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Transmission dynamics of a Huanglongbing model with cross protection

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Abstract

Huanglongbing (HLB) is one of the most common widespread vector-borne transmission diseases through psyllid, which is called a kind of cancer of plant disease. In recent years, biologists have focused on the role of cross protection strategy to control the spread of HLB. In this paper, according to transmission mechanism of HLB, a deterministic model with cross protection is formulated. A threshold value R_0 is established to measure whether or not the disease is uniformly persistent. The existence of a backward bifurcation presents a further sub-threshold condition below R_0 for the spread of the disease. We also discuss the effects of cross protection and removing infected trees in spreading the disease. Numerical simulations suggest that cross protection is a promotion control measure, and replanting trees is bad for HLB control

Keywords: Huanglongbing model; cross protection; backward bifurcation; sub-threshold value

1 Introduction

Nowadays, Huanglongbing (HLB) is one of the most serious problems of citrus worldwide caused by the bacteria Candidatus Liberibacter spp., whose name in Chinese means "yellow dragon disease" [1]. The main symptoms on HLB include chlorosis of leaves, dieback and, in extreme cases, tree death. Additionally, infected trees develop fruit that is of poor quality and drops early, reducing yields of edible and marketable fruit from diseased trees [2]. The infected trees are usually destroyed or become unproductive in 5 to 8 years [1].

Most of the known plant viruses are transmitted by insect vectors. HLB, a destructive disease of citrus, can be transmitted by grafting from psyllid to citrus. The primary vector of the spread of the disease is the psyllid (Diaphorina Citri Kuwayama) [3].

In order to control HLB effectively, most of growers usually take the following measures: pesticides, tree removal, antibiotics [4], changes to tree spacing, natural enemies of psyllid. A few new intervention strategies are explored, including heat treatment [5], new tolerant or resistant tree stocks [6], nutrient additions [7], cross protection, intercropping [8]. Cross protection is one of biological methods. In recent years, cross protection is widely considered and applied in prevention and control of plant diseases.

Cross protection, first shown by McKinney [9] with tobacco mosaic virus (TMV), is a phenomenon whereby prior infection with one (protecting) plant virus will prevent or interfere with superinfection by another, usually related (challenging) virus [10]. In [11], the



authors explored the cross protection between MAV (protecting) virus and PAV (challenging) virus in cereal, which belong to barley yellow dwarf viruses (BYDVs). By vaccinating M6 CTV strains (protecting) in citrus aurantif olia, Cui et al. [12] proved the obvious effect of cross protection on Bendizao mandarin. Van Vuuren et al. [13] studied the effect of cross protection on HLB of Africa by vaccinating multiple citrus recession viral strains. Hartung [14], who improved T36 CTV strains, described the resistance effect of cross protection on citrus HLB.

In recent years, some mathematical models on plant disease have been studied by many researchers (see [15–19]). Meng and Li [15] discussed the effect of cultural control on the healthy growth of the host plant. Local stability for the free periodic solution and persistence of the disease are key issues in the study of epidemic models. In fact, these issues are solved. In [16], Meng et al. illustrated that biological control may be a better way for pest management strategies by adopting a new mathematical model. Zhang et al. [17] proposed and compared two different control strategies in the model. In [18], Zhao et al. proposed a plant disease model with Markov conversion and impulsive toxicant input. Then thresholds of extinction and persistence in mean were obtained.

To the best of the authors' knowledge, there has been little work on plant disease models with cross protection (see [10, 20, 21]). Gao et al. [20] took seasonality into account and put forward a nonautonomous plant disease model with cross protection. The results showed that cross protection played an important role in controlling the spread of the challenging virus in plants. Zhang et al. [21] proposed a model to study cross protection between the viruses in 1999. Zhang and Holt [10] improved the model in [21], in which cross protection can occur both naturally and through artificial intervention. Our main purpose is to investigate the transmission of HLB between citrus tree and psyllid populations with cross protection and evaluate the effect of cross protection in controlling the spread of HLB.

To achieve the above goals, we formulate a HLB model with cross protection and analyze the dynamical behavior theoretically including a backward bifurcation. Recently, there have been a number of studies on a backward bifurcation in the epidemic literature, for example, see [22–26]. Garba et al. [22] considered a dengue model with standard incidence formulation undergoing the phenomenon of backward bifurcation. Ahmed et al. [23] modeled the spread and control of dengue with limited public health resources, which exhibited the phenomenon of backward bifurcation. Li et al. [24] constructed an SIR epidemic model with nonlinear incidence and treatment. The results show that a backward bifurcation occurs if the capacity is small, and there exist bistable endemic equilibria if the capacity is low [27].

The paper is organized as follows. We formulate our HLB model with cross protection in Section 2. In Section 3, we determine the existence and stability of equilibrium point of the model. Moreover, we prove the existence of a backward bifurcation around the disease-free equilibrium. In Section 4, we discuss the persistence of the disease. Numerical simulation and discussion are given in Section 5.

2 Model formulation

We now study the impact of cross protection with vector as described above on the transmission dynamics and control strategies. We firstly formulate a deterministic model of HLB by considering citrus trees totalling N_h in a grove, which we divide into four categories: healthy, infected with the protecting virus alone, infected with the HLB virus

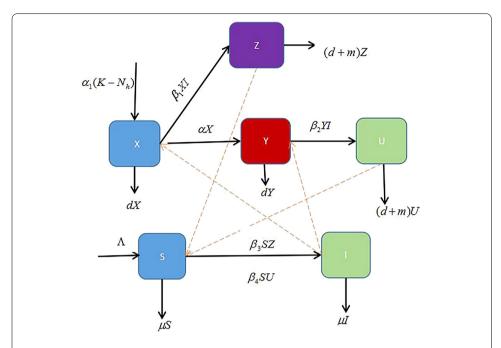


Figure 1 A schematic of the model system showing transitions to different categories for trees and psyllids. Black arrows show the transitions between compartments. Orange dashed arrows show the necessary interactions between trees and psyllids to obtain transmission.

(challenging) alone, and infected with both, designated as X(t), Y(t), Z(t), and U(t), respectively. Thus the total number of trees $N_h(t) = X(t) + Y(t) + Z(t) + U(t)$. We divide the vector population into a susceptible class S(t) and an infected class I(t). Let $N_v = S(t) + I(t)$ be the total number of psyllids. The model flow diagram is depicted in Figure 1. The model is a system of six ordinary differential equations:

$$\begin{cases} \frac{dX}{dt} = \alpha_1(K - N_h) - \alpha X - dX - \beta_1 XI, \\ \frac{dY}{dt} = \alpha X - dY - \beta_2 YI, \\ \frac{dZ}{dt} = \beta_1 XI - (d + m)Z, \\ \frac{dU}{dt} = \beta_2 YI - (d + m)U, \\ \frac{dS}{dt} = \Lambda - \beta_3 SZ - \beta_4 SU - \mu S, \\ \frac{dI}{dt} = \beta_3 SZ + \beta_4 SU - \mu I, \end{cases}$$

$$(2.1)$$

where α_1 is the rate of replanting a citrus tree, α is the vaccination rate, β_1 is the probability that a susceptible tree becomes infected from contact with an infected psyllid with HLB virus, β_2 is the probability that a tree with protecting virus becomes infected from contact with an infected psyllid, β_3 is the probability that a susceptible psyllid becomes infected from contact with an infected tree, β_4 is the probability that a susceptible psyllid becomes infected from contact with an infected tree with two kinds of viruses, μ is the natural mortality of psyllid population, m is the roguing rate of infected trees, d is the natural death rate of a citrus tree, Λ is the constant recruitment rate of a psyllid, K is the maximum total number of citrus trees that can be planted in the grove. By the biological meaning, we assume that all parameters in model (2.1) are positive, and $\alpha \leq 1$ and $\alpha_1 \leq 1$.

The initial conditions for (2.1) are

$$X(0) \ge 0,$$
 $Y(0) \ge 0,$ $Z(0) \ge 0,$ $U(0) \ge 0,$ $S(0) \ge 0,$ $I(0) \ge 0.$ (2.2)

We will study the transmission dynamics of HLB disease in the rest of this paper. Before giving the main result, we present the following lemmas.

Lemma 2.1 Suppose (X(t), Y(t), Z(t), U(t), S(t), I(t)) is a solution of system (2.1) with initial conditions (2.2), then $(X(t), Y(t), Z(t), U(t), S(t), I(t)) \ge 0$ for all $t \ge 0$.

Lemma 2.2 Every solution (X(t), Y(t), Z(t), U(t), S(t), I(t)) of system (2.1) eventually enters

$$\Omega = \left\{ (X,Y,Z,U,S,I) \in \mathbb{R}_+^6 : 0 \le X + Y + Z + U \le \frac{\alpha_1 K}{d + \alpha_1}, 0 \le S + I \le \frac{\Lambda}{\mu} \right\},$$

and Ω is a positively invariant set for (2.1).

Proof From model (2.1), we get

$$\frac{dN_h(t)}{dt} = \alpha_1 K - (d + \alpha_1) N_h(t) - m \left(Z(t) + U(t) \right) \tag{2.3}$$

and

$$\frac{dN_{\nu}(t)}{dt} = \Lambda - \mu N_{\nu}(t). \tag{2.4}$$

Thus, $\frac{dN_h(t)}{dt} \leq 0$ if $N_h(t) \geq \frac{\alpha_1 K}{d+\alpha_1}$, and $\frac{dN_v(t)}{dt} \leq 0$ if $N_v(t) \geq \frac{\Lambda}{\mu}$, which implies that Ω is positively invariant with respect to system (2.1). This completes the proof.

3 Existence and stability of equilibrium points

To better organize the analysis, in the following we denote $k_1 = d + \alpha$, $k_2 = d + \alpha_1$, $k_3 = d + m$, $k_4 = d + m + \alpha_1$, $k_5 = d + \alpha + \alpha_1$, and $k_6 = d + m + \mu$.

3.1 Existence of equilibrium points

In this subsection, we determine the existence of the equilibrium points of model (2.1). It is straightforward to establish that there is, for all parameter values, a disease-free equilibrium $E_0 = (X_0, Y_0, Z_0, U_0, S_0, I_0) = (\frac{\alpha_1 K d}{k_1 k_2}, \frac{\alpha \alpha_1 K}{k_1 k_2}, 0, 0, \frac{\Lambda}{\mu}, 0)$.

The stability of E_0 can be described by using the next generation operator method [28, 29]. According to the notation in [29], the Jacobian matrices F (of new infection terms) and V (of remaining transition terms) are given, respectively [30]. We have

$$F = \begin{pmatrix} 0 & 0 & \beta_1 X_0 \\ 0 & 0 & \beta_2 Y_0 \\ \frac{\beta_3 \Lambda}{\mu} & \frac{\beta_4 \Lambda}{\mu} & 0 \end{pmatrix} \quad \text{and} \quad V = \begin{pmatrix} k_3 & 0 & 0 \\ 0 & k_3 & 0 \\ 0 & 0 & \mu \end{pmatrix}.$$

Therefore, the basic reproductive number for system (2.1) is

$$R_0 = \rho \left(FV^{-1} \right) = \sqrt{\frac{\beta_2 \beta_4 \alpha \alpha_1 K \Lambda + \beta_1 \beta_3 \alpha_1 K \Lambda d}{\mu^2 k_1 k_2 k_3}},\tag{3.1}$$

here ρ is the spectral radius of a matrix.

Now we turn to discussing a possible endemic equilibrium point $E^*(X^*, Y^*, Z^*, U^*, S^*, I^*)$ in the interior of the feasible region Ω . Here $X^*, Y^*, Z^*, U^*, S^*, I^* > 0$ satisfy the following equilibrium equations:

$$\alpha_1(K - N_h^*) - \alpha X^* - dX^* - \beta_1 X^* I^* = 0, \tag{3.2}$$

$$\alpha X^* - dY^* - \beta_2 Y^* I^* = 0, (3.3)$$

$$\beta_1 X^* I^* - (d+m)Z^* = 0, (3.4)$$

$$\beta_2 Y^* I^* - (d+m) U^* = 0, \tag{3.5}$$

$$\Lambda - \beta_3 S^* Z^* - \beta_4 S^* U^* - \mu S^* = 0, \tag{3.6}$$

$$\beta_3 S^* Z^* + \beta_4 S^* U^* - \mu I^* = 0. \tag{3.7}$$

Adding (3.6) and (3.7), the coordinates of an endemic equilibrium point (X^* , Y^* , Z^* , U^* , S^* , I^*) must satisfy

$$S^* = \frac{\Lambda}{\mu} - I^*.$$

According to (3.3)-(3.7), we get

$$Y^* = \frac{\alpha \mu^2 k_3}{\beta_1 \beta_3 (\Lambda - \mu I^*)(d + \beta_2 I^*) + \alpha \beta_2 \beta_4 (\Lambda - \mu I^*)}.$$

Thus

$$X^* = \frac{\mu^2 k_3 (d + \beta_2 I^*)}{\beta_1 \beta_3 (\Lambda - \mu I^*) (d + \beta_2 I^*) + \alpha \beta_2 \beta_4 (\Lambda - \mu I^*)},$$

$$Z^* = \frac{\mu^2 \beta_1 I^* (d + \beta_2 I^*)}{\beta_1 \beta_3 (\Lambda - \mu I^*) (d + \beta_2 I^*) + \alpha \beta_2 \beta_4 (\Lambda - \mu I^*)},$$

$$U^* = \frac{\alpha \mu^2 \beta_2 I^*}{\beta_1 \beta_3 (\Lambda - \mu I^*) (d + \beta_2 I^*) + \alpha \beta_2 \beta_4 (\Lambda - \mu I^*)}.$$

Substituting X^* , Y^* , Z^* , U^* , S^* into (3.2), we obtain that the coordinates I^* of an equilibrium solution will be the positive root of the quadratic equation

$$h(I) = aI^2 + bI + c = 0, (3.8)$$

where

$$a = \alpha_1 K \mu \beta_1 \beta_2 \beta_3 + \mu^2 \beta_1 \beta_2 k_4 > 0$$

$$b = \alpha_1 K \beta_1 \beta_3 (d\mu - \Lambda \beta_2) + \alpha \alpha_1 K \mu \beta_2 \beta_4 + \mu^2 \beta_2 k_3 k_5 + \mu^2 \beta_1 dk_4 + \alpha \alpha_1 \mu^2 \beta_2,$$

$$c = \mu^2 k_1 k_2 k_3 (1 - R_0^2).$$

If the discriminant $\Delta = b^2 - 4ac$ is positive, equation (3.8) has two real roots

$$I_1 = \frac{-b - \sqrt{\Delta}}{2a}, \qquad I_2 = \frac{-b + \sqrt{\Delta}}{2a}.$$

Since all the state variables in model (2.1) are nonnegative, so $S^*(I^*) > 0$ requires the coordinate I^* to satisfy the inequality

$$I^* < \frac{\Lambda}{\mu}$$
.

To completely determine the existence of the positive equilibrium of system (2.1), we must consider the following three possible cases:

- (1) Assume $R_0 > 1$, then c < 0 and thus $\Delta > 0$. It is clear that h(I) = 0 has a simple positive root, which we denote by I_2 . In this case system (2.1) has a unique endemic equilibrium, which we denote by E_2 .
- (2) Suppose $R_0 = 1$, then c = 0, and the equation h(I) = 0 has two roots, which are 0 and $-\frac{b}{a}$. Hence system (2.1) has a unique endemic equilibrium, denoted by E_2 , if and only if b < 0.
- (3) Suppose $R_0 < 1$, then c > 0, and there are two possible subcases:
 - (i) If b > 0, h(I) = 0 does not have any positive root.
 - (ii) h(I) = 0 has two positive roots I_1 and I_2 if and only if $\Delta > 0$ and b < 0; further, h(I) = 0 has a double positive root I^* if and only if $\Delta = 0$ and b < 0.

We can summarize the previous calculations in the following theorem.

Theorem 3.1 *System* (2.1) *can have up to two positive equilibria. More precisely,*

- (1) if $R_0 > 1$, there exists a unique endemic equilibrium E_2 ;
- (2) if $R_0 = 1$, there exists a unique endemic equilibrium E_2 if and only if b < 0; otherwise, there is no endemic equilibrium;
- (3) if $R_0 < 1$, and
 - (i) if b > 0, there is no endemic equilibrium;
 - (ii) system (2.1) has two endemic equilibria E_1 and E_2 if and only if $\Delta > 0$ and b < 0; and these two equilibria coalesce into E^* if and only if $\Delta = 0$ and b < 0; otherwise, there is no endemic equilibrium.

3.2 Stability of the disease-free equilibrium point

In this subsection, we show the stability of the disease-free equilibrium for model (2.1).

Theorem 3.2 For system (2.1), the disease-free equilibrium E_0 is locally asymptotically stable if $R_0 < 1$ and unstable if $R_0 > 1$.

Proof The Jacobian matrix of system (2.1) about E_0 can be computed as

$$J(E_0) = \begin{pmatrix} -k_5 & -\alpha_1 & -\alpha_1 & -\alpha_1 & 0 & -\frac{\beta_1\alpha_1Kd}{k_1k_2} \\ \alpha & -d & 0 & 0 & 0 & -\frac{\beta_2\alpha\alpha_1K}{k_1k_2} \\ 0 & 0 & -k_3 & 0 & 0 & \frac{\beta_1\alpha_1Kd}{k_1k_2} \\ 0 & 0 & 0 & -k_3 & 0 & \frac{\beta_2\alpha\alpha_1K}{k_1k_2} \\ 0 & 0 & -\frac{\beta_3\Lambda}{\mu} & -\frac{\beta_4\Lambda}{\mu} & -\mu & 0 \\ 0 & 0 & \frac{\beta_3\Lambda}{\mu} & \frac{\beta_4\Lambda}{\mu} & 0 & -\mu \end{pmatrix}.$$

One eigenvalue of $J(E_0)$ is $-\mu$, which is negative, the others are the roots of the following quintic polynomial equation:

$$\lambda^{5} + (A + C)\lambda^{4} + (D + AC + B)\lambda^{3} + (E + AD + BC)\lambda^{2} + (AE + BD)\lambda + BE = 0$$

where

$$A = d + k_5 > 0,$$

$$B = k_1 k_2 > 0,$$

$$C = k_3 + k_6 > 0,$$

$$D = k_3 k_6 + \mu k_3 (1 - R_0^2),$$

$$E = \mu k_3^2 (1 - R_0^2),$$

$$CD - E = k_3 k_6 [k_3 + k_6 + \mu (1 - R_0^2)],$$

$$AC - 2B = 2m(\alpha + \alpha_1) - 2\alpha\alpha_1 + \mu\alpha + \mu\alpha_1 + 2d(m + k_6),$$

$$A^2 - 2B = \alpha^2 + \alpha_1^2 + 2d\alpha + 2d\alpha_1 + 2d^2 > 0.$$

Obviously, if $R_0 < 1$, then D > 0, E > 0, CD - E > 0. In view of $0 < \alpha \le 1$ and $0 < \alpha_1 \le 1$, we can get AC - 2B > 0.

The Hertz determinants of the first to fifth order polynomial are as follows:

$$\begin{split} &\Delta_1 = A + C > 0, \\ &\Delta_2 = A^2C + AB + AC^2 + CD - E > 0, \\ &\Delta_3 = (CD - E) \big[A^3 + A(AC - 2B) + E + AD \big] + A^2C^2B + ACB^2 + ABC^3, \\ &\Delta_4 = (CD - E) \big[A^4E + ABD \big(A^2 - 2B \big) + A^2DE + ABD^2 + AB^3 + A^2B^2C \\ &\quad + A^2E(AC - 2B) + AE^2 + AB^2C^2 + A^2B(CD - E) \big], \\ &\Delta_5 = BE\Delta_4. \end{split}$$

If $R_0 < 1$, then we know $\Delta_3 > 0$, $\Delta_4 > 0$, $\Delta_5 > 0$. According to the criterion of Routh-Hurwitz, we can obtain that the disease-free equilibrium E_0 is locally asymptotically stable if and only if $R_0 < 1$.

Theorem 3.3 For system (2.1), if $\hat{R} < 1$, then the disease-free equilibrium E_0 is globally asymptotically stable, where

$$\hat{R} = \sqrt{\frac{\beta_2\beta_4\alpha\alpha_1K\Lambda + \beta_1\beta_3\alpha_1K\Lambda d}{\mu^2dk_3k_5}}.$$

Proof Obviously, $R_0 < \hat{R}$. It follows from Theorem 3.2 that the disease-free equilibrium is locally asymptotically stable if $\hat{R} < 1$. Thus we only show that it attracts all nonnegative solutions of model (2.1).

From the first, second, and fifth equations of system (2.1), we have

$$\begin{cases} \frac{dX}{dt} \le \alpha_1 K - (d + \alpha + \alpha_1) X, \\ \frac{dY}{dt} \le \alpha X - dY, \\ \frac{dS}{dt} \le \Lambda - \mu S. \end{cases}$$

Thus we get that

$$\limsup_{t\to\infty}X(t)\leq\frac{\alpha_1K}{k_5},\qquad \limsup_{t\to\infty}Y(t)\leq\frac{\alpha\alpha_1K}{dk_5},\qquad \limsup_{t\to\infty}S(t)\leq\frac{\Lambda}{\mu}.$$

From the third, fourth, and sixth equations of system (2.1), we have

$$\begin{cases} \frac{dZ}{dt} \leq \frac{\beta_1 \alpha_1 K}{k_5} I - k_3 Z, \\ \frac{dU}{dt} \leq \frac{\beta_2 \alpha \alpha_1 K}{dk_5} I - k_3 U, \\ \frac{dI}{dt} \leq \frac{\beta_3 \Lambda}{\mu} Z + \frac{\beta_4 \Lambda}{\mu} U - \mu I. \end{cases}$$

Consider the following comparison system:

$$\begin{cases} \frac{dy_1}{dt} = \frac{\beta_1 \alpha_1 K}{k_5} y_3 - k_3 y_1, \\ \frac{dy_2}{dt} = \frac{\beta_2 \alpha_1 K}{dk_5} y_3 - k_3 y_2, \\ \frac{dy_3}{dt} = \frac{\beta_3 \Lambda}{\mu} y_1 + \frac{\beta_4 \Lambda}{\mu} y_2 - \mu y_3. \end{cases}$$
(3.9)

System (3.9) is a linear and monotone system. The characteristic equation corresponding to system (3.9) is

$$(\lambda + k_3)[\lambda^2 + k_6\lambda + a_1] = 0, (3.10)$$

where

$$a_1 = \frac{\mu^2 dk_3 k_5 - \beta_2 \beta_4 \alpha \alpha_1 K \Lambda - \beta_1 \beta_3 \alpha_1 K \Lambda d}{\mu dk_5}.$$

It is easy to know that real parts of all eigenvalues of (3.10) are negative provided that $\hat{R} < 1$. So any solution which passes a nonnegative initial value of system (3.9) must satisfy the following equation:

$$\lim_{t \to \infty} y_i(t) = 0 \quad (i = 1, 2, 3).$$

Let $0 < Z(0) < y_1(0)$, $0 < U(0) < y_2(0)$, $0 < I(0) < y_3(0)$. If $(y_1(t), y_2(t), y_3(t))$ is any solution of system (3.9) which passes a nonnegative initial value $(y_1(0), y_2(0), y_3(0))$, according to the comparison principle of differential equations, we can obtain that $Z(t) \le y_1(t)$, $U(t) \le y_2(t)$, $I(t) \le y_3(t)$, for all $t \ge 0$.

Therefore, in view of Lemma 2.1, we have

$$\lim_{t\to\infty} Z(t) = 0, \qquad \lim_{t\to\infty} U(t) = 0, \qquad \lim_{t\to\infty} I(t) = 0.$$

The proof is completed.

3.3 Existence of a backward bifurcation

In most epidemiological models, the disease-free equilibrium loses its local stability through a forward bifurcation at $R_0 = 1$, at the same time a stable endemic equilibrium appears at this parameter value. This phenomenon can also be described as a supercritical transcritical bifurcation. However, under certain circumstances, such as nonlinear incidence, nonlinear recovery rate, and vector-borne transmission, a backward bifurcation may occur although $R_0 < 1$ (see [31]). The system exhibits an endemic equilibrium along with a stable disease-free equilibrium. There is then a subcritical transcritical bifurcation at $R_0 = 1$.

Now we take the vaccination rate of a citrus tree α as a bifurcation parameter. Solve for $\bar{\mu}$ from $R_0 = 1$, giving

$$\bar{\mu} = \sqrt{\frac{\beta_2\beta_4\alpha\alpha_1K\Lambda + \beta_1\beta_3\alpha_1K\Lambda d}{k_1k_2k_3}}.$$

We can use Theorem 4.1 in [32] to explore when system (2.1) undergoes either a forward or a backward bifurcation when $R_0 = 1$. So two quantities, labeled \tilde{A} and \tilde{B} , need to be computed. In order to compute \tilde{A} and \tilde{B} , a change of coordinates involving the right and left eigenvectors of the Jacobian matrix $J(E_0)$ associated with the eigenvalue $\lambda = 0$ is required. We will express \tilde{A} and \tilde{B} in terms of parameters.

The Jacobian matrix $J(E_0)$ has a right eigenvector given by $w = (w_1, w_2, w_3, w_4, w_5, w_6)^T$, where

$$\begin{split} w_1 &= \frac{m\alpha_1\beta_2Y_0w_6 - \beta_1X_0dk_4w_6}{k_1k_2k_3}, \qquad w_2 &= \frac{-\alpha\beta_1X_0k_4w_6 - \beta_2Y_0(\alpha\alpha_1 + k_3k_5)w_6}{k_1k_2k_3}, \\ w_3 &= \frac{\beta_1X_0w_6}{k_3}, \qquad w_4 &= \frac{\beta_2Y_0w_6}{k_3}, \qquad w_5 = -w_6, \qquad w_6 = w_6. \end{split}$$

It should be noted that $w_2 < 0$ and $w_5 < 0$. The Jacobian matrix $J(E_0)$ has a left eigenvector given by $v = (v_1, v_2, v_3, v_4, v_5, v_6)$, where

$$v_1 = v_2 = v_5 = 0,$$
 $v_3 = \frac{\beta_3 S_0 v_6}{k_3},$ $v_4 = \frac{\beta_4 S_0 v_6}{k_3},$ $v_6 = v_6.$

We can choose w_6 and v_6 satisfy

$$v_6 \cdot w_6 = \left(\frac{\beta_2 \beta_4 \alpha \alpha_1 K \Lambda + \beta_1 \beta_3 \alpha_1 K \Lambda d}{\mu k_1 k_2 k_3^2} + 1\right)^{-1} > 0$$

such that $v \cdot w = 1$.

In order to follow the notations introduced in the literature [32], we set $x_1 = X - \frac{\alpha_1 Kd}{k_1 k_2}$, $x_2 = Y - \frac{\alpha \alpha_1 K}{k_1 k_2}$, $x_3 = Z$, $x_4 = U$, $x_5 = S - \frac{\Lambda}{\mu}$, $x_6 = I$, $W = (x_1, x_2, x_3, x_4, x_5, x_6)^T$, $\phi = \mu - \bar{\mu}$. Thus system (2.1) can be rewritten as follows:

$$\frac{dW}{dt} = F = (f_1, f_2, f_3, f_4, f_5, f_6)^T.$$

By direct computation we can get the associated non-zero partial derivatives of F at the disease-free equilibrium:

$$\frac{\partial^2 f_1}{\partial x_1 \partial x_6}(\mathbf{0}, 0) = -\beta_1, \qquad \frac{\partial^2 f_2}{\partial x_2 \partial x_6}(\mathbf{0}, 0) = -\beta_2, \qquad \frac{\partial^2 f_3}{\partial x_1 \partial x_6}(\mathbf{0}, 0) = \beta_1,$$

$$\frac{\partial^2 f_4}{\partial x_2 \partial x_6}(\mathbf{0}, 0) = \beta_2, \qquad \frac{\partial^2 f_5}{\partial x_3 \partial x_5}(\mathbf{0}, 0) = -\beta_3, \qquad \frac{\partial^2 f_5}{\partial x_4 \partial x_5}(\mathbf{0}, 0) = -\beta_4,$$

$$\frac{\partial^2 f_6}{\partial x_3 \partial x_5}(\mathbf{0}, 0) = \beta_3, \qquad \frac{\partial^2 f_6}{\partial x_4 \partial x_5}(\mathbf{0}, 0) = -\beta_4,$$

and all other derivatives are equal to zero.

Consequently, we can compute the two quantities \tilde{A} , \tilde{B} .

$$\tilde{A} = \sum v_k w_i w_j \frac{\partial^2 f_k}{\partial x_i \partial x_j} (\mathbf{0}, 0) = \frac{-g(\alpha)}{k_3^2 k_1 k_2} v_6 w_6^2,$$

where

$$\begin{split} g(\alpha) &= A_1 \alpha^2 + A_2 \alpha + A_3, \\ A_1 &= \beta_2 \beta_4 [\beta_2 \Lambda k_4 + \mu k_2 k_3] > 0, \\ A_2 &= \beta_1 \beta_2 \beta_4 \Lambda d k_4 + \beta_2 \beta_4 k_2 k_3 (\beta_2 \Lambda + \mu d) + \mu d \beta_1 \beta_3 k_2 k_3 - m \alpha_1 \beta_1 \beta_2 \beta_3 \Lambda, \\ A_3 &= \beta_1^2 \beta_3 \Lambda d^2 k_4 + \beta_1 \beta_3 \mu d^2 k_2 k_3 > 0. \end{split}$$

Denote Δ' is discriminant of $g(\alpha)$. Then $g(\alpha)=0$ have two positive real roots $\alpha^*=\frac{-A_2-\sqrt{\Delta'}}{2A_1}$ and $\alpha^{**}=\frac{-A_2+\sqrt{\Delta'}}{2A_1}$ if and only if $\Delta'>0$ and $A_2<0$.

Note that $\frac{\partial^2 f_5}{\partial x_5 \partial \phi}(\mathbf{0},0)=\frac{\partial^2 f_6}{\partial x_6 \partial \phi}(\mathbf{0},0)=1$, and all other derivatives $\frac{\partial^2 f_5}{\partial x_1 \partial \phi}(\mathbf{0},0)$ are equal to

Note that $\frac{\partial^2 f_5}{\partial x_5 \partial \phi}(\mathbf{0}, 0) = \frac{\partial^2 f_6}{\partial x_6 \partial \phi}(\mathbf{0}, 0) = 1$, and all other derivatives $\frac{\partial^2 f_8}{\partial x_i \partial \phi}(\mathbf{0}, 0)$ are equal to zero. So we can calculate \tilde{B} by substituting the vectors ν and w and the respective partial derivatives into the expression

$$\tilde{B} = \sum v_k w_i \frac{\partial^2 f_k}{\partial x_i \partial \phi} (\mathbf{0}, 0) = w_6 v_6 > 0.$$

According to the above discussion, we can conclude that $\tilde{A} > 0$ and $\tilde{B} > 0$ if and only if $\Delta' > 0$, $A_2 < 0$, and $\alpha^* < \alpha < \alpha^{**}$, which is the defining condition for a backward bifurcation [32].

Theorem 3.4 System (2.1) undergoes, at $R_0 = 1$, a backward bifurcation if and only if $\Delta' > 0$, $A_2 < 0$, and $\alpha^* < \alpha < \alpha^{**}$; otherwise, system (2.1) undergoes a forward bifurcation.

Remark 3.1 In the case of a backward bifurcation, there exists a saddle-node bifurcation point R_0^c such that for $0 < R_0 < R_0^c$, a unique stable disease-free equilibrium point exists, and, for $R_0^c < R_0 < 1$, the stable disease-free equilibrium point coexists with two endemic points. We can determine R_0^c by setting $\Delta = 0$, and get

$$R_0^c = \sqrt{1 - \frac{b^2}{4a\mu^2 k_1 k_2 k_3}}. (3.11)$$

Remark 3.2 From Remark 3.1, we know that the backward bifurcation gives a further sub-threshold condition beyond the reproduction number for the control of HLB, i.e., $R_0 < R_0^c < 1$. The existence of the backward bifurcation illustrates that the long term HLB activity in a citrus orchard depends on the initial population sizes of citrus trees and psyllids.

4 Permanence

In this section, we demonstrate the permanence of system (2.1). We first give some notations and a lemma.

Let \tilde{K} be a matrix space, $f: \tilde{K} \to \tilde{K}$ be a continuous map, and $K_0 \subseteq \tilde{K}$ be an open set. Define

$$\partial K_0 = \tilde{K} \setminus K_0$$
, and $M_{\partial} = \{ x \in \partial K_0 : f^n(x) \in \partial K_0, \forall n \in N \}.$

 A_{∂} is a maximal compact invariant set of f in ∂K_0 . A finite sequence $\{M_1, \dots, M_k\}$ are disjoint, compact, and invariant subsets of ∂K_0 , and each of them is isolated in ∂K_0 .

Lemma 4.1 (See [33]) Assume that

- (I) $f(K_0) \subset K_0$ and f has a global attractor A.
- (II) The maximal compact invariant set $A_{\partial} = A \cap M_{\partial}$ of f in ∂K_0 , possibly empty, has an acyclic covering $\tilde{M} = \{M_1, \dots, M_k\}$ with the following properties:
 - (a) M_i is isolated in \tilde{K} .
 - (b) $W^s(M_i) \cap K_0 = \emptyset$ for each $1 \le i \le k$.

Then f is uniformly persistent with respect to $(K_0, \partial K_0)$, i.e., there is $\eta > 0$ such that for any compact internally chain transitive set L with $L \nsubseteq \{M_i, \text{ for all } 1 \leq i \leq k\}$, $\inf_{x \in L} d(x, \partial K_0) > \eta$.

Theorem 4.1 If $R_0 > 1$, system (2.1) is permanent.

Proof Since $R_0 > 1$, then we can choose sufficiently small $\varepsilon > 0$ such that

$$\Upsilon \triangleq \frac{\gamma_1 + \gamma_2}{\mu k_2 k_3 (d + \beta_2 \varepsilon) (d + \alpha + \beta_1 \varepsilon) (\beta_3 \varepsilon + \beta_4 \varepsilon + \mu)} > 1,$$
(4.1)

where

$$\gamma_1 = \beta_1 \beta_3 \Big(\Lambda - \varepsilon (\beta_3 \varepsilon + \beta_4 \varepsilon + \mu) \Big) (d + \beta_2 \varepsilon) \Big(\alpha_1 K d - k_2 \varepsilon (d + \alpha + \beta_1 \varepsilon) \Big),
\gamma_2 = \beta_2 \beta_4 \Big(\Lambda - \varepsilon (\beta_3 \varepsilon + \beta_4 \varepsilon + \mu) \Big) \Big(\alpha \alpha_1 K d - k_2 \varepsilon (d + \beta_2 \varepsilon) (d + \alpha + \beta_1 \varepsilon) \Big).$$

To apply Lemma 4.1, for system (2.1), we define $\tilde{K} = \{(X,Y,Z,U,S,I) \in R_+^6\}$, $K_0 = \{(X,Y,Z,U,S,I) \in \tilde{K} : X \ge 0, Y \ge 0, Z > 0, U > 0, S \ge 0, I > 0\}$, and $\partial K_0 = \tilde{K} \setminus K_0$, and denote $u(t,x^0)$ as the unique solution of system (2.1) with the initial value $x^0 = (X^0,Y^0,Z^0,U^0,S^0,I^0)$.

Define the Poincaré map $P: \tilde{K} \to \tilde{K}$ associated with system (2.1) as follows:

$$P(x^0) = u(1, x^0), \quad \forall x^0 \in \tilde{K}.$$

It is easy to see that both \tilde{K} and K_0 are positively invariant and P is point dissipative. Set

$$M_{\partial} = \{ (X^0, Y^0, Z^0, U^0, S^0, I^0) \in \partial K_0 | P^m(X^0, Y^0, Z^0, U^0, S^0, I^0) \in \partial K_0, \forall m \in \mathbb{N} \}.$$

We claim that

$$M_{\partial} = \{(X, Y, 0, 0, S, 0) | X \ge 0, Y \ge 0, S \ge 0\}.$$

Obviously, $\{(X, Y, 0, 0, S, 0) | X \ge 0, Y \ge 0, S \ge 0\} \subseteq M_{\partial}$. Next we want to show

$$M_{\partial} \setminus \{(X, Y, 0, 0, S, 0) | X \ge 0, Y \ge 0, S \ge 0\} = \emptyset.$$

If it does not hold, then there exists a point $(X^0, Y^0, Z^0, U^0, S^0, I^0) \in M_\partial \setminus \{(X, Y, 0, 0, S, 0) | X \ge 0, Y \ge 0, S \ge 0\}$.

Case (i). $Z^0 = 0$, $U^0 > 0$, $I^0 > 0$. It is obvious that X(t) > 0, I(t) > 0 for any t > 0. Then, from the third equation of system (2.1), $\frac{dZ}{dt}|_{t=0} = \beta_1 X(0) I(0) > 0$ holds. It follows that $(X, Y, Z, U, S, I) \notin \partial K_0$ for $0 < t \ll 1$. This is a contradiction.

Similarly, we can prove the other cases: (a) $Z^0 > 0$, $U^0 = 0$, $I^0 > 0$, and (b) $Z^0 > 0$, $U^0 > 0$, $U^0 = 0$.

Case (ii). $Z^0 = U^0 = 0$, $I^0 > 0$. It is obvious that X(t) > 0, Y(t) > 0, I(t) > 0 for any t > 0. Then, from the third, fourth equations of system (2.1), we get $\frac{dZ}{dt}|_{t=0} = \beta_1 X(0)I(0) > 0$, $\frac{dU}{dt}|_{t=0} = \beta_2 Y(0)I(0) > 0$ hold. It follows that $(X,Y,Z,U,S,I) \notin \partial K_0$ for $0 < t \ll 1$. This is a contradiction.

Similarly, we can prove the other cases: (c) $Z^0 = I^0 = 0$, $U^0 > 0$, and (d) $U^0 = I^0 = 0$, $Z^0 > 0$.

That is to say, for any $(X^0, Y^0, Z^0, U^0, S^0, I^0) \notin \{(X, Y, 0, 0, S, 0) | X \ge 0, Y \ge 0, S \ge 0\}$, then $(X^0, Y^0, Z^0, U^0, S^0, I^0) \notin M_{\partial}$. Therefore we have

$$M_{\partial} = \{(X, Y, 0, 0, S, 0) | X \ge 0, Y \ge 0, S \ge 0\}.$$

In the following, we need to prove

$$W^s(E_0) \cap K_0 = \emptyset$$
.

We write $x^0 = (X^0, Y^0, Z^0, U^0, S^0, I^0) \in K_0$. By the continuity of the solutions with respect to the initial conditions, we know that, for any given $\varepsilon > 0$, there exists $\delta_0 > 0$ such that for all $x^0 \in K_0$ with $|x^0 - E_0| \le \delta_0$, it holds that

$$||u(t,x^0) - u(t,E_0)|| \le \varepsilon, \quad \forall t \in [0,1].$$

Now we proceed by contradiction to prove that

$$\limsup_{t \to \infty} d(P^m(x^0), E_0) \ge \delta_0. \tag{4.2}$$

If (4.2) does not hold, then

$$\limsup_{t\to\infty}d\big(P^m\big(x^0\big),E_0\big)<\delta_0,$$

for some $x^0 \in K_0$.

Without loss of generality, we suppose that

$$d(P^m(x^0), E_0) < \delta_0, \quad \forall m \in \mathbb{N}.$$

By the continuity of the solutions with respect to the initial values, we obtain

$$||u(t, P^m(x^0)) - u(t, E_0)|| \le \varepsilon, \quad \forall t \in [0, 1], \forall m \in \mathbb{N}.$$

For any $\tilde{t}_1 \ge 0$, there exists an integer $m \ge 0$ such that $\tilde{t}_1 = m + t'$, where $t' \in [0,1]$. Then we have

$$||u(\tilde{t}_1,x^0)-u(\tilde{t}_1,E_0)|| = ||u(t',P^m(x^0))-u(t',E_0)|| \le \varepsilon,$$

for any $\tilde{t}_1 \geq 0$, which implies that

$$0 \le Z(t) \le \varepsilon, \qquad 0 \le U(t) \le \varepsilon, \qquad 0 \le I(t) \le \varepsilon.$$
 (4.3)

From (2.1) and (4.3), we have

$$\begin{cases} \frac{dX}{dt} \ge \alpha_1 K - \frac{\alpha_1^2 K}{k_2} - (d + \alpha + \beta_1 \varepsilon) X, \\ \frac{dY}{dt} \ge \alpha X - (d + \beta_2 \varepsilon) Y, \\ \frac{dS}{dt} \ge \Lambda - (\beta_3 \varepsilon + \beta_4 \varepsilon + \mu) S. \end{cases}$$

Consequently, we can easily obtain that there exists T > 0 such that for all t > T

$$X(t) \ge \frac{\alpha_1 K d}{k_2 (d + \alpha + \beta_1 \varepsilon)} - \varepsilon, \qquad Y(t) \ge \frac{\alpha \alpha_1 K d}{k_2 (d + \alpha + \beta_1 \varepsilon) (d + \beta_2 \varepsilon)} - \varepsilon,$$

$$S(t) \ge \frac{\Lambda}{\beta_3 \varepsilon + \beta_4 \varepsilon + \mu} - \varepsilon.$$

$$(4.4)$$

Substituting (4.4) into the third, fourth, and sixth equations of system (2.1), we have that for t > T

$$\begin{cases}
\frac{dZ}{dt} \ge \beta_1 I(\frac{\alpha_1 K d}{k_2 (d + \alpha + \beta_1 \varepsilon)} - \varepsilon) - k_3 Z, \\
\frac{dU}{dt} \ge \beta_2 I(\frac{\alpha \alpha_1 K d}{k_2 (d + \alpha + \beta_1 \varepsilon) (d + \beta_2 \varepsilon)} - \varepsilon) - k_3 U, \\
\frac{dI}{dt} \ge \beta_3 Z(\frac{\Lambda}{\beta_3 \varepsilon + \beta_4 \varepsilon + \mu} - \varepsilon) + \beta_4 U(\frac{\Lambda}{\beta_3 \varepsilon + \beta_4 \varepsilon + \mu} - \varepsilon) - \mu I.
\end{cases} \tag{4.5}$$

Consider the following comparison system:

$$\begin{cases} \frac{d\tilde{Z}}{dt} = \beta_{1}\tilde{I}(\frac{\alpha_{1}Kd}{k_{2}(d+\alpha+\beta_{1}\varepsilon)} - \varepsilon) - k_{3}\tilde{Z}, \\ \frac{d\tilde{U}}{dt} = \beta_{2}\tilde{I}(\frac{\alpha\alpha_{1}Kd}{k_{2}(d+\alpha+\beta_{1}\varepsilon)(d+\beta_{2}\varepsilon)} - \varepsilon) - k_{3}\tilde{U}, \\ \frac{d\tilde{I}}{dt} = \beta_{3}\tilde{Z}(\frac{\Lambda}{\beta_{3}\varepsilon+\beta_{4}\varepsilon+\mu} - \varepsilon) + \beta_{4}\tilde{U}(\frac{\Lambda}{\beta_{3}\varepsilon+\beta_{4}\varepsilon+\mu} - \varepsilon) - \mu\tilde{I}. \end{cases}$$

$$(4.6)$$

Denote the coefficient matrix of system (4.6) by H, here

$$H = \begin{pmatrix} -k_3 & 0 & \beta_1(\frac{\alpha_1 K d}{k_2 (d + \alpha + \beta_1 \varepsilon)} - \varepsilon) \\ 0 & -k_3 & \beta_2(\frac{\alpha \alpha_1 K d}{k_2 (d + \alpha + \beta_1 \varepsilon) (d + \beta_2 \varepsilon)} - \varepsilon) \\ \beta_3(\frac{\Lambda}{\beta_3 \varepsilon + \beta_4 \varepsilon + \mu} - \varepsilon) & \beta_4(\frac{\Lambda}{\beta_3 \varepsilon + \beta_4 \varepsilon + \mu} - \varepsilon) & -\mu \end{pmatrix}.$$

Thus, we get the characteristic equation of H:

$$(\lambda + k_3)(\lambda^2 + k_6\lambda + c) = 0,$$

where

$$k_6 = d + m + \mu > 0$$
, $c = \mu k_2 k_3 (d + \beta_2 \varepsilon) (d + \alpha + \beta_1 \varepsilon) (\beta_3 \varepsilon + \beta_4 \varepsilon + \mu) (1 - \Upsilon)$.

It follows from (4.1) that c < 0 provided that $R_0 > 1$. Then there exists a unique positive root λ^* of characteristic polynomial of H. By [34], there exists a positive characteristic vector denoted by $(\tilde{Z}_1, \tilde{U}_1, \tilde{I}_1)$ such that $e^{\lambda^* t}(\tilde{Z}_1, \tilde{U}_1, \tilde{I}_1)$ is a solution of system (4.6). Further, for any given initial values (Z(0), U(0), I(0)), there exists sufficiently small positive q such that $q\tilde{Z}_1 < Z(0)$, $q\tilde{U}_1 < U(0)$, $q\tilde{I}_1 < I(0)$. Any solution $(\tilde{Z}(t), \tilde{U}(t), \tilde{I}(t))$ of system (4.6) which passes initial value $\tilde{Z}(0) = q\tilde{Z}_1$, $\tilde{U}(0) = q\tilde{U}_1$, $\tilde{I}(0) = q\tilde{I}_1$ must satisfy $\tilde{Z}(t) \to \infty$, $\tilde{U}(t) \to \infty$, $\tilde{I}(t) \to \infty$, as $t \to \infty$. According to the comparison principle in differential equations, the solution (Z(t), U(t), I(t)) of system (4.5) with initial values (Z(0), U(0), I(0)) must satisfy $Z(t) > \tilde{Z}(t)$, $U(t) > \tilde{U}(t)$, $I(t) > \tilde{I}(t)$. Therefore, $Z(t) \to \infty$, $U(t) \to \infty$, $I(t) \to \infty$, as $t \to \infty$. This is a contradiction. Thus, we have proved that (4.2) holds and P is weakly uniformly persistent with respect to $(K_0, \partial K_0)$.

We can easily obtain that P has a global attractor E_0 . It is easy to obtain that E_0 is an isolated invariant set in \tilde{K} and $W^s(E_0) \cap K_0 = \emptyset$. We know that E_0 is acyclic in M_{∂} , and every solution in M_{∂} converges to E_0 . According to Zhao [33], we have that P is uniformly persistent with respect to $(K_0, \partial K_0)$. This implies that the solution of system (2.1) is uniformly persistent with respect to $(K_0, \partial K_0)$. This completes the proof.

5 Numerical simulation

In this section, we first provide results from numerical simulations of model (2.1) that demonstrate and support our theoretical results. The model will be applied to study the transmission of HLB in the South of Jiangxi, China. We need to estimate the model parameters in order to carry out the numerical simulations. The values of parameters of model (2.1) are given in Table 1. We explain the parameter values as follows:

• The average life expectancy of trees was from 20 years to 30 years [35]. We can take 25 as the current average life expectancy. Thus, the natural death rate of citrus trees $d = \frac{1}{25} = 0.04$.

Parameters	Values	Unit	References
d	0.04	year ⁻¹	[35]
μ	5.7394	year ⁻¹	[36]
K	2,000	-	[36]
α_1	0.6	year ⁻¹	Estimation
$oldsymbol{eta}_1$	0.000243333	year ⁻¹	[36]
β_2	0.0000365	year ⁻¹	Estimation
β_3	0.000194667	year ⁻¹	[36]
$oldsymbol{eta}_4$	0.000214133	year ⁻¹	Estimation
Λ	6,028,433	year ⁻¹	[36]
α	0~1	year ⁻¹	-
m	0 ~ 1	year ⁻¹	-

Table 1 Parameter values used for numerical simulations of the HLB model

- The annual average temperature of Jiangxi Province is from 8.6 to 20.6 degree centigrade in 2010. So we can choose the average temperature $T = 17^{\circ}$ C.
- It follows from the literature [36–38] that the natural mortality of psyllids is taken as the form $\mu = \frac{1}{L}365$, in which $L = -0.14221*T^2 + 4.31998*T + 31.25498$. Thus, we can get $\mu = 5.7394$.
- The maximum number of trees that can be planted in the grove is 2,000, i.e., K = 2,000. According to the implementation of control measures for HLB in the South of Jiangxi, we take the replanting rate $\alpha_1 = 0.6$.
- Using the same transmission forms in [36], we get $\beta_1 = \frac{0.45625(d+\alpha_1)}{\alpha_1 K} = 0.000243333$, $\beta_3 = \frac{0.365(d+\alpha_1)}{\alpha_1 K} = 0.000194667$. Further, we take $\beta_2 = 0.015\beta_1$ and $\beta_4 = 1.1\beta_3$, then $\beta_2 = 0.00000365$ and $\beta_4 = 0.000214133$.
- From literature [36] and [37], we know the recruitment rate of psyllid $\Lambda = \frac{3\alpha_1 K*EFD*P_{ea}*MDR}{\mu(d+\alpha_1)}, \text{ where } EFD = 0.0107*365*T*(T-13)*\sqrt{30.8-T}, \\ P_{ea} = 0.47192 + 0.0109*T, MDR = 5.286*10^{-5}*365*T*(T-10.02)*\sqrt{34.17-T}, \\ \text{then we can calculate } \Lambda = 6,028,433.$

All citrus trees infected by HLB must be removed in the South of Jiangxi. But HLB has an incubation period during which the infected trees do not show symptoms, so we take the removing rate m=0.6 by empirical estimation. If we choose the vaccination rate $\alpha=0.1$, by (3.1), we can obtain the basic reproductive number for the South of Jiangxi $R_0=2.75$. Sensitivity analysis of all constant parameters that are included in R_0 is performed (see Figure 2). For the parameters, including Λ , μ , K, m, β_4 , β_3 , β_2 , β_1 , α , d, α_1 , we vary their value by 10% and plot the effects on R_0 . From Figure 2, we can clearly observe that the natural mortality of psyllid population (μ) has the most effects on R_0 of all the constant parameters. The reason is the parameter is involved in both directions of transmission: from a tree to a psyllid and vice versa. Note that parameters α , m, μ have the opposite effects on R_0 . For example, an increase in α decreases R_0 , whereas other parameters are positively correlated with R_0 . Apart from α_1 (invariability), parameters β_1 , β_3 , K have the effect on R_0 . By increasing the rate of vaccinating protecting virus α , the roguing rate m, the mortality of psyllid population μ , it is possible to reduce the prevalence of the disease.

In addition, from Figure 2 we can find that the replanting rate (α_1) is less sensitive to R_0 , but the different values of α_1 can affect the peak values of the infected trees and the times to reach peak value. Figure 3 reflects that, along with the increase in value α_1 , the peak value delays in time and increases in value. Therefore, the risk of HLB spread would reduce with the decrease of replanting magnitude.

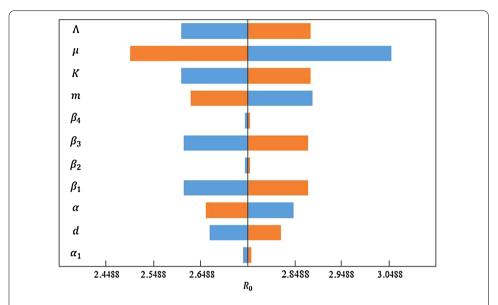


Figure 2 The sensitivity of R_0 to changes in constant parameters. Each parameter is varied by 10% to assess the impact on R_0 . Decreasing each parameter by 10% (e.g., 0.9α) is indicated in blue; increasing each parameter by 10% (e.g., 1.1α) is indicated in orange.

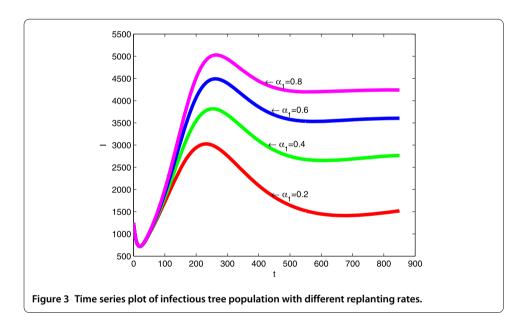


Figure 4 shows the dependence of the basic reproductive number R_0 on two control strengths of vaccination and removing the infected tree. R_0 decreases as m and α increase from 0 to 1, and it is more sensitive when m and α are small. It implies that proper cross protection or removing infected trees can effectively control the spread of HLB.

Next, in order to show the effects of cross protection on the total infective population, we fix the vaccination rate $\alpha=0,0.4,0.8$, respectively. The numerical results (see Figure 5) show that there is high infected value without cross protection ($\alpha=0$); however, there are low density values after inoculating the protecting virus strains. It shows that the protecting virus without causing undue harm plays a key role in HLB virus control in plants. It appears to offer a promising measure for HLB control.

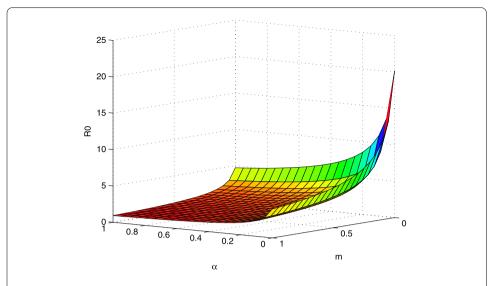
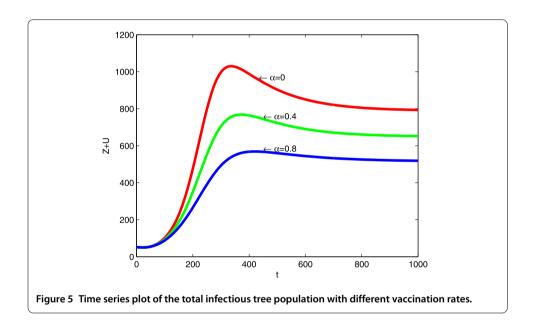
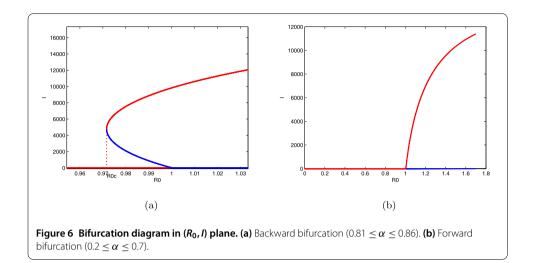


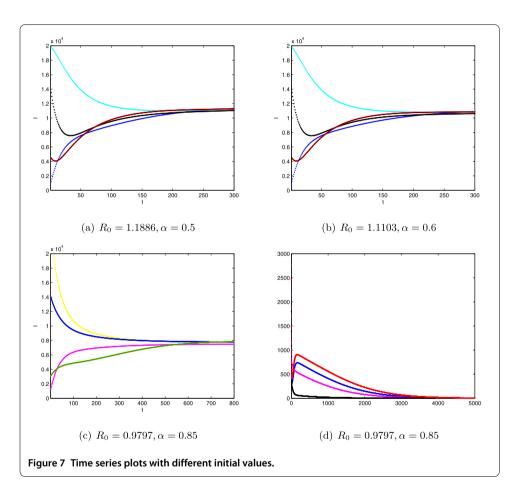
Figure 4 The dependence of the basic reproductive number on the strength of vaccination and removing infected tree.



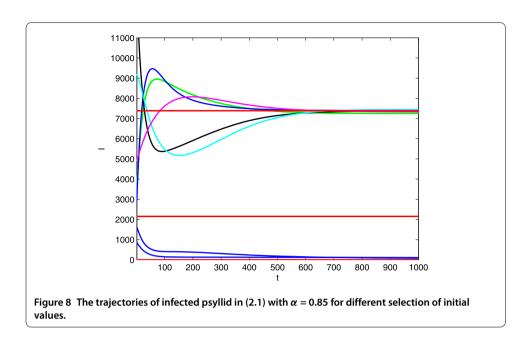
Finally, numerical simulations are carried out to illustrate the effectiveness of the obtained results. For the simulations that follow, we applied this set of parameters shown in Table 1 unless otherwise stated.

Set m = 0.988. According to the result of Theorem 3.4, we know that if $\alpha \in [0.81, 0.86]$, a backward bifurcation can occur, that is, for $R_0 < 1$, a unique disease-free equilibrium and two subcritical endemic equilibria coexist, but for $R_0 > 1$, a unique endemic equilibrium exists (see Figure 6(a)). Moreover, if $\alpha \in [0, 0.81) \cup (0.86, 1]$, a forward bifurcation occurs, that is, for $R_0 < 1$, a unique disease-free equilibrium exists, which is stable, but its stability is lost at $R_0 = 1$, in which a stable endemic equilibrium arises by a transcritical bifurcation (see Figure 6(b)).





Time series of I are plotted in Figure 7(a)-(d) showing the disease-free equilibrium and two endemic equilibria. Fix $\alpha=0.5$, then $R_0=1.1886>1$; and fix $\alpha=0.6$, then $R_0=1.1103>1$. By Theorem 4.1, we have that the disease will be endemic (see Figure 7(a)-(b)). Taking $\alpha=0.85$, by (3.1) and (3.11), we can calculate $R_0=0.9797$, $R_0^c=0.9708$, then $R_0^c< R_0<1$. If initial values close to $E_0=(84,1,790,0,0,1,050,367,0)$ are chosen, then the solution of system (2.1) converges to the stable disease-free equilibrium E_0 (see Figure 7



(d)). Further, if initial values close to endemic equilibria $E_2 = (99, 1,253,172,32,1,042,977,7,390)$ are chosen, then the solution of system (2.1) converges to the endemic equilibria E_2 (see Figure 7 (c)). So the outbreak of HLB depends on the initial size of every population. The disease can die out if the initial values lie in the basin of attraction of E_0 , or it can persist if the initial values lie in the basin of attraction of E_2 . Figure 8 shows that the bigger endemic equilibrium is stable, the smaller is unstable, and the disease-free equilibrium is stable. This clearly shows the co-existence of two locally-asymptotically stable equilibria when $E_0 < 1$.

6 Conclusions

In this paper, a deterministic model with bilinear incidence is formulated to study the impact of cross protection on the spread and control of HLB. When we choose appropriate parameters, there exists a backward bifurcation. If $R_0 > 1$, then there is a unique endemic equilibrium and the disease is uniformly persistent. If $R_0 < 1$, there may be two endemic equilibria, and the endemic equilibrium can coexist with the disease-free equilibrium. This illustrates that $R_0 < 1$ cannot ensure the eradication of the disease, and decreasing R_0 below the sub-threshold R_0^c would be a propositional control strategy. If $R_0^c < R_0 < 1$, only when the numbers of infected cases are small enough, it is a sufficient condition to eliminate HLB. Numerical examples are given to demonstrate the effectiveness of the theoretical results.

Our investigations suggest that cross protection and removing infected trees play an important role in controlling the spread of HLB. Cross protection also dramatically affects the disease transmission dynamics. Moreover, increasing the replanting rate is bad for disease control. The result strongly suggests and supports the previous observations [39, 40].

Acknowledgements

The research has been supported by the National Natural Science Foundation of China (11561004) and the Natural Science Foundation of Jiangxi Province (20171BAB201006).

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

The main idea and theoretical proof of this paper were proposed by LL and SG. Programming of numerical simulation was completed by YL and YG. All authors read and approved the final manuscript.

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Received: 10 May 2017 Accepted: 7 October 2017 Published online: 06 November 2017

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