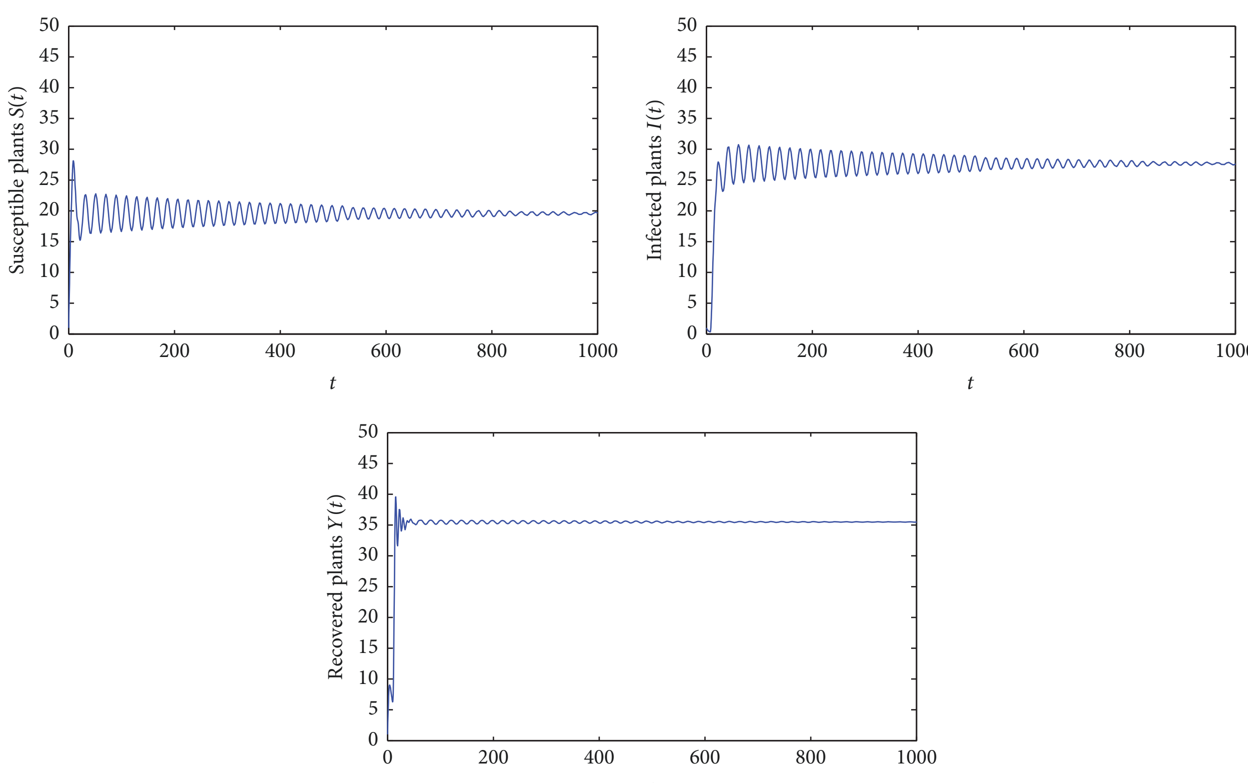

Figure 3: E^* is asymptotically stable, where $\tau_1 = 7.1 < \tau_{10} = 7.4719$ and $\tau_2 = 2$.

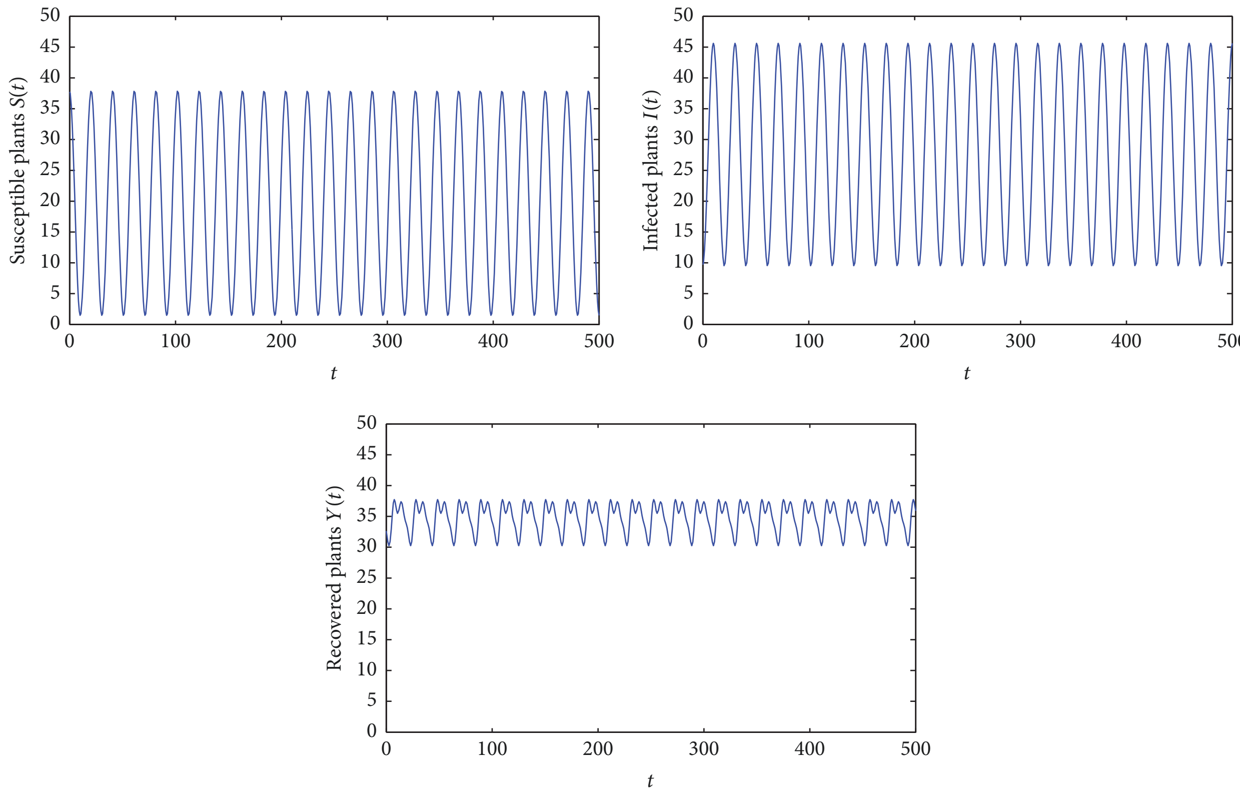

Figure 4: System (3) undergoes a Hopf bifurcation at the endemic equilibrium E^*, where $\tau_1 = 7.6 > \tau_{10} = 7.4719$ and $\tau_2 = 2$.

agriculture workers must be alert to the virus even if they have noticed that fewer plants are becoming infected.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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