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Modeling leafhopper populations and their role in transmitting plant diseases.

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MODELING LEAFHOPPER POPULATIONS AND THEIR ROLE IN
TRANSMITTING PLANT DISEASES
(Thesis format: Integrated Article)

by

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Abstract

This M.Sc. thesis focuses on the interactions between crops and leafhoppers.

Firstly, a general delay differential equations system is proposed, based on the infection age structure, to investigate disease dynamics when disease latencies are considered. To further the understanding on the subject, a specific model is then introduced. The basic reproduction numbers $\mathcal{R}_0$ and $\mathcal{R}_1$ are identified and their threshold properties are discussed. When $\mathcal{R}_0 < 1$, the insect-free equilibrium is globally asymptotically stable. When $\mathcal{R}_0 > 1$ and $\mathcal{R}_1 < 1$, the disease-free equilibrium exists and is locally asymptotically stable. When $\mathcal{R}_1 > 1$, the disease will persist.

Secondly, we derive another general delay differential equations system to examine how different life stages of leafhoppers affect crops. The basic reproduction numbers $\mathcal{R}_0$ is determined: when $\mathcal{R}_0 < 1$, the insect-free equilibrium is globally asymptotically stable. When $\mathcal{R}_0 > 1$, a positive equilibrium appears. To investigate the qualitative behaviours of this equilibrium, two special cases based on the monotonicity of birth rates of leafhoppers with respect to the adult population are studied.

Keywords: Leafhoppers, crops, age-structured model, basic reproduction number, local asymptotical stability, global asymptotical stability, delays, persistence.

Co-Authorship Statement

Chapter 2-3 of this thesis consist of the following papers:

Chapter 2: Ji Ruan and Xingfu Zou: Modeling crop disease dynamics transmitted by leafhoppers.

Chapter 3: Ji Ruan and Xingfu Zou: Modeling leafhopper population and their effects on crops.

The original draft for each of the above articles is prepared by the author. Subsequent revisions are performed by the author and Dr. Xingfu Zou. The analytical and numerical works are performed by the author under the supervision of Dr. Xingfu Zou.

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Chapter 1

Introduction

Leafhopper is a common name applied to any species from the family Cicadellidae. These minute insects, colloquially known as hoppers, suck sap from grass, shrubs, or trees. Potatoes, alfalfa, and beets constitute especially good hosts. Apple, birch, chestnut, maple and numerous other tree species can also host the pests [7, 20]. The species have been reported as a very serious problem in Canada, causing huge losses in crops. [8, 9, 13, 18, 22].

1.1 The Life Cycle of Leafhoppers

Although leafhoppers are divided into a high number of subfamilies (about 40), most of the subfamilies share a very similar life cycle [21]. Generally speaking, in North America, leafhopper species overwinter in the southern United States, and migrate northward in spring. They arrive in Canada in early summer. After mating, eggs are laid inside the veins on the underside of leaves. A female leafhopper lives about a month, producing one to six eggs daily. Normally, after about 10 days hatching, leafhoppers go to the nymph stage, during which they will pass through five instars before emerging as adults [16, 19].

Eggs are laid singly within the petioles and veins on the under surfaces of host foliage. The approximate optimum temperature for egg laying is 24°C with no egg laying above 32°C or below 17°C. The eggs, which are about 1 mm in length, hatch in approximately 10 days. Females may deposit 1–6 eggs per day over their life span [16].

Leafhopper nymphs (immature stage) pass through five distinct stages within a period of 12–35 days. Nymphal development is most rapid at 19°C, no development occurs below 12°C, and development is inhibited above 41°C. The total period from egg to reproductive maturity

ranges from 2 weeks to 1 month, under favourable conditions. Nymphs are extremely sensitive to desiccation and to dislodgement from the host by wind-driven rain [16].

Leafhopper adults are elongated, wedge-shaped and somewhat triangular in cross-section. They jump and fly off readily. Depending on species, they range in size from 0.32 cm to 1.3 cm and their bodies are coloured yellow, green, gray or they may be marked with colour patterns. Adults can live about 40 – 90 days [15].

1.2   Habitat and Food Resource(s)

Species can be somewhat specific to certain host plants. As a group they feed on leaves of a wide variety of plants including many types of grasses, flowers, vegetables, fruit trees, shrubs, deciduous trees, palms and weeds. The rose leafhopper, *Edwardsiana rosae* (Linnaeus), feeds primarily on plants of the rose family, although foliage of other woody plants (blackberry, cornus, oak, prunus, populus, raspberry, ulmus, acer and others) serve as food. The potato leafhopper, *Empoasca fabae* (Harris), feeds on legumaceous plants like alfalfa, as well as on apple, birch, chestnut, maples, and other trees. Species in the genus, *Erythroneura*, feed on sycamore leaves, but also on apple, grape and willow. The aster or six-spotted leafhopper, *Macrosteles quadrilineatus* Forbes, feeds on vegetables and annual flowers and spreads the aster yellows virus to woody plants like periwinkle and thunbergia species. Nymphs and adults feed on the underside of leaves. Some leafhoppers are readily attracted to lights [15, 20].

1.3   The Damage

Leafhoppers have become a serious problem in many parts of Canada. Generally, the damage is caused by their consumption of crops and the transmission of crop diseases.

The leafhopper is a sucking insect, removing plant sap directly from the vascular (water and food transport) system in the leaflet, petioles, and sometimes the stem. Both adults and nymphs feed on the leaves. Feeding injury sometimes appears very similar to disease symptoms or nutrient imbalance. By adversely affecting the vascular system, leafhoppers reduce photosynthesis, which decreases productivity, stunts the plant, and sometimes kills young seedlings. The salivary substance forms a plug in the vascular system in addition to acting as a phytotoxin. Plant damage is frequently intensified during periods of moisture stress [16, 15].

A more serious problem is that leafhoppers spread pathogens causing many crop diseases, such as the aster yellow disease [6], the sugarcane yellow leaf disease [5], the flavescence doree (FD) disease [12], the purple-top wilt disease [19] and other diseases. Most leafhoppers are not born with pathogens that cause plant diseases. However, they acquire pathogens by feeding on plant species. Both adults and nymphs are capable of carrying and transmitting diseases. The diseases transmitted by leafhoppers are characterized by the production of disturbances that arise primarily in the vascular system, usually in the region of the phloem. Symptoms consist of yellowing, dwarfing, stunting, streaking, leaf rolling or curling, rosetting, witches' broom effects, and other related abnormalities [1, 18, 6, 19]. The diseases sometimes will cause huge losses in crop yields, if not placed under proper controls [11, 14]. The outbreaks of crop diseases in these fields that are vectored by leafhoppers pose great threats to the whole farming industry; therefore, it is of significance to investigate how to control this damage.

In this thesis, we construct models that study both the consumption and the disease-transmitting effects of leafhoppers, and trying to understand the interactions between crops and leafhoppers.

1.4   Recent Work

Many efforts have been devoted to investigating leafhoppers, and rich results have been obtained.

As mentioned in Section §1.1, the hatching and maturation of leafhoppers are greatly affected by environmental factors, more specifically, temperature and moisture. The effects of temperature on hatching and maturation of nymphs have been intensively studied [2, 3, 12], providing a better understanding of the development of leafhoppers under changing weather conditions. Rigamonti et. al. [12], considering the fact that the hatching and maturing process are undermined or elongated under low temperatures, suggest a better timing of management activities to control the pests. In the meantime, other efforts [4, 5, 14] have been devoted to studying humidity effects, which allow us to identify the correlation between moisture and leafhopper dynamics in the fields. Besides, they argue that moisture has a positive effect on preventing plant diseases from spreading. Many statistical tools have been used when studying environmental effects and rich results have been obtained; however, the models have limitations for theoretical use because most of the relationships between factors are determined empirically using data from only one location. In addition, the previous models fail to take

crops into consideration. Therefore, we are looking for some deterministic models that will provide implications on the interactions between leafhoppers and crops.

Unfortunately, not many deterministic models regarding leafhoppers have been put forward. F. Nakasuji et. al. [10] advance an ODE system to model the epidemiology of infectious diseases of leafhoppers and crops. However, instead of giving the theoretical analysis, the authors focus on the parametrization of the model. Besides, the model fails to consider the leafhoppers' consumption of crops, the life structure of leafhoppers, as well as the delay effects of diseases.

To date, the pathological and physiological properties of the virus-vector relationship and the ecological traits of the vector population have been studied intensively. This provides us with a theoretical background to investigate leafhoppers and their effects on crops. In this thesis, we will be studying the phenomenon by means of age-structured approach [17]. Based on the fact that disease infection in both leafhoppers and crops is hierarchic (i.e. susceptible, latent, infected) and the life cycle of leafhoppers is structured (i.e. egg, nymph, adult), this thesis investigates the interactions between leafhoppers and crops in two perspectives: the infection age structure and the biological age structure.

1.5   Organization of the Project

In Chapter §2, a delay differential equations system, based on the infection age structure model, is introduced. We verify the wellposedness of the system and discuss the stability of the equilibria. Moreover, the persistence theory is applied to show that, under certain conditions, the disease establishes and an equilibrium with all components being positive appears. Numerical simulations are provided to verify the results, and furthermore, to offer the complementary information.

In Chapter §3, we propose another delay differential equations system to investigate the effects that different life stages of leafhoppers pose on crops. In this model, diseases are not included. The wellposedness of the system is verified and the stability of the equilibria is discussed. Both qualitative and quantitative methods are applied to study the system.

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Chapter 2

Modeling crop disease dynamics transmitted by leafhoppers

2.1 Introduction

Leafhoppers, also known as hoppers, belong to the order Homoptera and the family Cicadellidae [26]. The family is distributed all over the world, and constitutes the second-largest *Hemipteran* family, with at least 20,000 described species. A variety of plants, such as potatoes, beets, alfalfa, and birch trees [23], can host these pests. Adult leafhoppers are 3–4 mm in length, green to brown in color. As their name implies, they jump from leaf to leaf. Nymphs (young leafhoppers resembling adults in appearance) are lighter green in color [21].

Most leafhopper species share a similar life cycle. They lay their eggs in the veins on the undersides of leaves in April and May. Within approximately 10 days, nymphs will hatch out of the eggs and go through five development stages, which are called instars, before becoming adults. Development lasts 4–6 weeks. Adults will go on to live around 40 days with some staying alive for up to 90 days. During their adult life, leafhoppers will lay hundreds of eggs, producing several generations in between April and October [21].

The importance of leafhoppers stems from their consumption of plants, and more significantly, the transmission of many plant diseases. As was reported [2], the first plant virus shown to be insect-transmitted was one transmitted by a leafhopper. This virus has caused a destructive disease, called rice dwarf, in Japan for more than 100 years [17]. Since the discovery of rice dwarf, leafhopper-transmitted viruses have been found in nearly all of the agricultural areas of the world, such as aster yellow disease [12], sugarcane yellow leaf disease [8], flaves-

cence doree (FD) disease [18], and purple-top wilt disease [24]. Some of these cause some of the most destructive plant diseases. At least 110 species of leafhoppers in seven families are listed as vectors of viruses that affect a wide range of plant species. It should be expected, of course, that further studies will reveal additional viruses transmitted by some of these vectors, and additional vectors of some of the viruses. Most leafhoppers are not born with pathogens that cause plant diseases. However, they acquire pathogens by feeding on plants. Both adults and nymphs are capable of carrying and transmitting diseases. The diseases transmitted by leafhoppers are characterized by the production of disturbances that arise primarily in the vascular system, usually in the region of the phloem. Symptoms include yellowing, dwarfing, stunting, streaking, leaf rolling or curling, rosetting, witches' broom effects, and other related abnormalities [2, 23, 12, 24].

The studies, focusing on disease aspects, undertaken so far are mainly about disease transmission and disease control [4, 19, 25]. The information available on the vector primarily refers to life cycles, behavioural aspects, spatiotemporal distributions and sampling for supervised control [1, 3, 6, 10, 15]. Those models have limitations for theoretical use because most of the relationships between factors are determined empirically using data from only one location. Besides, few of them study the interactions between leafhoppers and crops [17]. Thus, our motivation in this chapter is to build a general model that could contribute to understanding how diseases transmit between leafhoppers and crops, and thereby provide information for pest control management.

Age structure models [11, 22] serve as a good tool to study the disease dynamics. Based on the fact that diseases in both leafhoppers and crops are structured (i.e. susceptible, latent and infected), it is natural and reasonable to take the structure into consideration. Making use of the infection age as well as the typical method of characteristics for structured population, we derive a model that has two discrete delays, accounting for the latencies in leafhoppers and crops. Furthermore, we assume an isolated, spatially well-mixed environment, where the insect population is evenly distributed [27].

The rest of the chapter is organized as below. In Section §2.2, we derive a general disease model. The wellposedness of the model and stability of the trivial equilibrium and insect-free equilibrium are investigated in Section §2.3. Section §2.4 deals with a specific age-structured model, for which we can obtain more detailed analysis of the model, including the stability of the equilibria and the persistence of the disease. Simulations are given in Section §2.5 to verify the qualitative results.

2.2 Derivation of the General Model

In this section, a general model will be derived. Assume that, in an isolated, spatially well-mixed environment, a certain leafhopper species transmits a certain type of disease within a certain crop species. Suppose that there is a fixed infection latent period of length τ_1 within leafhoppers and another fixed latent period τ_2 within crops. Although latencies differ among individuals in general, for the sake of simplicity, we assume fixed latencies which can be considered as an approximation of the mean latencies within the hosts and vectors here. Assume that $\tau_1 > \tau_2$ (for most of the crop diseases, it is known that latencies in leafhoppers are larger than latencies in crops [2, 24]). Due to latencies, the infected classes are further divided into latent and infectious classes for both hosts and vectors. Let $S_1(t)$, $L_1(t)$ and $I_1(t)$ be the sub-population of susceptible, latent and infectious leafhoppers, respectively; and let $S_2(t)$, $L_2(t)$ and $I_2(t)$ be the biomass of susceptible, latent and infectious crops, respectively. Here, the unit of the population is chosen to be number; in addition, we treat the biomass as the weight of crops, i.e. the units could be kilogram or pound, and etc. To be consistent with the International System of Units, we use kilogram as the unit of the biomass.

To derive the model, we follow the ideas in [11, 16] to make use of the infection age a. Let $\ell_1(t, a)$ be the density of the leafhopper population with infection age a at time t. Similar to the equation incorporating the natural age structure in Metz and Diekmann [9], the density $\ell_1(t, a)$ is described by the following first-ordered partial differential equation

$$\frac{\partial \ell_1(t, a)}{\partial t} + \frac{\partial \ell_1(t, a)}{\partial a} = -(d_1 + \bar{d}_1(a))\ell_1(t, a), \tag{2.1}$$

where constant d_1 is the natural death rate of leafhoppers, and $\bar{d}_1(a)$ is the disease-induced mortality. From the definition of $\ell_1(t, a)$, the leafhopper population in the latent and infectious classes at time t can be expressed by

$$L_1(t) = \int_0^{\tau_1} \ell_1(t, a)da, \quad \text{and} \quad I_1(t) = \int_{\tau_1}^{\infty} \ell_1(t, a)da.$$

Let $\ell_2(t, a)$ be the biomass density of crops with infection age a at time t. The underlying PDE is

$$\frac{\partial \ell_2(t, a)}{\partial t} + \frac{\partial \ell_2(t, a)}{\partial a} = -\bar{d}_2(a)\ell_2(t, a), \tag{2.2}$$

where $\bar{d}_2(a) = \bar{d}_2$ is the disease-induced reduction in the biomass. One may notice the difference between equation (2.2) and equation (2.1). The reason is that it is not conventional to

apply birth/death rate to the biomass (especially when the biomass is measured by kilogram); but rather, we describe the change in biomass by growth rate, which includes both birth and death. By equation (2.2),

$$L_2(t) = \int_0^{\tau_2} \ell_2(t, a)da, \quad \text{and} \quad I_2(t) = \int_{\tau_2}^{\infty} \ell_2(t, a)da,$$

are the biomass of the latent and infectious crops at time t, respectively.

Before deriving the delay differential equations system, we will first work out the birth rate of leafhoppers and the growth rate of crops. We assume that the per capita birth rates of leafhoppers in all compartments are identical. It is of biological reasons that the per capita birth rate of leafhoppers is affected by the total leafhopper population and food resources, which, in this thesis, are the biomass of crops. Denote the per capita birth rate of leafhoppers by $B_1(N_2(t), N_1(t))$, where $N_2(t) = S_2(t) + L_2(t) + I_2(t)$ is the total biomass of crops and $N_1(t) = S_1(t) + L_1(t) + I_1(t)$ is the total population of leafhoppers. Therefore, the birth rates of the susceptible, latent, and infectious leafhoppers are $B_1(N_2(t), N_1(t))S_1(t)$, $B_1(N_2(t), N_1(t))L_1(t)$ and $B_1(N_2(t), N_1(t))I_1(t)$, respectively. For crops, we assume the food resources are limitless, which means the intrinsic growth rates per kilogram are only affected by its population. We further assume that the growth rates per kilogram of each compartment are identical and denote them as $B_2(N_2(t))$. Hence, the intrinsic growth rates of the susceptible, latent, and infectious crops are $B_2(N_2(t))S_2(t)$, $B_2(N_2(t))L_2(t)$ and $B_2(N_2(t))I_2(t)$, respectively.

Next, we derive the delay differential equations system. We start with the equations about the leafhopper population. It is reasonable to assume that $\lim_{a \to \infty} p(t, a) = 0$, which will be denoted as $p(t, \infty) = 0$ as a shorthand notation. Noting that the population with zero infection age comes not only from the population of the new infected individuals, but also from the population born to be latent. This latter phenomenon is called transovarial transmission [17], which, in the thesis, is defined to be proportional to the total population of the newborns that are reproduced by the latent adults:

$$\alpha_1 B_1(N_2(t), N_1(t))L_1(t),$$

where $0 \le \alpha_1 \le 1$ is the rate of transovarial transmission. Similarly, assume that λ_1 portion of the offspring that reproduced by infectious leafhoppers, where $0 \le \lambda_1 \le 1$. The rest of the

offspring goes to the susceptible compartment. Therefore,

$$\ell_1(t, 0) = p_1(I_2(t), S_1(t))S_1(t) + \alpha_1 B_1(N_2(t), N_1(t))L_1(t),$$

where $p_1(I_2(t), S_1(t))S_1(t)$ is the infection function.

To conveniently show the main idea we use to build the model, we further assume that the disease induced-mortality is a constant:

$$\bar{d}_1(a) = \bar{d}_1. \tag{2.3}$$

Thus the PDE system for the population of leafhoppers is given as

$$\frac{\partial \ell_1(t, a)}{\partial t} + \frac{\partial \ell_1(t, a)}{\partial a} = -(d_1 + \bar{d}_1)\ell_1(t, a) \tag{2.4}$$

with initial conditions

$$\begin{cases} \ell_1(t, 0) = p_1(I_2(t), S_1(t))S_1(t) + \alpha_1 B_1(N_2(t), N_1(t))L_1(t) \\ \ell_1(t, \infty) = 0 \end{cases}. \tag{2.5}$$

The general solution of this PDE is

$$\begin{cases} \ell_1(t, a) = \ell_1(t - a, 0)e^{-\int_0^a (d_1 + \bar{d}_1)ds} & t \ge a \\ \ell_1(t, a) = \ell_1(0, a - t)e^{-\int_0^t (d_1 + \bar{d}_1)ds} & t < a \end{cases}. \tag{2.6}$$

Based on the PDE system (2.4), (2.5) and the general solution (2.6), we can derive a DDE system to describe the leafhopper population dynamics. Integrating both sides of equation (2.4) with respect to the infection age a from 0 to τ_1 leads to

$$\int_0^{\tau_1} \left(\frac{\partial \ell_1(t, a)}{\partial t} + \frac{\partial \ell_1(t, a)}{\partial a} \right) da = -\int_0^{\tau_1} (d_1 + \bar{d}_1)\ell_1(t, a)da$$

$$\Rightarrow \frac{dL_1(t)}{dt} = -(d_1 + \bar{d}_1)L_1(t) - \ell_1(t, \tau_1) + \ell_1(t, 0).$$

Thus the PDE system together with (2.6) leads to

$$
\begin{cases}
\frac{dL_1(t)}{dt} = \alpha_1 B_1(N_2(t), N_1(t))L_1(t) + p_1(I_2(t), S_1(t))S_1(t) - (d_1 + \bar{d}_1)L_1(t) & t < \tau_1 \\
\frac{dL_1(t)}{dt} = \alpha_1 B_1(N_2(t), N_1(t))L_1(t) + p_1(I_2(t), S_1(t))S_1(t) & t \geq \tau_1 \\
\qquad - p_1(S_1(t - \tau_1), I_2(t - \tau_1))S_1(t - \tau_1)e^{-(d_1 + \bar{d}_1)\tau_1} - (d_1 + \bar{d}_1)L_1(t)
\end{cases}.
$$

A similar process gives, for the infected leafhoppers,

$$
\frac{dI_1(t)}{dt} = -(d_1 + \bar{d}_1)I_1(t) - \ell_1(t, \tau_1 + \tau_2) + \ell_1(t, \tau_1).
$$

Then following the general solution of the underlying model (2.1), and the boundary conditions, we have

$$
\begin{cases}
\frac{dI_1(t)}{dt} = \gamma_1 B(N_2(t), N_1(t))I_1(t) - (d_1 + \bar{d}_1)I_1(t) & t < \tau_1 \\
\frac{dI_1(t)}{dt} = \gamma_1 B(N_2(t), N_1(t))I_1(t) + p_1(I_2(t - \tau_1), S_1(t - \tau_1))S_1(t - \tau_1)e^{-(d_1 + \bar{d}_1)\tau_1} & t \geq \tau_1 \\
\qquad - (d_1 + \bar{d}_1)I_1(t)
\end{cases}.
$$

It follows that for $t < \tau_1$, the population dynamics can be described by

$$
\begin{cases}
\frac{dL_1(t)}{dt} = \alpha_1 B_1(N_2(t), N_1(t))L_1(t) + p_1(I_2(t), S_1(t))S_1(t) - (d_1 + \bar{d}_1)L_1(t) \\
\frac{dI_1(t)}{dt} = \gamma_1 B(N_2(t), N_1(t))I_1(t) - (d_1 + \bar{d}_1)I_1(t)
\end{cases};
$$

for $t \geq \tau_1$, we have

$$
\begin{cases}
\frac{dL_1(t)}{dt} = \alpha_1 B_1(N_2(t), N_1(t))L_1(t) + p_1(I_2(t), S_1(t))S_1(t) \\
\qquad - p_1(I_2(t - \tau_1), S_1(t - \tau_1))S_1(t - \tau_1)e^{-(d_1 + \bar{d}_1)\tau_1} - (d_1 + \bar{d}_1)L_1(t) \\
\frac{dI_1(t)}{dt} = \gamma_1 B(N_2(t), N_1(t))I_1(t) + p_1(I_2(t - \tau_1), S_1(t - \tau_1))S_1(t - \tau_1)e^{-(d_1 + \bar{d}_1)\tau_1} - (d_1 + \bar{d}_1)I_1(t)
\end{cases};
$$

and the equation for the susceptible leafhoppers is

$$
\frac{dS_1}{dt} = B_1(N_2(t), N_1(t))[S_1(t) + (1 - \alpha_1)L_1(t) + (1 - \gamma_1)I_1(t)] - \beta_1(I_2(t), S_1(t))S_1(t) - d_1 S_1(t).
$$

As with the above process, we derive the equations to describe the crop biomass dynamics: when $t < \tau_2$, the latent and infectious classes of crops are modeled by

$$
\begin{cases}
\frac{dL_2(t)}{dt} = \alpha_2 B_2(N_2(t))L_2(t) + p_2(S_2(t), I_1(t))I_1(t) - q(L_2(t), N_1(t))N_1(t) - \bar{d}_2 L_2(t) \\
\frac{dI_2(t)}{dt} = \gamma_2 B_2(N_2(t))I_2(t) - q(I_2(t), N_1(t))I_2(t) - \bar{d}_2 I_2(t)
\end{cases};
$$

when $t \geq \tau_2$, we obtain

$$
\begin{cases}
\frac{dL_2(t)}{dt} = \alpha_2 B_2(N_2(t))L_2(t) + p_2(S_2(t), I_1(t))I_1(t) - p_2(S_2(t - \tau_2), I_1(t - \tau_2))I_1(t - \tau_2)e^{-\bar{d}_2\tau_2} \\
\qquad\quad - q(L_2(t), N_1(t))N_1(t) - \bar{d}_2 L_2(t) \\
\frac{dI_2(t)}{dt} = \gamma_2 B_2(N_2(t))I_2(t) + p_2(S_2(t - \tau_2), I_1(t - \tau_2))I_1(t - \tau_2)e^{-\bar{d}_2\tau_2} - \bar{d}_2 I_2 \\
\qquad\quad - q(I_2(t), N_1(t))N_1(t)
\end{cases} ;
$$

and the equation for the susceptible crops is

$$
\frac{dS_2(t)}{dt} = B_2(N_2(t))[S_2(t) + (1 - \alpha_2)L_2(t) + (1 - \gamma_2)I_2(t)] - p_2(S_2(t), I_1(t))I_1(t)
$$
$$
- q(S_2(t), N_1(t))N_1(t),
$$

where $p_2(S_2(t), I_1(t))$ is the amount of crop biomass that are infected by an infectious leafhopper; $q(S_2(t), N_1(t))$ denotes the consumption rate of an average leafhopper on crops; and α_2 and γ_2 account for the rate of transovarial transmission for latent and infectious leafhoppers, respectively.

Since we are mainly interested in the long-term behaviour of the system, we will study the system when $t \geq \tau_1$, which is given by

$$
\begin{cases}
\frac{dS_1(t)}{dt} = B_1(N_2(t), N_1(t))[S_1(t) + (1 - \alpha_1)L_1(t) + (1 - \gamma_1)I_1(t)] - d_1 S_1(t) \\
\qquad\quad - p_1(I_2(t), S_1(t))S_1(t) \\
\frac{dL_1(t)}{dt} = \alpha_1 B_1(N_2(t), N_1(t))L_1(t) + p_1(I_2(t), S_1(t))S_1(t) \\
\qquad\quad - p_1(I_2(t - \tau_1), S_1(t - \tau_1))S_1(t - \tau_1)e^{-(d_1 + \bar{d}_1)\tau_1} - (d_1 + \bar{d}_1)L_1(t) \\
\frac{dI_1(t)}{dt} = \gamma_1 B_1(N_2(t), N_1(t))I_1(t) + p_1(I_2(t - \tau_1), S_1(t - \tau_1))S_1(t - \tau_1)e^{-(d_1 + \bar{d}_1)\tau_1} \\
\qquad\quad - (d_1 + \bar{d}_1)I_1(t) \\
\frac{dS_2(t)}{dt} = B_2(N_2(t))[S_2(t) + (1 - \alpha_2)L_2(t) + (1 - \gamma_2)I_2(t)] - p_2(S_2(t), I_1(t))I_1(t) \\
\qquad\quad - q(S_2(t), N_1(t))N_1(t) \\
\frac{dL_2(t)}{dt} = \alpha_2 B_2(N_2(t))L_2(t) + p_2(S_2(t), I_1(t))I_1(t) - q(L_2(t), N_1(t))N_1(t) - \bar{d}_2 L_2(t) \\
\qquad\quad - p_2(S_2(t - \tau_2), I_1(t - \tau_2))I_1(t - \tau_2)e^{-\bar{d}_2\tau_2} \\
\frac{dI_2(t)}{dt} = \gamma_2 B_2(N_2(t))I_2(t) + p_2(S_2(t - \tau_2), I_1(t - \tau_2))I_1(t - \tau_2)e^{-\bar{d}_2\tau_2} - \bar{d}_2 I_2(t) \\
\qquad\quad - q(I_2(t), N_1(t))N_1(t)
\end{cases} . \quad (2.7)
$$

However, the initial conditions of system (2.7) depend on the systems when $t < \tau_1$, so we give the systems. For $0 \leq t < \tau_2$, no new infected hosts nor vectors will become infectious, and

hence, the disease dynamics are governed by the following system of ODEs:

$$
\begin{cases}
\frac{dS_1(t)}{dt} = B_1(N_2(t), N_1(t))[S_1(t) + (1 - \alpha_1)L_1(t) + (1 - \gamma_1)I_1(t)] - d_1 S_1(t) \\
\qquad\quad - p_1(I_2(t), S_1(t))S_1(t) \\
\frac{dL_1(t)}{dt} = \alpha_1 B_1(N_2(t), N_1(t))L_1(t) + p_1(I_2(t), S_1(t))S_1(t) - (d_1 + \bar{d}_1)L_1(t) \\
\frac{dI_1(t)}{dt} = \gamma_1 B_1(N_2(t), N_1(t))I_1(t) - (d_1 + \bar{d}_1)I_1(t) \\
\frac{dS_2(t)}{dt} = B_2(N_2(t))[S_2(t) + (1 - \alpha_2)L_2(t) + (1 - \gamma_2)I_2(t)] - p_2(S_2(t), I_1(t))I_1(t) \\
\qquad\quad - q(S_2(t), N_1(t))N_1(t) \\
\frac{dL_2(t)}{dt} = \alpha_2 B_2(N_2(t))L_2(t) + p_2(S_2(t), I_1(t))I_1(t) - q(L_2(t), N_1(t))N_1(t) - \bar{d}_2 L_2(t) \\
\frac{dI_2(t)}{dt} = \gamma_2 B_2(N_2(t))I_2(t) - q(I_2(t), N_1(t))N_1(t) - \bar{d}_2 I_2(t)
\end{cases}
\tag{2.8}
$$

When $\tau_2 \le t < \tau_1$, the disease dynamics are given by another system of DDEs:

$$
\begin{cases}
\frac{dS_1(t)}{dt} = B_1(N_2(t), N_1(t))[S_1(t) + (1 - \alpha_1)L_1(t) + (1 - \gamma_1)I_1(t)] - d_1 S_1(t) \\
\qquad\quad - p_1(I_2(t), S_1(t))S_1(t) \\
\frac{dL_1(t)}{dt} = \alpha_1 B_1(N_2(t), N_1(t))L_1(t) + p_1(I_2(t), S_1(t))S_1(t) - (d_1 + \bar{d}_1)L_1(t) \\
\frac{dI_1(t)}{dt} = \gamma_1 B_1(N_2(t), N_1(t))I_1(t) - (d_1 + \bar{d}_1)I_1(t) \\
\frac{dS_2(t)}{dt} = B_2(N_2(t))[S_2(t) + (1 - \alpha_2)L_2(t) + (1 - \gamma_2)I_2(t)] - p_2(S_2(t), I_1(t))I_1(t) \\
\qquad\quad - q(S_2(t), N_1(t))N_1(t) \\
\frac{dL_2(t)}{dt} = \alpha_2 B_2(N_2(t))L_2(t) + p_2(S_2(t), I_1(t))I_1(t) - q(L_2(t), N_1(t))N_1(t) - \bar{d}_2 L_2(t) \\
\qquad\quad - p_2(S_2(t - \tau_2), I_1(t - \tau_2))I_1(t - \tau_2)e^{-\bar{d}_2 \tau_2} \\
\frac{dI_2(t)}{dt} = \gamma_2 B_2(N_2(t))I_2(t) + p_2(S_2(t - \tau_2), I_1(t - \tau_2))I_1(t - \tau_2)e^{-\bar{d}_2 \tau_2} - \bar{d}_2 I_2(t) \\
\qquad\quad - q(I_2(t), N_1(t))N_1(t)
\end{cases}
\tag{2.9}
$$

To ensure that the model makes biological sense, the following assumptions need to be specified [7]. The per capita birth rate of leafhoppers should satisfy the following rules:

A11 $B_1(N_2, N_1) > 0$ for $N_1, N_2 > 0$; $B_1(0, \cdot) = 0$, and $B_1(\cdot, 0^+) > 0$

A12 $B_1(N_2, N_1)$ is continuously differentiable with

$$
\frac{\partial B_1(N_2, N_1)}{\partial N_1} < 0, \qquad \frac{\partial B_1(N_2, N_1)}{\partial N_2} > 0.
$$

A13 $\lim_{N_1 \to +\infty} B_1(N_2, N_1)N_1 < C$, where C is a constant positive value.

Note that $A13$ gives the existence of a carrying capacity K_1 of the leafhopper population.

The per capita growth rate of crops also satisfies the following assumptions:

A21 $B_2(N_2) > 0$ if $N_2 > 0$, and $B_2(0^+) > 0$.

A22 $B_2(N_2)$ is continuously differentiable with

$$\frac{dB_2}{dN_2} < 0.$$

A23 There exists a constant K, such that $B_2(K) = 0$; and $N(t)$, which is governed by $dN(t)/dt = G(N(t))N(t)$, is bounded.

Note that $A22$ and $A23$ imply that $B_2^{-1}(N_2)$ exists. $A23$ gives the existence of a carrying capacity K such that $B_2(N_2) > 0$ for $N_2 < K$, and $B_2(N_2) < 0$ for $N_2 > K$.

The infection functions follow the rules:

A31 $p_i(x, y) \geq 0$ if $x, y \geq 0$, $i = 1, 2$.

A32 $p_i(x, y)$, $i = 1, 2$ is continuously differentiable with

$$\frac{\partial p_i(x, y)}{\partial x} \geq 0, \qquad \frac{\partial p_i(x, y)}{\partial y} \geq 0.$$

A33 $p_i(\cdot, 0) = 0$ and $p_i(0, \cdot) = 0$, $i = 1, 2$.

The attack functions follow similar rules as well:

A41 $q(\theta_2, N_1) \geq 0$ if $N_1, \theta_2 \geq 0$, where $\theta \in \{S, L, I\}$.

A42 $q(\theta_2, N_1)$ is continuously differentiable with

$$\frac{\partial q(\theta_2, N_1)}{\partial N_1} \geq 0, \qquad \frac{\partial q(\theta_2, N_1)}{\partial \theta_2} \geq 0.$$

A43 $q(\cdot, 0) = 0$ and $q(0, \cdot) = 0$.

2.3   Analysis of the General Model

In this section, we will show positivity and boundedness to verify that the system is well-posed. Also, we will prove the instability of the trivial equilibrium, and the local asymptotical stability of the insect-free equilibrium when $\mathcal{R}_0 < 1$. In this chapter, $\mathcal{R}_0$ is defined as the expected number of susceptible offsprings produced by a susceptible adult in its lifetime.

Model (2.7) is a system of delay differential equations. For such a system, initial functions need to be specified and well-posedness needs to be addressed. The following theorem establishes the positivity and boundedness of the solutions to (2.7).

Theorem 2.3.1 *Let* $(S_1(t), L_1(t), I_1(t), S_2(t), L_2(t), I_2(t))$ *be the solution of system (2.7) satisfying* $S_i(0) \geq 0, L_i(0) \geq 0,$ *and* $I_i(0) \geq 0,$ $i = 1, 2.$ *Then* $S_1(t), L_1(t), I_1(t), S_2(t), L_2(t)$ *and* $I_2(t)$ *are all non-negative and bounded for all* $t \geq 0$ *at which the solution exists.*

Proof. With such a set of initial values given, one can solve the ODE system (2.8) to get a unique and non-negative solution for $t \in [0, \tau_2]$. Using the values of this solution in the interval $[0, \tau_2]$, one can further solve the DDE system (2.9) to get a unique and non-negative solution defined for $t \in [\tau_2, \tau_1]$. The combination of these two solutions gives the initial conditions for system (2.7) in $[0, \tau_1]$. To prove the non-negativity of system (2.7), we start with the $I_1(t)$ equation. Since $\beta_1(S_1(t - \tau_1), I_2(t - \tau_1))S_1(t - \tau_1)e^{-(d_1+\bar{d}_1)\tau_1} \geq 0$ in $[\tau_1, \tau_1 + \tau_2]$,

$$\frac{dI_1(t)}{dt} \geq \gamma_1 B_1(N_2(t), N_1(t))I_1(t) - (d_1 + \bar{d}_1)I_1(t)$$

$$\Rightarrow I_1(t) \geq I_1(0) \exp\left(\int_0^t (B_1(N_2(\theta), N_1(\theta)) - (d_1 + \bar{d}_1))d\theta\right) \geq 0.$$

A similar method verifies the non-negativity of $I_2(t)$ in $[\tau_1, \tau_1 + \tau_2]$. Furthermore, we reformulate the $L_1(t)$ equation as

$$L_1(t) = \int_0^{\tau_1} p_1(I_2(t - \theta), S_1(t - \theta))S_1(t - \theta)e^{-(d_1+\bar{d}_1)\theta}d\theta + \alpha_1 B_1(N_2(t), N_1(t))L_1(t). \quad (2.10)$$

The positivity of $S_1(t)$ and $I_2(t)$ in $[0, \tau_1]$ implies the positivity of $L_1(t)$ in $[\tau_1, \tau_1 + \tau_2]$. $L_2(t)$ is non-negative as well. Based on the positivity of $L_1(t)$ and $I_1(t)$,

$$\frac{dS_1(t)}{dt} \geq B_1(N_2(t), N_1(t))S_1(t) - p_1(I_2(t), S_1(t))S_1(t) - d_1 S_1(t)$$

$$\Rightarrow S_1(t) \geq S_1(0) \exp\left(\int_0^t (B_1(N_2(\theta), N_1(\theta)) - p_1(I_2(\theta), S_1(\theta)) - d_1)d\theta\right) \geq 0.$$

A similar approach gives $S_2(t) \geq 0$.

Using the values of this solution in the interval $[\tau_1, \tau_1 + \tau_2]$, one can further solve the DDE system (2.7) to get a unique and non-negative solution defined for $t \in [\tau_1 + \tau_2, \tau_1 + 2\tau_2]$. Proceeding with this method, we prove the non-negativity of the solutions [14].

Next we show that the solutions of system (2.7) remain bounded. Based on the positivity of the solutions, it follows

$$
\begin{aligned}
\frac{dN_2(t)}{dt} &= \frac{dS_2(t)}{dt} + \frac{dL_2(t)}{dt} + \frac{dI_2(t)}{dt} \\
&= B_2(N_2(t))N_2(t) - q_1(S_2(t), N_1(t))S_2(t) - q_1(L_2(t), N_1(t))L_2(t) \\
&\quad - q_1(I_2(t), N_1(t))I_2(t) - \bar{d}_2 L_2(t) - \bar{d}_2 I_2(t) \\
&\leq B_2(N_2(t))N_2(t).
\end{aligned}
$$

The above inequality gives the comparison system

$$
\frac{dX(t)}{dt} = B_2(X(t))X(t),
$$

which has a bounded solution based on $A22$ and $A23$. Therefore, $N_2(t)$ is bounded. By positivity, $S_2(t)$, $L_2(t)$, and $I_2(t)$ are bounded.

Similarly,

$$
\begin{aligned}
\frac{dN_1(t)}{dt} &= \frac{dS_1(t)}{dt} + \frac{dL_1(t)}{dt} + \frac{dI_1(t)}{dt} \\
&= B_1(N_2(t), N_1(t))N_1(t) - d_1 S_1(t) - (d_1 + \bar{d}_1)L_1(t) - (d_1 + \bar{d}_1)I_1(t) \\
&\leq B_1(N_2(t), N_1(t))N_1(t) - d_1 N_1(t).
\end{aligned}
$$

The corresponding comparison system, therefore, is

$$
\frac{dY(t)}{dt} = B_1(N_2(t), Y(t))Y(t) - d_1 Y(t).
$$

$B_1(N_2(t), Y(t))Y(t)$ is bounded based on $A12$ and $A13$, say by Y_B; hence, $Y(t)$ is bounded. By the comparison principle for delay differential equations system, $N_1(t)$ is bounded as well, showing that $S_1(t)$, $L_1(t)$, and $I_1(t)$ are bounded. Here, we have completed the proof of the well-posedness of system (2.7). ∎

Next we investigate the stability of system (2.7). We start with the trivial equilibrium E_0 with all the components being zero.

Theorem 2.3.2 *The trivial equilibrium $E_0 = (0, 0, 0, 0, 0, 0)$ is always unstable.*

Proof. Linearizing system (2.7) at the trivial equilibrium leads to

$$
\begin{cases}
\frac{dS_1(t)}{dt} = -d_1 S_1(t) \\
\frac{dL_1(t)}{dt} = -(d_1 + \bar{d}_1)L_1(t) \\
\frac{dI_1(t)}{dt} = -(d_1 + \bar{d}_1)I_1(t) \\
\frac{dS_2(t)}{dt} = B_2(0)S_2(t) \\
\frac{dL_2(t)}{dt} = -\bar{d}_2 L_2(t) \\
\frac{dI_2(t)}{dt} = \gamma_2 B_2(0)I_2(t) - \bar{d}_2 I_2(t)
\end{cases}.
$$

The characteristic equation thereby is given by $|\lambda I - J|$, where

$$
J = \begin{pmatrix}
-d_1 & 0 & 0 & 0 & 0 & 0 \\
0 & -d_1 - \bar{d}_1 & 0 & 0 & 0 & 0 \\
0 & 0 & -d_1 - \bar{d}_1 & 0 & 0 & 0 \\
0 & 0 & 0 & B_2(0) & 0 & 0 \\
0 & 0 & 0 & 0 & -\bar{d}_2 & 0 \\
0 & 0 & 0 & 0 & 0 & \gamma_2 B_2(0) - \bar{d}_2
\end{pmatrix}.
$$

One of the eigenvalues of J is $B_2(0)$, which is positive and implies that the trivial equilibrium is unstable. Based on the last equation of the linearized system, it is easy to obtain that the biomass of crops grows exponentially around the trivial equilibrium. ∎

An insect-free equilibrium of model (2.7) is the equilibrium with the insect and disease related components being zeros. That is, such an equilibrium has the form

$$
E_1 = (0, 0, 0, x, 0, 0).
$$

A simple calculation gives $E_1 = (0, 0, 0, B_2^{-1}(0), 0, 0) = (0, 0, 0, K, 0, 0)$. The following theorem establishes the local asymptotical stability of the insect-free equilibrium.

Theorem 2.3.3 *The insect-free equilibrium E_1 is locally asymptotically stable when*

$$
\mathcal{R}_0 = \frac{B_1(K, 0)}{d_1} < 1,
$$

and unstable when $\mathcal{R}_0 > 1$.

Proof. Based on the linearization of system (2.7) at E_1:

$$
\begin{cases}
\frac{dS_1(t)}{dt} = (B_1(K,0) - d_1)S_1(t) + (1 - \alpha_1)B_1(K,0)L_1(t) + (1 - \gamma_1)B_1(K,0)I_1(t) \\
\frac{dL_1(t)}{dt} = -(d_1 + \bar{d}_1)L_1(t) + \alpha_1 B_1(K,0)L_1(t) \\
\frac{dI_1(t)}{dt} = -(d_1 + \bar{d}_1)I_1(t) + \gamma_1 B_1(K,0)I_1(t) \\
\frac{dS_2(t)}{dt} = B_2'(K)KS_2(t) + B_2'(K)KL_2(t) + B_2'(K)KI_2(t) \\
\frac{dL_2(t)}{dt} = -\bar{d}_2 L_2(t) \\
\frac{dI_2(t)}{dt} = -\bar{d}_2 I_2(t)
\end{cases},
$$

one can derive the characteristic equation

$$|\lambda I - J| = 0,$$

where $J =$

$$
\begin{pmatrix}
B_1(K,0) - d_1 & (1 - \alpha_1)B_1(K,0) & (1 - \gamma_1)B_1(K,0) & 0 & 0 & 0 \\
0 & \alpha_1 B_1(K,0) - d_1 - \bar{d}_1 & 0 & 0 & 0 & 0 \\
0 & 0 & \gamma_1 B_1(K,0) - d_1 - \bar{d}_1 & 0 & 0 & 0 \\
0 & 0 & 0 & B_2'(K)K & B_2'(K)K & B_2'(K)K \\
0 & 0 & 0 & 0 & -\bar{d}_2 & 0 \\
0 & 0 & 0 & 0 & 0 & -\bar{d}_2
\end{pmatrix}.
$$

The characteristic equation can be calculated as

$$(\lambda - B_1(K,0) + d_1)(\lambda + d_1 + \bar{d}_1)(\lambda - \gamma_1 B_1(K,0) + d_1 + \bar{d}_1)(\lambda - B_2'(K)K)(\lambda + \bar{d}_2)(\lambda + \bar{d}_2) = 0.$$

The eigenvalues are $B_1(K,0) - d_1$, $\alpha_1 B_1(K,0) - d_1 - \bar{d}_1$, $\gamma_1 B_1(K,0) - d_1 - \bar{d}_1$, $B_2'(K)K$, $-\bar{d}_2$. Since $\mathcal{R}_0 < 1$, $-d_1 + B_1(K,0) < 0$. $\gamma_1 B_1(K,0) - d_1 - \bar{d}_1 < B_1(K,0) - d_1 < 0$; similarly, $\alpha_1 B_1(K,0) - d_1 - \bar{d}_1 < 0$. And $B_2'(K)K < 0$ based on assumption $A22$. Therefore, all the eigenvalues are negative, which means that, when the basic reproduction number is less than one, the insect-free equilibrium is locally asymptotically stable. However, when $\mathcal{R}_0 > 1$, the insect-free equilibrium is no longer stable, since eigenvalues with positive real part appear. ∎

Remark 2.3.1 *Since*

$$\mathcal{R}_0 = \underbrace{B_1(K,0)}_{\text{per capita birth rate of leafhoppers}} \underbrace{\frac{1}{d_1}}_{\text{expected life time of leafhoppers}},$$

and considering the meaning of the parameters involved, one can easily see the biological meaning of $\mathcal{R}_0$: $\mathcal{R}_0$ is the average number of the offspring that are reproduced by an adult in its lifetime. If $\mathcal{R}_0 < 1$, which means that one adult leafhopper can only reproduce less than one offsprings, the leafhopper population will eventually die out. However, if $\mathcal{R}_0 > 1$, the leafhopper population will thrive.

2.4   Analysis of a Specific Model

When $\mathcal{R}_0 > 1$, E_1 becomes unstable. However, we can not get further information about the population from the general model. In this section, we choose some specific functions that satisfy all the assumptions in Section §2.2, which allows us to further analyze the system.

Based on the literature [7], we choose

$$B_1(N_2(t), N_1(t)) = \frac{mN_2(t)}{1 + nN_2(t)} b_0 e^{-cN_1(t)},$$

$$B_2(N_2(t)) = r\left(1 - \frac{N_2(t)}{K}\right),$$

$$p_1(I_2(t), S_1(t)) = \beta_1 I_2(t), \quad p_2(S_2(t), I_1(t)) = \beta_2 I_1(t),$$

$$q(N_1(t), \theta_2(t)) = \alpha N_1(t) \ \ (\theta \in \{S, L, I\}).$$

where b_0 is the intrinsic birth rate of leafhoppers and c denotes the self-limitation effects within leafhoppers – the birth function $B_1(N_2, N_1)$ with the above form is known as the Ricker function; $mN_2(t)/(1 + nN_2(t))$, which is an increasing function with respect to the crop biomass, represents the influence of food resources on the reproductive ability of leafhoppers; β_1 and β_2 are the infection rates; α denotes the crop-attack rate; $B_2(N_2(t))$ is the logistic function, with r being intrinsic growth rate, and K being carrying capacity.

Therefore, the corresponding system when $t > \tau_1$ is

$$
\begin{cases}
\frac{dS_1(t)}{dt} = \frac{mN_2(t)}{1+nN_2(t)}b_0e^{-cN_1(t)}[S_1(t) + (1-\alpha_1)L_1(t) + (1-\gamma_1)I_1(t)] - \beta_1I_2(t)S_1(t) - d_1S_1(t) \\
\frac{dL_1(t)}{dt} = \alpha_1\frac{mN_2(t)}{1+nN_2(t)}b_0e^{-cN_1(t)}L_1(t) + \beta_1I_2(t)S_1(t) - \beta_1I_2(t-\tau_1)S_1(t-\tau_1)e^{-(d_1+\bar{d}_1)\tau_1} \\
\qquad - (d_1 + \bar{d}_1)L_1(t) \\
\frac{dI_1(t)}{dt} = \gamma_1\frac{mN_2(t)}{1+nN_2(t)}b_0e^{-cN_1(t)}I_1(t) + \beta_1I_2(t-\tau_1)S_1(t-\tau_1)e^{-(d_1+\bar{d}_1)\tau_1} - (d_1+\bar{d}_1)I_1(t) \\
\frac{dS_2(t)}{dt} = r\left(1 - \frac{N_2(t)}{K}\right)[S_2(t) + (1-\alpha_2)L_2(t) + (1-\gamma_2)I_2(t)] - \beta_2S_2(t)I_1(t) - \alpha N_1(t)S_2(t) \\
\frac{dL_2(t)}{dt} = \alpha_2r\left(1 - \frac{N_2(t)}{K}\right)L_2(t) + \beta_2S_2(t)I_1(t) - \beta_2S_2(t-\tau_2)I_1(t-\tau_2)e^{-\bar{d}_2\tau_2} - \bar{d}_2L_2(t) \\
\qquad - \alpha N_1(t)L_2(t) \\
\frac{dI_2(t)}{dt} = \gamma_2r\left(1 - \frac{N_2(t)}{K}\right)I_2(t) + \beta_2S_2(t-\tau_2)I_1(t-\tau_2)e^{-\bar{d}_2\tau_2} - \alpha N_1(t)I_2(t) - \bar{d}_2I_2(t).
\end{cases}
$$

$$(2.11)$$

In the following sections, we discuss the stability of the equilibria.

2.4.1   Trivial Equilibrium and Insect-Free Equilibrium

For the above chosen function b, h_1, h_2 and G, we know that $E_0 = (0,0,0,0,0,0)$ is always unstable, and $E_1 = (0,0,0,K,0,0)$ is locally asymptotically stable if

$$
\mathcal{R}_0 = \frac{mKb_0}{(1+nK)d_1} < 1,
$$

and unstable if $\mathcal{R}_0 > 1$. Indeed, the insect-free equilibrium is globally asymptotically stable under certain conditions. To show this statement, we first prove that the insect-free equilibrium is globally attractive.

Theorem 2.4.1 *The insect-free equilibrium $E_1 = (0,0,0,K,0,0)$ is globally attractive, if $\mathcal{R}_0 < 1$ and* $\max\{\alpha_2r, \gamma_2r\} < \bar{d}_2$.

Proof. To prove the global attractivity, we need to show that

$$
\lim_{t\to+\infty}(S_1(t), L_1(t), I_1(t), S_2(t), L_2(t), I_2(t)) = (0,0,0,K,0,0).
$$

for any set of non-negative initial conditions.

By adding the last three equations in system (2.11), we obtain that

$$\frac{dN_2(t)}{dt} = \frac{dS_2(t)}{dt} + \frac{dL_2(t)}{dt} + \frac{dI_2(t)}{dt}$$
$$\leq r\left(1 - \frac{N_2(t)}{K}\right)N_2(t),$$

which gives the comparison system

$$\frac{dX(t)}{dt} = r\left(1 - \frac{X(t)}{K}\right)X(t). \tag{2.12}$$

Equation (2.12) is a logistic equation, where $\lim_{t\to\infty} X(t) = K$ is satisfied. By the comparison theorem, when t is sufficiently large,

$$N_2(t) < K + \delta,$$

where δ can be any small positive value.

We have proven in Theorem 2.3.1 that, when t is sufficiently large,

$$\frac{dN_1(t)}{dt} = \frac{dS_1(t)}{dt} + \frac{dL_1(t)}{dt} + \frac{dI_1(t)}{dt}$$
$$\leq \frac{mK + m\delta}{1 + nK + n\delta}b_0 e^{-cN_1(t)}N_1(t) - d_1 N_1(t)$$
$$\leq \frac{b_0 mK + b_0 m\delta}{1 + nK + n\delta}N_1(t) - d_1 N_1(t).$$

Since $b_0 mK/(1+nK) < d_1$, we could choose δ to be sufficiently small so that $(b_0 mK + bm\delta)/(1 + nK + n\delta) < d_1$. Thus, the comparison system,

$$\frac{dX(t)}{dt} = \frac{b_0 mK + b_0 m\delta}{1 + nK + n\delta}X(t) - d_1 X(t),$$

has solution $X(t)$, which satisfies

$$\lim_{t\to+\infty} X(t) = 0.$$

By the comparison principle,

$$\lim_{t\to+\infty} N_1(t) = 0.$$

Based on the positivity of the solutions,

$$\lim_{t \to +\infty} S_1(t) = 0, \quad \lim_{t \to +\infty} L_1(t) = 0, \quad \text{and} \quad \lim_{t \to +\infty} I_1(t) = 0.$$

It follows that

$$\begin{cases} \frac{dS_2(t)}{dt} = r\left(1 - \frac{N_2(t)}{K}\right)[S_2(t) + (1 - \alpha_2)L_2(t) + (1 - \gamma_2)I_2(t)] \\ \frac{dL_2(t)}{dt} = \alpha_2 r\left(1 - \frac{N_2(t)}{K}\right)L_2(t) - \bar{d}_2 L_2(t) \\ \frac{dI_2(t)}{dt} = \gamma_2 r\left(1 - \frac{N_2(t)}{K}\right)I_2(t) - \bar{d}_2 I_2(t) \end{cases} \tag{2.13}$$

is the asymptotic system of the last three equations in system (2.11). In system (2.13), since $\max\{\alpha_2 r, \gamma_2 r\} < \bar{d}_2$, $I_2(t) \to 0$ and $L_2(t) \to 0$ as $t \to \infty$. Then, the asymptotic equation of the first equation in system (2.13) is

$$\frac{dS_2(t)}{dt} = r\left(1 - \frac{S_2(t)}{K}\right)S_2(t),$$

which means $S_2(t) \to K$ as $t \to \infty$. Hence, we have completed the proof. ∎

Based on Theorem 2.4.1 and the local asymptotical stability of E_1, we have established the following theorem.

Theorem 2.4.2 *The insect-free equilibrium E_1 is globally asymptotical stable, if $\mathcal{R}_0 < 1$ and $\max\{\alpha_2 r, \gamma_2 r\} < \bar{d}_2$.*

Remark 2.4.1 *$\bar{d}_2$, the disease-induced mortality of crops, plays a very important role in the qualitative behaviours of the system. When $\bar{d}_2$ is very small, then the insect-free equilibrium is always unstable. A tentative explanation is that, if the elimination rate of the infected crops is small, it gives rise to a relative large amount of infect crops, which sustains the disease; in another case, if $\bar{d}_2$ is large enough, then the elimination rate of infected crops is too large to support the spread of the disease. In fact, the condition, $\max\{\alpha_2 r, \gamma_2 r\} < \bar{d}_2$, holds for the most cases since α_2 and γ_2 are generally very small [17].*

2.4.2 Disease Free Equilibrium

A disease-free equilibrium of model (2.11) is the equilibrium with the disease-related components being zeros, while the other components are positive. That is, such an equilibrium has

the form

$$E_2 = (S_1, 0, 0, S_2, 0, 0),$$

where $S_1 > 0$ and $S_2 > 0$. First of all, we need to establish the existence of the disease-free equilibrium.

Theorem 2.4.3 *If $\mathcal{R}_0 > 1$, a unique disease-free equilibrium E_2 exists.*

Proof. To prove the existence of the disease-free equilibrium, it is sufficient to show that the following equation system has a unique positive solution:

$$\begin{cases} \frac{mS_2}{1+nS_2} b_0 e^{-cS_1} S_1 - d_1 S_1 = 0 \\ r\left(1 - \frac{S_2}{K}\right) S_2 - \alpha S_1 S_2 = 0 \end{cases}. \tag{2.14}$$

Based on the above system, we have

$$\frac{mK - \frac{K}{r}\alpha S_1}{1 + nK - \frac{K}{r}\alpha S_1} b_0 e^{-cS_1} = d_1. \tag{2.15}$$

In equation (2.15), if $S_1 = 0$, then the left-hand side of the equation equals $bmK/(1 + nK)$, which is larger than d_1, provided $\mathcal{R}_0 > 1$. And if S_1 is sufficiently large, then the left-hand side of equation (2.15) approaches to zero, which is smaller than d_1. Since the left-hand side of equation (2.15) is a continuous function with respect to S_1, there exists at least one positive value of S_1 that satisfies equation (2.15). Moreover, the left-hand side of equation (2.15) is a strictly decreasing function with respect to S_1; in other words, the root of the equation (2.15) is unique. Likewise, $S_2 > 0$ exists uniquely. ∎

The following theorem discusses the stability of the insect-free equilibrium.

Theorem 2.4.4 *The disease-free equilibrium $E_2 = (S_1, 0, 0, S_2, 0, 0)$ is locally asymptotically stable, if*

$$\mathcal{R}_1 = \frac{\beta_1 S_1}{(-\gamma_1 d_1 + d_1 + \bar{d}_1)e^{(d_1+\bar{d}_1)\tau_1}} \frac{\beta_2 S_2}{(\bar{d}_2 + (1 - \gamma_2)\alpha S_2)e^{\bar{d}_2\tau_2}} < 1.$$

It loses its stability when $\mathcal{R}_1 > 1$.

Proof. The characteristic equation of the linearized system of (2.7) at the disease-free equilibrium is given by

$$|\lambda I - J_1 - J_2 e^{-\lambda \tau_1} - J_3 e^{-\lambda \tau_2}| = 0,$$

where

$$
J_1 =
\begin{pmatrix}
c_1(1 - cS_1) - d_1 & c_1(1 - \alpha_1 - cS_1) & c_1(1 - \gamma_1 - cS_1) & c_2 & c_2 & c_2 \\
0 & \alpha_1 d_1 - (d_1 + \bar{d}_1) & 0 & 0 & 0 & \beta_1 S_1 \\
0 & 0 & \gamma_1 d_1 - d_1 - \bar{d}_1 & 0 & 0 & 0 \\
-\alpha S_2 & -\alpha S_2 & -(\alpha + \beta_2)S_2 & r - r\frac{2S_2}{K} - \alpha S_1 & r - \frac{2rS_2}{K} & -\gamma_2 r - (\gamma_2 + 1)\frac{r}{K}S_2 \\
0 & 0 & \beta_2 S_2 & 0 & (\alpha_2 - 1)\alpha S_1 - \bar{d}_2 & 0 \\
0 & 0 & 0 & 0 & 0 & \gamma_2 r\left(1 - \frac{S_2}{K}\right) - \alpha S_1 - \bar{d}_2
\end{pmatrix},
$$

$$
J_2 =
\begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \beta_1 S_1 e^{(d_1 + \bar{d}_1)\tau_1} \\
0 & 0 & 0 & 0 & 0 & \beta_1 S_1 e^{(d_1 + \bar{d}_1)\tau_1} \\
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix},
$$

$$
J_3 =
\begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \beta_2 S_2 e^{-\bar{d}_2 \tau_2} & 0 & 0 & 0 \\
0 & 0 & \beta_2 S_2 e^{-\bar{d}_2 \tau_2} & 0 & 0 & 0
\end{pmatrix},
$$

$$c_1 = \frac{mb_0 S_2 e^{-cS_1}}{1 + nS_2},$$

$$c_2 = \frac{mb_0 e^{-cS_1} S_1}{(1 + nS_2)^2}.$$

By equation (2.14),

$$\frac{mb_0 S_2}{1 + nS_2} e^{-cS_1} = d_1, \quad \text{and} \quad r - r\frac{S_2}{K} - \alpha S_1 = 0,$$

the characteristic equation can be calculated as

$$
\left[(\lambda + cd_1S_1)\left(\lambda + \frac{S_2}{K}\right) + \frac{\alpha S_1 d_1}{1 + nS_2} \right] (\lambda + (1 - \alpha_1)d_1 + \bar{d}_1)(\lambda + (1 - \alpha_2)\alpha S_1 + \bar{d}_2)
$$
$$
\left[(\lambda - \gamma_1 d_1 + d_1 + \bar{d}_1)(\lambda + \bar{d}_2 + (1 - \gamma_2)\alpha S_2) - \beta_1\beta_2 S_1 S_2 e^{-(d_1 + \bar{d}_1)\tau_1} e^{-\bar{d}_1\tau_1} e^{-(\tau_1 + \tau_2)\lambda} \right] = 0. \tag{2.16}
$$

It is obvious that equation (2.16) has two negative real eigenvalues $-(1 - \alpha_1)d_1 - \bar{d}_1$ and $-(1 - \alpha_2)\alpha S_1 - \bar{d}_2$. Therefore, the local stability is determined by the roots of:

$$
\left[(\lambda + cd_1S_1)\left(\lambda + \frac{S_2}{K}\right) + \frac{\alpha S_1 d_1}{1 + nS_2} \right]
$$
$$
\left[(\lambda - \gamma_1 d_1 + d_1 + \bar{d}_1)(\lambda + \bar{d}_2 + (1 - \gamma_2)\alpha S_2) - \beta_1\beta_2 S_1 S_2 e^{-(d_1 + \bar{d}_1)\tau_1} e^{-\bar{d}_1\tau_1} e^{-(\tau_1 + \tau_2)\lambda} \right] = 0. \tag{2.17}
$$

Let

$$
\begin{aligned}
h_1(\lambda) &= (\lambda + cd_1S_1)\left(\lambda + \frac{S_2}{K}\right) + \frac{\alpha S_1 d_1}{1 + nS_2} \\
&= \lambda^2 + \left(cd_1S_1 + \frac{S_2}{K}\right)\lambda + cd_1S_1\frac{S_2}{K} + \frac{\alpha S_1 d_1}{1 + nS_2}, \\
h_2(\lambda) &= (\lambda - \gamma d_1 + d_1 + \bar{d}_1)(\lambda + \bar{d}_2 + (1 - \gamma_2)\alpha S_2) - \beta_1\beta_2 S_1 S_2 e^{-(d_1 + \bar{d}_1)\tau_1} e^{-\bar{d}_1\tau_1} e^{-(\tau_1 + \tau_2)\lambda} \\
&= \lambda^2 + (-\gamma_1 d_1 + d_1 + \bar{d}_1 + \bar{d}_2 + (1 - \gamma_2)\alpha S_2)\lambda + (\bar{d}_2 + (1 - \gamma_2)\alpha S_2)(-\gamma_1 d_1 + d_1 + \bar{d}_1) \\
&\quad - \beta_1\beta_2 S_1 S_2 e^{-(d_1 + \bar{d}_1)\tau_1} e^{-\bar{d}_1\tau_1} e^{-(\tau_1 + \tau_2)\lambda}.
\end{aligned}
$$

The roots of $h_1(\lambda)$ have negative real parts, which means that the local stability of the insect-free equilibrium is determined by the roots of $h_2(\lambda)$.

To simplify the calculation, we denote

$$
\begin{aligned}
A &= -\gamma_1 d_1 + d_1 + \bar{d}_1 + \bar{d}_2 + (1 - \gamma_2)\alpha S_2, \\
B &= (\bar{d}_2 + (1 - \gamma_2)\alpha S_2)(-\gamma_1 d_1 + d_1 + \bar{d}_1), \\
C &= \beta_1\beta_2 S_1 S_2, \\
D &= e^{-(d_1 + \bar{d}_1)\tau_1} e^{-\bar{d}_1\tau_1}.
\end{aligned}
$$

When $\tau_1 = \tau_2 = 0$, $h_2(\lambda) = 0$ reduces to

$$
\lambda^2 + A\lambda + B - C = 0,
$$

the roots of which have negative real parts under $\mathcal{R}_1 < 1$ (i.e. $B < C$).

Note that all roots of $h_2(\lambda) = 0$ depend continuously on τ_1 and τ_2. Therefore, as the delays increase, the roots of $h_2(\lambda) = 0$ can only enter the right-half in complex plane by crossing the imaginary axis. Let $\lambda = iw$ with $w > 0$ be a pure imaginary root of $h_2(\lambda) = 0$, then

$$h_2(iw) = (iw)^2 + iAw + B - (CD \cos w(\tau_1 + \tau_2) - iCD \sin w(\tau_1 + \tau_2) = 0.$$

Taking moduli in the above equation and grouping in terms of the powers of w give

$$w^4 + (A^2 - 2B)w^2 + B^2 - C^2 D^2 = 0. \tag{2.18}$$

Since $\mathcal{R}_1 = CD/B < 1$ and $A^2 - 2B \geq 0$, $w^4 + (A^2 - 2B)w^2 + B^2 - C^2 D^2 > 0$ for all w. In other words, equation (2.18) has no roots with positive real parts. Thus, when $\mathcal{R}_1 < 1$, the disease-free equilibrium is locally asymptotically stable.

However, if $\mathcal{R}_1 > 1$, the equation

$$h_2(\lambda) = 0$$

has roots with positive real parts, thus indicating that the equilibrium loses its stability. ∎

Remark 2.4.2 *Rewrite $\mathcal{R}_1$ as*

$$\mathcal{R}_1 = \underbrace{\beta_1 S_1}_{\substack{\text{infection rate of} \\ \text{infectious leafhoppers}}} \underbrace{\frac{1}{-\gamma_1 d_1 + d_1 + \bar{d}_1}}_{\text{expected life time of infectious leafhoppers}} \underbrace{e^{-(d_1 + \bar{d}_1)\tau_1}}_{\substack{\text{survival probability of infectious} \\ \text{leafhoppers during latent period}}}$$

$$\underbrace{\beta_2 S_2}_{\substack{\text{infection rate of} \\ \text{infectious crops}}} \underbrace{\frac{1}{\bar{d}_2 + (1 - \gamma_2)\alpha S_2}}_{\text{expected life time of infectious crops}} \underbrace{e^{-\bar{d}_2 \tau_2}}_{\substack{\text{survival probability of infectious} \\ \text{crops during latent period}}}.$$

Thus, the biological interpretation of $\mathcal{R}_1$ is the expected number of secondary infections produced by one infectious individual in its entire lifetime.

2.4.3 Disease Persistence and Positive Equilibrium

In this section, we apply the persistence theory to show that the disease is uniformly strongly persistent if $\mathcal{R}_1 > 1$, and, moreover, that a positive equilibrium E_3 exists. To proceed, we first show that the disease is weakly persistent.

Theorem 2.4.5 *Assume that* $\mathcal{R}_1 > 1$, $\alpha_1 m K b_0/(1 + nK) < (d_1 + \bar{d}_1)$, *and* $\max\{\alpha_2 r, \gamma_2 r\} < \bar{d}_2$.
Then the disease will weakly persist in the sense that there is an $\epsilon > 0$ *such that for any*
solutions to system (2.11), *we have*

$$\limsup_{t \to +\infty} \max\{I_i(t), i = 1, 2\} \geq \epsilon. \tag{2.19}$$

Proof. For the sake of contradiction, assume that equation (2.19) is false. Then for any $\epsilon > 0$,
there is a $T_1 > \max\{\tau_1, \tau_2\}$, such that

$$0 < I_i(t) < \epsilon \quad \text{for} \quad t \geq T_1, i = 1, 2. \tag{2.20}$$

It follows that, when t is sufficiently large,

$$\frac{dS_1}{dt} \leq \frac{mS_2 + mL_2 + m\epsilon}{1 + nS_2 + nL_2 + n\epsilon} b_0 e^{-c(S_1+L_1)}(S_1 + (1 - \alpha_1)L_1 + (1 - \gamma_1)\epsilon) - d_1 S_1, \tag{2.21}$$

$$\frac{dS_2}{dt} \leq r\left(1 - \frac{S_2 + L_2}{K}\right)(S_2 + (1 - \alpha_2)L_2 + (1 - \gamma_2)\epsilon) - \alpha(S_1 + L_1)S_2, \tag{2.22}$$

$$\frac{dL_1}{dt} \leq \alpha_1 \frac{mKb_0}{1 + nK} L_1 + \beta_1 \epsilon S_1 - (d_1 + \bar{d}_1)L_1, \tag{2.23}$$

and

$$\frac{dL_2}{dt} \leq \alpha_2 r L_2 + \beta_2 \epsilon S_2 - \bar{d}_2 L_2 - \alpha S_1 L_2. \tag{2.24}$$

Theorem 2.3.1 guarantees that S_1 and S_2 are bounded, i.e. $S_1 < \bar{S}_1$, and $S_2 < \bar{S}_2$, where
$\bar{S}_1$ and $\bar{S}_2$ are some positive values. Then inequality (2.23) and inequality (2.24) become

$$\frac{dL_1}{dt} \leq \beta_1 \epsilon \bar{S}_1 + \alpha_1 \frac{mKb_0}{1 + nK} L_1 - (d_1 + \bar{d}_1)L_1 \tag{2.25}$$

and

$$\frac{dL_2}{dt} \leq \beta_2 \epsilon \bar{S}_2 + \alpha_2 r L_2 - \bar{d}_2 L_2, \tag{2.26}$$

which suggests that, when t is sufficiently large, for any small given positive value δ,

$$L_1 \leq \frac{\beta_1 \epsilon \bar{S}_1}{d_1 + \bar{d}_1 - \alpha_1 mKb_0/(1 + nK)} + \delta \tag{2.27}$$

and

$$L_2 \leq \frac{\beta_2 \epsilon \bar{S}_2}{\bar{d}_2 - \alpha_2 r} + \delta. \tag{2.28}$$

Inequalities (2.21) and (2.22), together with inequalities (2.27) and (2.28), when t is sufficiently large, give

$$
\begin{cases}
\frac{dS_1}{dt} \le \frac{mS_2 + m\frac{\beta\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + m\delta + m\epsilon}{1 + nS_2 + n\frac{\beta\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + n\delta + n\epsilon} b_0 e^{-cS_1} \left(S_1 + (1-\alpha_1)\left(\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + \delta\right) + (1-\gamma_1)\epsilon \right) - d_1 S_1 \\
\frac{dS_2}{dt} \le r\left(1 - \frac{S_2}{K}\right)\left(S_2 + (1-\alpha_2)\left(\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + \delta\right) + (1-\gamma_2)\epsilon\right) - \alpha S_1 S_2
\end{cases}
\tag{2.29}
$$

Thus we obtain the following comparison system for $S_1(t)$ and $S_2(t)$:

$$
\begin{cases}
\frac{dX_{11}}{dt} = \frac{mX_{12} + m\frac{\beta\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + m\delta + m\epsilon}{1 + nX_{12} + n\frac{\beta\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + n\delta + n\epsilon} b_0 e^{-cX_{11}} \left(X_{11} + (1-\alpha_1)\left(\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + \delta\right) + (1-\gamma_1)\epsilon \right) - d_1 X_{11} \\
\frac{dX_{12}}{dt} = r\left(1 - \frac{X_{12}}{K}\right)\left(X_{12} + (1-\alpha_2)\left(\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + \delta\right) + (1-\gamma_2)\epsilon\right) - \alpha X_{11} X_{12}
\end{cases}
\tag{2.30}
$$

A positive equilibrium exists (see Appendix A.1 for details) and is denoted by $(X_{11}^*(\epsilon,\delta), X_{12}^*(\epsilon,\delta))$. Notice that $X_{11}^*(\epsilon,\delta)$ and $X_{12}^*(\epsilon,\delta)$ are all continuous in ϵ and δ with $X_{11}^*(\epsilon,\delta) \to S_1$, $X_{12}^*(\epsilon,\delta) \to S_2$ as $\epsilon \to 0$ and $\delta \to 0$.

Linearizing system (2.30) at the positive equilibrium, we are able to show that the positive equilibrium is locally asymptotically stable when $\mathcal{R}_0 = mbK/d_1(1+nK) > 1$ and when ϵ and δ are sufficiently small (see Appendix A.1 for details). Periodic solutions can be eliminated by using the Bendixson-Dulac theorem [13], since

$$
\frac{\partial}{\partial X_{11}}\left(\frac{X_{11}'}{X_{11}X_{12}}\right) + \frac{\partial}{\partial X_{12}}\left(\frac{X_{12}'}{X_{11}X_{12}}\right) < 0,
$$

provided $X_{11} > 0$ and $X_{12} > 0$. As ODE system (2.30) is 2-dimensional, the positive equilibrium $(X_{11}^*(\epsilon,\delta), X_{12}^*(\epsilon,\delta))$ is globally asymptotically stable provided $\mathcal{R}_0 > 1$, and ϵ and δ are sufficiently small. Therefore, for any given $\eta_1 > 0$, there are $\epsilon_0, \delta_0 < \eta_1$ such that, for sufficiently large t,

$$
S_1(t) < S_1(\eta_1) = X_{11}^*(\epsilon,\delta) + \eta_1, \quad \text{and} \quad S_2(t) < S_2(\eta_1) = X_{12}^*(\epsilon,\delta) + \eta_1.
\tag{2.31}
$$

Based on inequalities (2.31), (2.26) and (2.27), it follows, when t is sufficiently large, that

$$
\begin{cases}
\frac{dS_1(t)}{dt} \ge \frac{mS_2(t)}{1 + nS_2(t)} b_0 e^{-c\left(S_1(t) + \epsilon + \frac{\beta_1\epsilon\bar{S}_1}{d_1 + \bar{d}_1 - \alpha_1 mKb/(1+nK)} + \delta\right)} S_1(t) - \beta_1 \epsilon S_1(t) - d_1 S_1(t) \\
\frac{dS_2(t)}{dt} \ge r\left(1 - \frac{S_2(t) + \epsilon + \frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + \delta}{K}\right) S_2(t) - \alpha\left(S_1(t) + \epsilon + \frac{\beta_1\epsilon\bar{S}_1}{d_1 + \bar{d}_1 - \alpha_1 mKb/(1+nK)} + \delta\right) S_2(t) \\
\quad - \beta_2 \epsilon S_2(t)
\end{cases}
\tag{2.32}
$$

which gives the comparison system

$$
\begin{cases}
\frac{dX_{21}(t)}{dt} = \frac{mX_{22}(t)}{1+nX_{22}(t)}b_0 e^{-c\left(X_{21}(t)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right)}X_{21}(t) - \beta_1\epsilon X_{21}(t) - d_1 X_{21}(t) \\
\frac{dX_{22}(t)}{dt} = r\left(1 - \frac{X_{22}(t)+\epsilon+\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta}{K}\right)X_{22}(t) - \alpha\left(X_{21}(t) + \epsilon + \frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)} + \delta\right)X_{22}(t) \\
\qquad\quad - \beta_2\epsilon X_{22}(t)
\end{cases} \quad (2.33)
$$

Denote the equilibrium of system (2.33) as $X_{21}^*(\epsilon,\delta)$ and $X_{22}^*(\epsilon,\delta)$. Likewise, we can prove that $X_{21}^*(\epsilon,\delta) \to S_1$ and $X_{22}^*(\epsilon,\delta) \to S_2$, as $\epsilon \to 0$ and $\delta \to 0$ (see Appendix A.2 for details). For sufficiently large t, and any given positive value η_2

$$
S_1(t) > S_1(\eta_2) = X_{21}^*(\epsilon,\delta) - \eta_2, \quad \text{and} \quad S_2(t) > S_2(\eta_2) = X_{22}^*(\epsilon,\delta) - \eta_2. \quad (2.34)
$$

Thus, for I_1 and I_2 equations, we have

$$
\begin{cases}
\frac{dI_1(t)}{dt} \geq \gamma_1\frac{mS_2(\eta_2)}{1+nS_2(\eta_2)}b_0 e^{-c\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right)}I_1(t) + \beta_1 I_2(t-\tau_1)S_1(\eta_2)e^{(-d_1+\bar{d}_1)\tau_1} \\
\qquad\quad - (d_1 + \bar{d}_1)I_1(t) \\
\frac{dI_2(t)}{dt} \geq \gamma_2 r\left(1 - \frac{S_2(\eta_1)+\epsilon+\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta}{K}\right)I_2(t) + \beta_2 I_1(t-\tau_2)S_2(\eta_2)e^{\bar{d}_2\tau_2} \\
\qquad\quad - \alpha\left(S_1(\eta_1) + \epsilon + \frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)} + \delta\right)I_2(t) - \bar{d}_2 I_2(t)
\end{cases} \quad (2.35)
$$

Consider the following comparison system obtained from the right-hand side of system (2.35):

$$
\begin{cases}
\frac{dY_1(t)}{dt} = \gamma\frac{mS_2(\eta_2)}{1+nS_2(\eta_2)}b_0 e^{-c\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right)}Y_1(t) + \beta_1 Y_2(t-\tau_1)S_1(\eta_2)e^{(-d_1+\bar{d}_1)\tau_1} \\
\qquad\quad - (d_1 + \bar{d}_1)Y_1(t) \\
\frac{dY_2(t)}{dt} = \gamma_2 r\left(1 - \frac{S_2(\eta_1)+\epsilon+\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta}{K}\right)Y_2(t) + \beta_2 Y_1(t-\tau_2)S_2(\eta_2)e^{\bar{d}_2\tau_2} \\
\qquad\quad - \alpha\left(S_1(\eta_1) + \epsilon + \frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)} + \delta\right)Y_2(t) - \bar{d}_2 Y_2(t)
\end{cases} \quad (2.36)
$$

The local stability of the trivial equilibrium of system (2.36) is determined by the roots of

$$
|\lambda I - J_1 - J_2 e^{-\lambda\tau_1} - J_3 e^{-\lambda\tau_2}| = 0,
$$

where $J_1 =$

$$\left(\begin{matrix} \gamma_1 \frac{mb_0 S_2(\eta_2)}{1+nS_2(\eta_2)} \exp\left(-c\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right)\right)-d_1-\bar{d}_1 & 0 \\ 0 & \gamma_2 r\left(1-\frac{S_2(\eta_1)+\epsilon+\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta}{K}\right)-\alpha\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right)-\bar{d}_2 \end{matrix}\right),$$

$$J_2 = \begin{pmatrix} 0 & \beta_1 S_1(\eta_2)e^{-(d_1+\bar{d}_1)\tau_1} \\ 0 & 0 \end{pmatrix},$$

$$J_3 = \begin{pmatrix} 0 & 0 \\ \beta_2 S_2(\eta_2)e^{-\bar{d}_2\tau_2} & 0 \end{pmatrix}.$$

Thus,

$$|\lambda I - J_1 - J_2 e^{-\lambda\tau_1} - J_3 e^{-\lambda\tau_2}|$$

$$= \lambda^2 + \left[-\gamma_1\frac{mb_0 S_2(\eta_2)}{1+nS_2(\eta_2)}e^{-c\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb_0/(1+nK)}+\delta\right)} + \gamma_2 r\left(1-\frac{S_2(\eta_1)+\epsilon+\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta}{K}\right)\right.$$

$$\left. + \alpha\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right)+d_1+\bar{d}_1+\bar{d}_2\right]\lambda$$

$$+ \left[-\gamma_1\frac{mb_0 S_2(\eta_2)}{1+nS_2(\eta_2)}e^{-c\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb_0/(1+nK)}+\delta\right)} + d_1+\bar{d}_1\right]\times$$

$$\left[-\gamma_2 r\left(1-\frac{S_2(\eta_1)+\epsilon+\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta}{K}\right)+\alpha\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb_0/(1+nK)}+\delta\right)+\bar{d}_2\right]$$

$$- \beta_1 S_1(\eta_2)\beta_2 S_2(\eta_2)e^{(-d_1+\bar{d}_1)\tau_1}e^{-\bar{d}_2\tau_2}.$$

As discussed before, if

$$\mathcal{R}_{\epsilon,\delta,\eta_1,\eta_2} = \frac{\beta_1 S_1(\eta_2)\beta_2 S_2(\eta_2)e^{(-d_1+\bar{d}_1)\tau_1}e^{-\bar{d}_2\tau_2}}{\left((-\gamma_1 d_1+\bar{d}_1)+d_1+\bar{d}_1\right)\left(-\gamma_2 r\left(1-(S_2(\eta_1)+\epsilon+\beta_2\epsilon\bar{S}_2/(\bar{d}_2-\alpha_2+\delta))/K\right)+\alpha\left(S_1(\eta_1)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right)+\bar{d}_2\right)} > 1,$$

then the trivial solution is unstable, implying that system (2.36) has unbounded solutions s-ince it is a linear system.

Note that $\lim_{\epsilon,\delta,\eta_1,\eta_2\to 0}\mathcal{R}_{\epsilon,\delta,\eta_1,\eta_2} = \mathcal{R}_1$. Since $\mathcal{R}_1 > 1$, by continuity, we can choose $\epsilon,\delta,\eta_1,\eta_2$ to be sufficiently small so that $\mathcal{R}_{\epsilon,\delta,\eta_1,\eta_2} > 1$. Therefore, system (2.36) has unbounded solutions. As suggested by system (2.35) and the comparison theorem for delay differential equations, system (2.11) also has unbounded solutions, contradicting the results in Theorem 2.3.1. This proves the theorem. ∎

We are now in a position to state and prove the main results in this section.

Theorem 2.4.6 *Assume that $\mathcal{R}_1 > 1$, $\alpha_1 mKb_0/(1 + nK) < (d_1 + \bar{d}_1)$, and $\max\{\alpha_2 r, \gamma_2 r\} < \bar{d}_2$. Then the disease is uniformly persistent in the sense that there exists an $\epsilon > 0$ such that for any solutions to system (2.11), we have*

$$\liminf_{t \to \infty} I_i(t) \geq \epsilon \ \text{for} \ i = 1, 2. \tag{2.37}$$

Moreover, there exists a positive equilibrium, that is, an equilibrium with all components positive.

Proof. Denote

$$X = \{(S_1, L_1, I_1, S_2, L_2, I_2) : S_j \geq 0, \ L_j \geq 0, \ \text{and} \ I_j \geq 0, \ j = 1, 2\},$$
$$X_0 = \{(S_1, L_1, I_1, S_2, L_2, I_2) \in X : S_j \geq 0, \ L_j \geq 0, \ \text{and} \ I_j > 0, \ j = 1, 2\}\},$$

and the boundary of X is given by $\partial X_0 = X \backslash X_0$. Then $\partial X_0 = \{(S_1, L_1, I_1, S_2, L_2, I_2) \in X : I_j = 0$ at least for one $j\}$. Theorem 2.4.5 has shown that ∂X_0 is a weak repeller for X_0. So to prove that ∂X_0 is also a strong repeller for X_0, we need to verify the conditions of Theorem 4.6 in Thieme [20].

First of all, X_0 is open and forward invariant under the solution semi-flow $\Phi(t)$ of system (2.11). Since $\bar{S}^0 = (S_1, S_2)$ is globally asymptotically stable in $\mathbb{R}^2_+$ for the system consisting of S_1 and S_2, by setting $L_1 = 0$, $L_2 = 0$, $I_1 = 0$ and $I_2 = 0$ in system (2.11), the compactness assumptions of Theorem 4.6 in Thieme [20] hold. Moreover, every orbit in ∂X_0 converges to $E_2 = (S_1, 0, 0, S_2, 0, 0)$. Besides, E_2 is isolated and acyclic. Hence, we have verified all the conditions of Theorem 4.6 in Thieme [20], and proven inequality (2.37).

Theorem 2.3.1 confirms that system (2.11) is point-dissipative in X since there is a bounded set that attracts all orbits of (2.11) in X. By Theorem 2.4 in Zhao [28], there is an equilibrium in X_0, denoted by $E^* = (S_1^*, L_1^*, I_1^*, S_2^*, L_2^*, I_2^*)$. It remains to be proven that $S_1^* > 0$, $S_2^* > 0$, $L_1^* > 0$ and $L_2^* > 0$. If $S_1^* = 0$, then, based on the first equation in system (2.11), $I_1^* = 0$, which contradicts the fact that $I_1^* > 0$; therefore, $S_1^* > 0$. Comparably, the second equation in system (2.11) shows that $L_1^* > 0$. If $S_2^* = 0$, then the last equation of system (2.11) becomes

$$0 = \gamma_2 r \left(1 - \frac{I_2^* + L_2^*}{K}\right) I_2^* - \alpha(S_1^* + L_1^* + I_1^*) I_2^* - \bar{d}_2 I_2^*$$
$$< (\gamma_2 r - \bar{d}_2) I_2^*$$
$$< 0.$$

A contradiction appears; therefore, $S_2^* > 0$. Similarly, the fifth equation in system (2.11) shows that $L_2^* > 0$. Hence, we have completed the proof. ∎

Remark 2.4.3 *According to the biological findings [2, 17, 23], the conditions, $\alpha_1 mKb_0/(1 + nK) < (d_1 + \bar{d}_1)$, and $\max\{\alpha_2 r, \gamma_2 r\} < \bar{d}_2$, hold for the most cases since α_1, α_2 and γ_2 are normally very small.*

2.5   Numerical Simulation

The following numerical simulations are given to verify the theoretical results we have obtained.

1. When $\mathcal{R}_0 < 1$, the insect-free equilibrium is globally asymptotically stable, which means that the insect population cannot persist. See Figure 2.1.

2. When $\mathcal{R}_0 > 1$ and $\mathcal{R}_1 < 1$, the insect-free equilibrium loses its stability, and the disease-free equilibrium exists and is locally asymptotically stable, which is consistent with Theorems 2.11 and 2.14. See Figure 2.2.

3. When $\mathcal{R}_1 > 1$, the positive equilibrium exists and is locally asymptotically stable. In this case, the disease will establish, as suggested in Theorem 2.4.6. See Figure 2.3.

2.6   Discussion and Future Work

We have derived a system of delay differential equations to describe the interaction dynamics between leafhoppers and crops, in which disease latencies within both leafhoppers and crops are incorporated. Our model only applies to a large scale isolated environment, outside of which leafhoppers will not travel. Previous models concerning leafhoppers mainly focus on environmental effects, such as temperature and moisture, on the life cycle of leafhoppers [3, 5, 18]. Moreover, few deterministic models have been advanced to study the interactions between leafhoppers and crops [17]. Therefore, our model constitutes a complementary work in this field and has obtained some results.

In this disease model, we have investigated the interactions between leafhoppers and crops based on the infection age structure. We start by proposing a general model in Section §2.2.
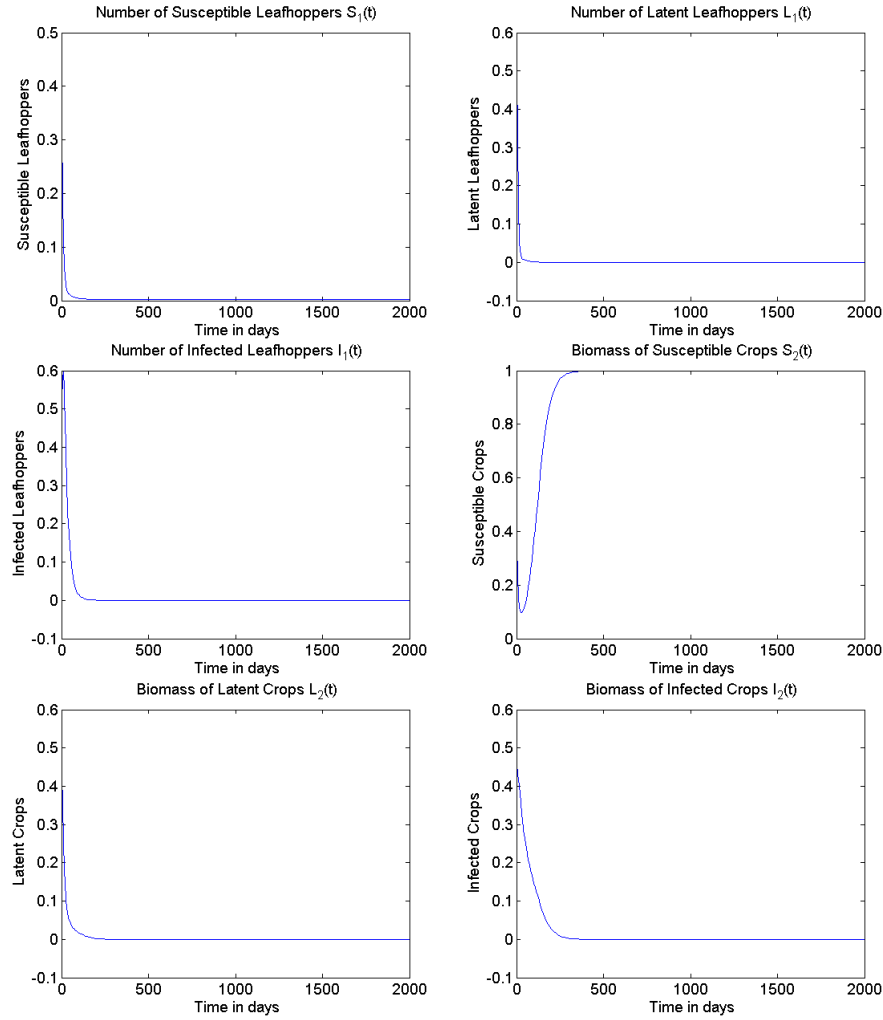
Figure 2.1: The insect population can not persist. Simulations are done with the following parameter values: $m = 1$, $n = 1$, $\alpha_1 = 0.05$, $\alpha_2 = 0.08$, $\beta_1 = 0.3$, $\beta_2 = 0.1$, $c = 1$, $b_0 = 0.03$, $d_1 = 0.03$, $\bar{d}_1 = 0.03$, $\bar{d}_2 = 0.03$, $r = 0.04$, $\gamma_1 = 0.05$, $\gamma_2 = 0.05$, $K = 1$, $\tau_1 = 10$, and $\tau_2 = 8$; and initial conditions: $(S_1(0), L_1(0), I_1(0), S_2(0), L_2(0), I_2(0)) = (0.5, 0.5, 0.5, 0.5, 0.5, 0.5)$.
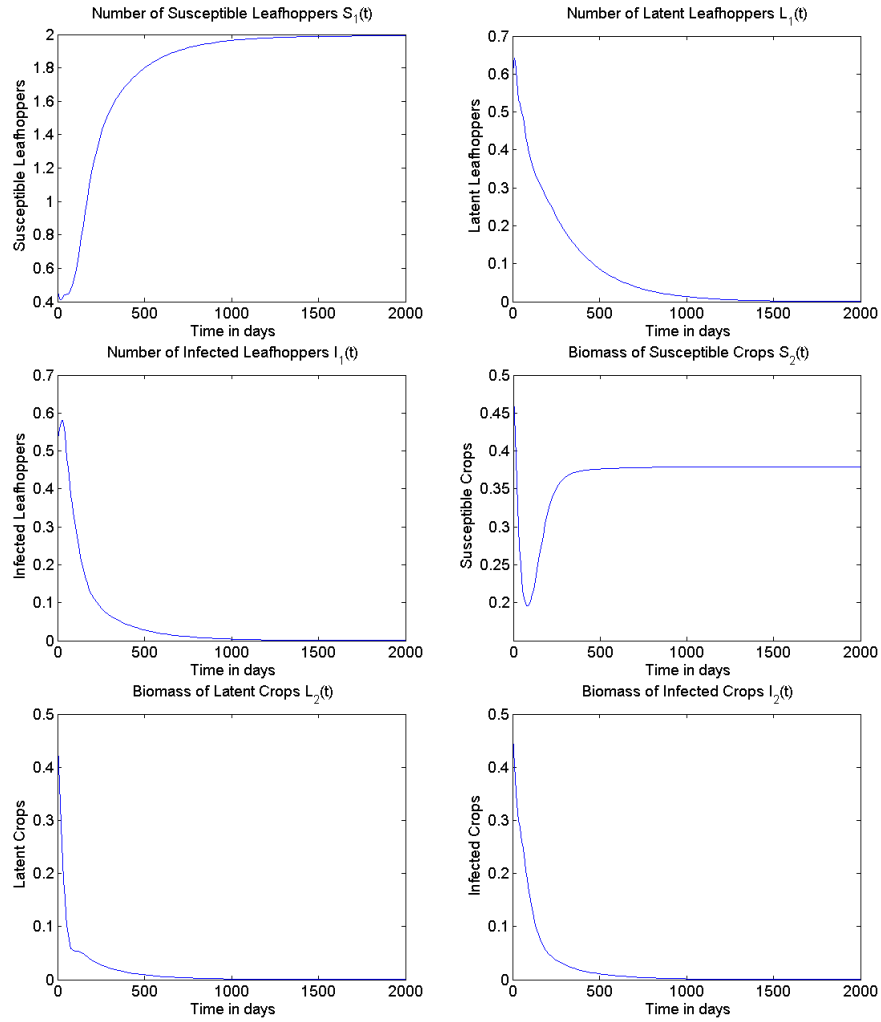
Figure 2.2: The insect population persists, but the disease can not establish. Simulations are done with the following parameter values: $m = 1$, $n = 1$, $\alpha_1 = 0.05$, $\alpha_2 = 0.08$, $\beta_1 = 0.3$, $\beta_2 = 0.1$, $c = 1$, $b_0 = 0.8$, $d_1 = 0.03$, $\bar{d}_1 = 0.03$, $\bar{d}_2 = 0.03$, $r = 0.04$, $\gamma_1 = 0.05$, $\gamma_2 = 0.05$, $K = 1$, $\tau_1 = 30$, and $\tau_2 = 28$; and initial conditions: $(S_1(0), L_1(0), I_1(0), S_2(0), L_2(0), I_2(0)) = (0.5, 0.5, 0.5, 0.5, 0.5, 0.5)$.

Figure 2.3: Both the insect population and the disease persist. Simulations are done with the following parameter values: $m = 1, n = 1, \alpha_1 = 0.05, \alpha_2 = 0.08, \beta_1 = 0.3, \beta_2 = 0.1, c = 1, b_0 = 0.8, d_1 = 0.03, \bar{d}_1 = 0.03, \bar{d}_2 = 0.03, r = 0.04, \gamma_1 = 0.05, \gamma_2 = 0.05, K = 1, \tau_1 = 10$, and $\tau_2 = 8$; and initial conditions: $(S_1(0), L_1(0), I_1(0), S_2(0), L_2(0), I_2(0)) = (0.5, 0.5, 0.5, 0.5, 0.5, 0.5)$.
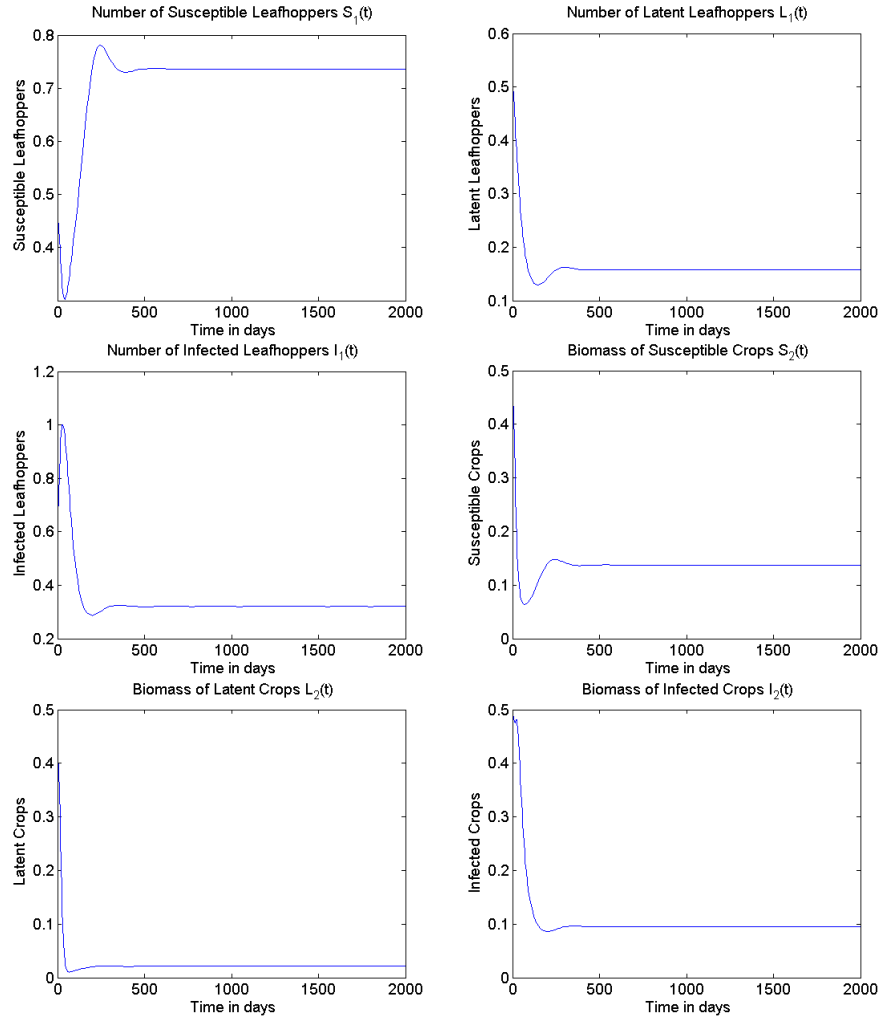
First of all, by showing the well-posedness of the model, we verify that the leafhopper popula-
tion and crop biomass do not go unbounded as well as below zero. By linearizing the system,
we prove the instability of the trivial equilibrium. We are able to see that the biomass grows
exponentially at the trivial equilibrium. To deepen our understanding on the subject, in Section
§2.4, we choose a specific model to analyze. Based on this model, we show that, if the repro-
duction ability of leafhoppers is very low i.e. $\mathcal{R}_0 < 1$, the leafhopper population will eventually
go extinct in the sense that the insect-free equilibrium is globally asymptotically stable. Here,
$\mathcal{R}_0$ is the average offspring that are reproduced by one adult leafhopper in its entire lifetime.
If $\mathcal{R}_0 < 1$, then one adult leafhopper can only reproduce less than one offspring in its life-
time; therefore, the leafhopper population cannot establish. We, furthermore, obtain that, when
$\mathcal{R}_0 > 1$ and $\mathcal{R}_1 < 1$, the disease-free equilibrium exists and is locally asymptotically stable. Un-
der this circumstance, the population of leafhoppers can thrive since $\mathcal{R}_0 > 1$. If $\mathcal{R}_1 > 1$, by the
persistence theory, the disease will persist, and, moreover, the positive equilibrium appears. In
this case, effective management actions need to be applied. Moreover, the simulations in Sec-
tion §2.5 have suggested that, when $\mathcal{R}_1 > 1$, the positive equilibrium is locally asymptotically
stable.

In this system, the delays play a vital role in determining whether the disease will establish
or not. Based on the formula of $\mathcal{R}_1$, we find that the increased delays have a negative impact on
the establishment of the disease by deceasing the value of $\mathcal{R}_1$ in an exponential fashion. This is
further verified by the simulations. In Figure 2.2, we choose both delays to be 30 and 28 days,
respectively, and the disease cannot persist. However, in Figure 2.3, when the delays are 10
and 8 days, respectively, with other parameters being unchanged, we find that the disease will
persist. A tentative explanation is that, if the incubation period is very long, not enough latent
leafhoppers will survive this period and become infectious; thus, the disease cannot establish.

The model implies an idea on how to better prevent the leafhopper-transmitted disease
from spreading, which is to get rid of the latent leafhoppers or crops as much as possible. To
examine this statement, we assume that an additional elimination rate of latent leafhoppers is
$\sigma L_1(t)$. Thus, based on our model, the corresponding $\mathcal{R}_1$ is given as

$$\mathcal{R}_1 = \frac{\beta_1 \beta_2 S_1 S_2}{(\bar{d}_2 + (1 - \gamma_2)\alpha S_2)(-\gamma_1 d_1 + d_1 + \bar{d}_1)e^{(d_1 + \bar{d}_1 + \sigma)\tau_1}e^{\bar{d}_2 \tau_2}}.$$

Since σ appears in the exponential term, it decreases the value of $\mathcal{R}_1$, as well as the likeli-
hood of outbreak of the disease, the fastest. This would provide some insights for leafhopper-
transmitted disease management, such as applying drugs that are efficient to eliminate latent

leafhoppers/crops, or getting rid of latent crops at a certain rate.

Moreover, the model can be modified to test the effectiveness of some existing disease management activities. For example, one of the management activities is to plant new susceptible crops at a certain rate [17], which can be incorporated into our model by adding a constant planting rate in the equation of susceptible crops. It is also suggested empirically that it is effective to control the disease by getting rid of the infected crops [12, 24]. However, this would inevitably destroy some healthy crops as a consequence. This activity can be investigated by subtracting a loss term in each of the three equations of crops in the model. By getting the expression of $\mathcal{R}_1$, we are able to test whether the corresponding management activity is effective or not; or at what parameter values, the effectiveness reaches the maximum.

This model has contributed to the understanding of the interactions between leafhoppers and crops; however, there are some aspects that can be improved in this model. First of all, we have assumed that the latent periods of the disease within leafhoppers and crops are all constant and identical. It is biologically more reasonable to consider different and non-constant delays for both host and vectors due to the variations of climate and geographic conditions.

Secondly, we can further analyze the stability situations of the positive equilibrium. The simulation results have shown that the positive equilibrium is locally (even globally!) asymptotically stable. However, this would involve the calculation of a degree six characteristic polynomial equation and the construction of a Lyapunov functional, following a very complicated analysis.

Adult leafhoppers are able to travel; thus, it is reasonable to take this travel into consideration. A good choice is to extend our model into a patch model, which considers an environment with various concentrations of individuals of the population being unevenly distributed across this area [27]. Although a patch model requires a substantial analysis, it would allow us to investigate how to prevent diseases in one region from spreading to other regions.

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Chapter 3

Modeling leafhopper population and their interactions with crops

3.1 Introduction

The family Cicadellidae, commonly known as leafhoppers or hoppers, is distributed all over the world, and constitutes the second-largest hemipteran family, with at least 20,000 described species [24]. These minute insects are plant feeders that suck plant sap from many plants. Their hind legs are modified for jumping, and are covered with hairs that facilitate the spreading of a secretion over their bodies that acts as a water repellent and carrier of pheromones. They undergo an incomplete metamorphosis, and have various host associations, varying from very generalized to very specific. Potatoes, alfalfa, and beets constitute especially good hosts. Apple, birch, chestnut, maple and numerous other tree species can also host the pests [12, 22].

Almost all the species share a very similar life cycle. In general, female inserts several eggs into the living tissue of the host plant. The eggs either remain dormant for a period ranging from a month to over a year, or develop and hatch within approximately 10 days. The young, known as nymphs, feed on plant sap by inserting their beaks into the vascular or parenchyma tissues of the host plant and go through a series of five moults, which are called instars, reaching the adult stage after a period of several weeks (normally 3-6 weeks) [20]. Leafhopper adults are elongated, wedge shaped and somewhat triangular in cross-section. They jump and fly off readily. Depending on the species, they range in size from 0.32 cm to 1.3 cm and their bodies are coloured yellow, green, gray or they may be marked with colour patterns [18, 21].

A natural question arises: what are the effects that different life stages (i.e. egg, nymph,

adult) of leafhoppers can impose on crops? Few attempts regarding this question have been made. The studies undertaken so far focus on how temperature and moisture affect the life cycle of leafhoppers [3, 5, 6, 8, 15, 16], and how diseases transmit between leafhoppers and crops [1, 3, 4, 9, 13, 17, 23]. Those models have limitations because either the interactions between leafhoppers and crops are not incorporated, or the life stages of leafhoppers are not distinguished. Therefore, to investigate the question that we brought up at the beginning of this paragraph, as well as provide more effective management activities specific to each life stage of the pests, more comprehensive models need to be put forward.

Age structure models [10, 19] serve as a good candidate to study the population dynamics. Based on the fact that the life cycle of leafhoppers is structured (i.e. egg, nymph, adult), it is natural and reasonable to take the age structure into consideration. Making use of the age structure as well as the typical method of characteristics for structured population, we derive a model that incorporates different life stages of leafhoppers. Furthermore, we assume an isolated, spatially well-mixed environment, where the insect population is evenly distributed [25], outside of which leafhoppers do not travel to.

The rest of this chapter is organized as follows. In Section §3.2, we construct a general age-structured model. The well-posedness of the model and the stability of the trivial equilibrium, as well as the stability of the insect-free equilibrium, are given in Section §3.3. To further our analysis on the subject, two specific models are introduced in Section §3.4. This section provides a detail analysis of the models, including the stability of the equilibria. We end this chapter by presenting some simulations to illustrate the analytical results.

3.2   Derivation of the General Model

In this section, we give the derivation of the general model. Assume that, in an isolated, spatial-ly well-mixed environment, a certain leafhopper species consumes a certain crop species. Due to different life stages, the life cycle of leafhoppers are divided into the egg stage, nymph stage and adult stage, respectively. Assume that the lengths of the egg stage and nymph stage are fixed by τ_1 and τ_2, respectively. Although lengths differ among individuals in general, for the sake of simplicity, we assume fixed lengths which can be considered as an approximation of the mean or median length within leafhoppers. Let $E(t)$, $N(t)$ and $A(t)$ be the sub-population of the egg stage, nymph stage and adult stage, respectively, at time t. Moreover, since leafhoppers consume on crops, the crop biomass will affect the leafhopper population dynamics. Let $g(t)$

denote the biomass at time t.

To understand the population dynamics of leafhoppers, we start with an age-structured model [10, 19], which is

$$\frac{\partial p(t,a)}{\partial t} + \frac{\partial p(t,a)}{\partial a} = -d(a)p(t,a),$$

where $p(t,a)$ is the density of the leafhopper population with respect to age a at time t, and $d(a)$, the age-specific mortality of leafhoppers, is a non-negative function of age. From the definition of $p(t,a)$, the population of eggs, nymphs, and adults can be expressed by

$$\begin{cases} E(t) = \int_0^{\tau_1} p(t,a)da \\ N(t) = \int_{\tau_1}^{\tau_1+\tau_2} p(t,a)da \\ A(t) = \int_{\tau_1+\tau_2}^{\infty} p(t,a)da \end{cases}.$$

To conveniently build the model, let us assume that the age-specific mortality is a piecewise-constant function:

$$d(a) = \begin{cases} d_1 & 0 \le a < \tau_1 \\ d_2 & \tau_1 \le a < \tau_1 + \tau_2 \\ d_3 & a \ge \tau_1 + \tau_2 \end{cases}.$$

Only mature adults have the ability to reproduce, which means $A(t)$ has a contribution to the per capita birth function of leafhoppers. Besides, the total biomass of crops will affect the per capita birth rate of leafhoppers as well. Normally, the more biomass, the larger the per capita birth rate. Denote the per capita birth rate as $b(t) = b(g(t), A(t))$. Thus the birth rate of leafhoppers at time t is $b(g(t), A(t))A(t)$. In other words, $p(t,0) = b(g(t), A(t))A(t)$. Besides, it is also reasonable to assume that $\lim_{a \to \infty} p(t,a) = 0$, which will be denoted as $p(t, \infty) = 0$ as a shorthand notation.

Thus the PDE system is given as

$$\begin{cases} \frac{\partial p(t,a)}{\partial t} + \frac{\partial p(t,a)}{\partial a} = -d(a)p(t,a) \\ p(t,0) = b(g(t), A(t))A(t) \\ p(t,\infty) = 0 \end{cases}. \tag{3.1}$$

The general solution of system (3.1) is

$$
\begin{cases}
p(t, a) = p(t - a, 0)e^{-\int_0^a d(s)ds} & t \geq a \\
p(t, a) = p(0, a - t)e^{-\int_0^t d(s)ds} & t < a
\end{cases}. \tag{3.2}
$$

Integrating both sides of the first equation in system (3.1) with respect to age from 0 to τ_1 leads to

$$
\int_0^{\tau_1} \left(\frac{\partial p(t, a)}{\partial t} + \frac{\partial p(t, a)}{\partial a} \right) da = - \int_0^{\tau_1} d_1 p(t, a) da
$$

$$
\Rightarrow \frac{dE(t)}{dt} = -d_1 E(t) - p(t, \tau_1) + p(t, 0).
$$

Applying the general solution of (3.1), we have

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) & t < \tau_1 \\
\frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) - b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} & t \geq \tau_1
\end{cases}.
$$

Similarly, the nymph population follows

$$
\frac{dN(t)}{dt} = -d_2 N(t) - p(t, \tau_1 + \tau_2) + p(t, \tau_1).
$$

Then, following the general solution of model (3.1), and the boundary conditions, the nymph population can be described as

$$
\begin{cases}
\frac{dN(t)}{dt} = -d_2 N(t) & t < \tau_1 \\
\frac{dN(t)}{dt} = -d_2 N(t) + b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} & \tau_1 \leq t < \tau_1 + \tau_2 \\
\frac{dN(t)}{dt} = -d_2 N(t) + b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} - \\
\qquad b(g(t - \tau_1 - \tau_2), A(t - \tau_1 - \tau_2))A(t - \tau_1 - \tau_2)e^{-d_1\tau_1 - d_2\tau_2} & t \geq \tau_1 + \tau_2
\end{cases}.
$$

Based on a similar approach, one can derive the equations for adults:

$$
\begin{cases}
\frac{dA(t)}{dt} = -d_3 A(t) & t < \tau_1 + \tau_2 \\
\frac{dA(t)}{dt} = -d_3 A(t) + b(g(t - \tau_1 - \tau_2), A(t - \tau_1 - \tau_2))A(t - \tau_1 - \tau_2)e^{-d_1\tau_1 - d_2\tau_2} & t \geq \tau_1 + \tau_2
\end{cases}.
$$

It follows that for $t < \tau_1$, the population dynamics are governed by the ODEs system:

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) \\
\frac{dN(t)}{dt} = -d_2 N(t) \\
\frac{dA(t)}{dt} = -d_3 A(t)
\end{cases} ;
$$

for $\tau_1 \leq t < \tau_1 + \tau_2$, they are described by

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) - b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} \\
\frac{dN(t)}{dt} = -d_2 N(t) + b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} \\
\frac{dA(t)}{dt} = -d_3 A(t)
\end{cases} ;
$$

and for $t \geq \tau_1 + \tau_2$, we have

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) - b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} \\
\frac{dN(t)}{dt} = -d_2 N(t) + b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} \\
\qquad\quad - b(g(t - \tau_1 - \tau_2), A(t - \tau_1 - \tau_2))A(t - \tau_1 - \tau_2)e^{-d_1\tau_1 - d_2\tau_2} \\
\frac{dA(t)}{dt} = -d_3 A(t) + b(g(t - \tau_1 - \tau_2), A(t - \tau_1 - \tau_2))A(t - \tau_1 - \tau_2)e^{-d_1\tau_1 - d_2\tau_2}
\end{cases} .
$$

Next, we derive the equation for the crop biomass. Assume that if there are no leafhoppers, the growth of the crop biomass is given by

$$
\frac{dg(t)}{dt} = G(g(t))g(t),
$$

where $G(g(t))$ is the per capita growth rate of crops. Assume that both adult and nymph leafhoppers consume crops at rates given by the attack rates $h_1(g(t), A(t))A(t)$ and $h_2(g(t), N(t))N(t)$, respectively. As a result, the dynamics of the crop biomass can be described by

$$
\frac{dg(t)}{dt} = G(g(t))g(t) - h_1(g(t), A(t))A(t) - h_2(g(t), N(t))N(t).
$$

The long-term behaviours of the system, when $t \geq \tau_1 + \tau_2$, are described by the DDEs:

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) - b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} \\
\frac{dN(t)}{dt} = -d_2 N(t) + b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} \\
\qquad\qquad - b(g(t - \tau_1 - \tau_2), A(t - \tau_1 - \tau_2))A(t - \tau_1 - \tau_2)e^{-d_1\tau_1 - d_2\tau_2} \\
\frac{dA(t)}{dt} = -d_3 A(t) + b(g(t - \tau_1 - \tau_2), A(t - \tau_1 - \tau_2))A(t - \tau_1 - \tau_2)e^{-d_1\tau_1 - d_2\tau_2} \\
\frac{dg(t)}{dt} = G(g(t))g(t) - h_1(g(t), A(t))A(t) - h_2(g(t), N(t))N(t)
\end{cases}
\tag{3.3}
$$

To investigate model (3.3), well-posedness needs to be specified. However, the initial conditions of this model depend on the systems when $t < \tau_1 + \tau_2$. When $0 \leq t < \tau_1$, no eggs will hatch out and no nymphs will become adults. The system is governed by the following ODEs system:

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) \\
\frac{dN(t)}{dt} = -d_2 N(t) \\
\frac{dA(t)}{dt} = -d_3 A(t) \\
\frac{dg(t)}{dt} = G(g(t))g(t) - h_1(g(t), A(t))A(t) - h_2(g(t), N(t))N(t)
\end{cases}
\tag{3.4}
$$

When $\tau_1 \leq t < \tau_1 + \tau_2$, the system is governed by the following DDEs system:

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) - b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} \\
\frac{dN(t)}{dt} = -d_2 N(t) + b(g(t - \tau_1), A(t - \tau_1))A(t - \tau_1)e^{-d_1\tau_1} \\
\frac{dA(t)}{dt} = -d_3 A(t) \\
\frac{dg(t)}{dt} = G(g(t))g(t) - h_1(g(t), A(t))A(t) - h_2(g(t), N(t))N(t)
\end{cases}
\tag{3.5}
$$

To ensure that the model makes biological sense, the following assumptions need to be specified [7]. The per capita birth rate of leafhoppers should satisfy the following rules:

A11 $b(g(t), A(t)) > 0$ for $g(t), A(t) > 0$; $b(0, \cdot) = 0$ and $b(\cdot, 0^+) > 0$

A12 $b(g(t), A(t))$ is continuously differentiable with

$$
\frac{\partial b(g, A)}{\partial A} < 0, \qquad \frac{\partial b(g, A)}{\partial g} > 0.
$$

A13 $\lim_{A(t) \to +\infty} b(g(t), A(t))A(t) < C$, where C is a positive constant.

Condition A13 gives the existence of a carrying capacity K_1 of the leafhopper population.

The per capita birth rate of crops also satisfies the following assumptions:

A21 $G(g(t)) > 0$ for $g(t) > 0$, and $G(0^+) > 0$.

A22 $G(g(t))$ is continuously differentiable with

$$\frac{dG}{dg} < 0.$$

A23 There exists a positive constant K, such that $G(K) = 0$, and $g(t)$, which is governed by $dg(t)/dt = G(g(t))g(t)$, is bounded.

Note that A22 and A23 imply that $G^{-1}(g)$ exists. A23 gives the existence of a carrying capacity K such that $G(g(t)) > 0$ for $g(t) < K$, and $G(g(t)) < 0$ for $g(t) > K$.

The attack functions follow similar rules as well:

A31 $h_1(g(t), A(t)) \geq 0$ and $h_2(g(t), N(t)) \geq 0$ if $g(t), A(t),$ and $N(t) \geq 0$.

A32 $h_1(g(t), A(t))$ and $h_2(g(t), N(t))$ are continuously differentiable with

$$\frac{\partial h_1(g, A)}{\partial A} \geq 0, \qquad \frac{\partial h_1(g, A)}{\partial g} \geq 0,$$
$$\frac{\partial h_2(g, A)}{\partial A} \geq 0, \qquad \frac{\partial h_2(g, A)}{\partial g} \geq 0.$$

A33 $h_i(\cdot, 0) = 0$ and $h_i(0, \cdot) = 0$, $i = 1, 2$.

3.3 Analysis of the General Model

In this section, we will give a brief qualitative analysis of the general model we have derived above. Model (3.3) is a system of delay differential equations. For such a system, initial functions need to be specified and well-posedness needs to be addressed. The following theorem establishes the positivity and boundedness of the solutions to system (3.3).

Theorem 3.3.1 *Let $(E(t), N(t), A(t), g(t))$ be the solution to system* (3.3) *with initial conditions* $E(0) \geq 0, N(0) \geq 0, A(0) \geq 0,$ *and* $g(0) \geq 0$. *Then* $E(t), N(t), A(t)$ *and* $g(t)$ *are all non-negative and bounded for all* $t \geq 0$ *at which the solution exists.*

Proof. With the initial values given, it is easy to show that the ODE system (3.4) has a unique and non-negative solution for $t \in [0, \tau_1]$. Using the values of this solution in the interval

$[\tau_1, \tau_1 + \tau_2]$, one can further solve the DDE system (3.5) to get a unique and non-negative solution defined for $t \in [\tau_1, \tau_1 + \tau_2]$. Combining these two solutions together, we obtain the initial conditions for system (3.3) on $[0, \tau_1 + \tau_2] = [0, \tau_1] \cup [\tau_1, \tau_1 + \tau_2]$. First of all, we show that $g(t)$ is non-negative. However, this depends on the expressions of $h_1(g, A)$ and $h_2(g, N)$. In this thesis, we choose $h_1(g, A)$ and $h_2(g, A)$ to be Holling's type functions, which means $h_1(g, A)$ and $h_2(g, N)$ have factor g. Rewrite h_1 and h_2 as $h'_1(g, A)g$ and $h'_2(g, A)g$, respectively. Thus,

$$g(t) = g(0) \exp\left(\int_0^t G(g(\theta)) - h'_1(g(\theta), A(\theta))A(\theta) - h'_2(g(\theta), N(\theta))N(\theta)d\theta\right) \geq 0.$$

For other types of h_1 and h_2, other methods need to be applied.

Next, we reformulate the rest of the equations in system (3.3) into the integral forms

$$E(t) = \int_0^{\tau_1} b(g(t - \theta), A(t - \theta))A(t - \theta)e^{-d_1\theta}d\theta,$$
$$N(t) = \int_0^{\tau_2} b(g(t - \tau_1 - \theta), A(t - \tau_1 - \theta))A(t - \tau_1 - \theta)e^{-d_1\tau_1 - d_2\theta}d\theta, \tag{3.6}$$
$$A(t) = A(0)e^{-d_3t} + e^{-d_1\tau_1 - d_2\tau_2}\int_0^t b(g(t - \theta), A(t - \theta))A(t - \theta)e^{d_3(t-\theta)}d\theta.$$

The last equation of (3.6) is based on the variation of constants formula. Based on assumptions $A11$, $A21$, and $A31$, and the positivity of the initial conditions, $E(t), N(t)$, and $A(t)$ are all non-negative.

Next, we show that the solutions to system (3.3) are bounded. By positivity,

$$\frac{dg(t)}{dt} = G(g(t))g(t) - h_1(g(t), A(t))A(t) - h_2(g(t), N(t))N(t) \leq G(g(t))g(t).$$

Assumption $A23$ together with a comparison argument implies that $g(t)$ is bounded. Before proving that $E(t)$, $N(t)$ and $A(t)$ are bounded, it is noticed that, from assumption $A13$, $b(A(t), g(t))A(t)$ is bounded, say by M_b. Define $M(t) = E(t) + N(t) + A(t)$ and $q = \min\{d_1, d_2, d_3\}$. By the non-negativity of the solutions, it follows that

$$\frac{dM(t)}{dt} = \frac{dE(t)}{dt} + \frac{dN(t)}{dt} + \frac{dA(t)}{dt}$$
$$= -d_1E(t) + b(A(t), g(t))A(t) - d_2N(t) - d_3A(t)$$
$$\leq M_b - qM(t),$$

which implies that $M(t)$ is bounded. Therefore, $E(t), N(t), A(t)$ and $g(t)$ are bounded. ∎

In the following theorem, we discuss the stability of the trivial equilibrium E_0, which is the equilibrium with all components being zero.

Theorem 3.3.2 *The trivial equilibrium* $E_0 = (0, 0, 0, 0)$ *is unstable.*

Proof. This proof can be obtained by linearizing system (3.3) at the trivial equilibrium, which yields

$$\begin{cases} \frac{dE(t)}{dt} = -d_1 E(t) \\ \frac{dN(t)}{dt} = -d_2 N(t) \\ \frac{dA(t)}{dt} = -d_3 A(t) \\ \frac{dg(t)}{dt} = G(0)g(t) \end{cases}. \tag{3.7}$$

Therefore, the characteristic equation is given by $|\lambda I - J| = 0$, where

$$J = \begin{pmatrix} -d_1 & 0 & 0 & 0 \\ 0 & -d_2 & 0 & 0 \\ 0 & 0 & -d_3 & 0 \\ 0 & 0 & 0 & G(0) \end{pmatrix}.$$

It is not hard to compute the eigenvalues of J, among which one of the eigenvalues is $G(0) > 0$. In other words, the trivial equilibrium is unstable. Based on the last equation in the linearized system (3.7), we find that the biomass grows exponentially around the trivial equilibrium. ∎

An insect-free equilibrium of model (3.3) is the equilibrium with the infection related components being zeros. That is, such an equilibrium has the form

$$E_1 = (0, 0, 0, x).$$

A simple calculation gives $E_1 = (0, 0, 0, K)$. We can show that E_1 is locally asymptotically stable under certain conditions.

Theorem 3.3.3 *The insect-free equilibrium* E_1 *is locally asymptotically stable when*

$$\mathcal{R}_0 = \frac{b(K, 0)}{d_3 e^{d_1 \tau_1 + d_2 \tau_2}} < 1,$$

and unstable when $\mathcal{R}_0 > 1$.

Proof. Linearizing system (3.3) at the E_1 leads to

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + b(K,0)A(t) - b(K,0)e^{-d_1\tau_1}A(t-\tau_1) \\
\frac{dN(t)}{dt} = -d_2 N(t) + b(K,0)e^{-d_1\tau_1}A(t-\tau_1) - b(K,0)e^{-d_1\tau_1-d_2\tau_2}A(t-\tau_1-\tau_2) \\
\frac{dA(t)}{dt} = -d_3 A(t) + b(K,0)e^{-d_1\tau_1-d_2\tau_2}A(t-\tau_1-\tau_2) \\
\frac{dg(t)}{dt} = G'(K)Kg(t)
\end{cases}.
$$

Therefore, the characteristic equation is given by

$$
|\lambda I - J_1 - J_2 e^{-\lambda\tau_1} - J_3 e^{-\lambda(\tau_1+\tau_2)}| = 0,
$$

where

$$
J_1 = \begin{pmatrix}
-d_1 & 0 & b(K,0) & 0 \\
0 & -d_2 & 0 & 0 \\
0 & 0 & -d_3 & 0 \\
0 & 0 & 0 & G'(K)K
\end{pmatrix},
$$

$$
J_2 = \begin{pmatrix}
0 & 0 & -b(K,0)e^{-d_1\tau_1} & 0 \\
0 & 0 & b(K,0)e^{-d_1\tau_1} & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{pmatrix},
$$

$$
J_3 = \begin{pmatrix}
0 & 0 & 0 & 0 \\
0 & 0 & -b(K,0)e^{-d_1\tau_1-d_2\tau_2} & 0 \\
0 & 0 & b(K,0)e^{-d_1\tau_1-d_2\tau_2} & 0 \\
0 & 0 & 0 & 0
\end{pmatrix}.
$$

The characteristic equation can be calculated as

$$
(\lambda + d_3 - b(K,0)e^{-d_1\tau_1-d_2\tau_2}e^{-\lambda(\tau_1+\tau_2)})(\lambda + d_1)(\lambda + d_2)(\lambda - G'(K)K) = 0. \tag{3.8}
$$

The last three factors on the left-hand side of equation (3.8) give three real roots: $-d_1$, $-d_2$ and $G'(K)K$, which are all negative.

Hence, the local asymptotical stability of the system is determined by

$$\lambda + d_3 - b(K, 0)e^{-d_1\tau_1 - d_2\tau_2}e^{-\lambda(\tau_1 + \tau_2)} = 0.$$

Rewrite the above equation as

$$[\lambda(\tau_1 + \tau_2) + d_3(\tau_1 + \tau_2)]e^{\lambda(\tau_1 + \tau_2)} - \frac{b(K, 0)(\tau_1 + \tau_2)}{e^{d_1\tau_1 + d_2\tau_2}} = 0. \tag{3.9}$$

Equation (3.9) is the famous Hayes equation. We can show that

$$a = d_3(\tau_1 + \tau_2) > -1,$$

$$\theta \sin \theta - a \cos \theta > 0 > b = -\frac{b(K, 0)(\tau_1 + \tau_2)}{e^{d_1\tau_1 + d_2\tau_2}},$$

always hold, since $\pi/2 < \theta < \pi$, when $\theta = -a \tan \theta$.

$$a + b = d_3(\tau_1 + \tau_2) - \frac{b(K, 0)(\tau_1 + \tau_2)}{e^{d_1\tau_1 + d_2\tau_2}} = d_3(\tau_1 + \tau_2)(1 - \mathcal{R}_0) > 0,$$

if $\mathcal{R}_0 < 1$; $a + b < 0$, if $\mathcal{R}_0 > 1$.

Employing Theorem A.5 in Hale & Verduyn Lunel [11], equation (3.9) has all roots with negative real parts, when $\mathcal{R}_0 < 1$; roots with positive real parts show up when $\mathcal{R}_0 > 1$. ∎

The insect-free equilibrium is indeed globally asymptotically stable. To prove it, we first show that this equilibrium is globally attractive.

Theorem 3.3.4 *The insect-free equilibrium E_1 is globally attractive when $\mathcal{R}_0 < 1$.*

Proof. First of all, we reformulate system (3.12) in terms of the integrals:

$$E(t) = \int_0^{\tau_1} b(g(t - \theta), A(t - \theta))A(t - \theta)e^{-d_1\theta}d\theta,$$

$$N(t) = \int_0^{\tau_2} b(g(t - \tau_1 - \theta), A(t - \tau_1 - \theta))A(t - \tau_1 - \theta)e^{-d_1\tau_1 - d_2\theta}d\theta, \tag{3.10}$$

$$A(t) = A(0)e^{-d_3t} + e^{-d_1\tau_1 - d_2\tau_2}\int_0^t b(g(t - \theta), A(t - \theta))A(t - \theta)e^{d_3(t-\theta)}d\theta.$$

If we could prove that $\lim_{t\to+\infty} A(t) = 0$, then it is easy to show that

$$\lim_{t\to+\infty} E(t) = \lim_{t\to+\infty} N(t) = 0, \quad \text{and} \quad \lim_{t\to+\infty} g(t) = K.$$

Therefore, $\lim_{t\to+\infty}(E(t), N(t), A(t), g(t)) = E_0 = (0, 0, 0, K)$.

By the virtue of the positivity of the solutions, to prove $\lim_{t\to+\infty} A(t) = 0$, it is sufficient to prove that $\limsup_{t\to+\infty} A(t) = 0$ whenever $\mathcal{R}_0 < 1$. To this end, from the third integral equation in system (3.10) and by use of the Lemma 4.2 [2], we have

$$
\begin{aligned}
\limsup_{t\to+\infty} A(t) &= \limsup_{t\to+\infty} \left(e^{-d_1\tau_1 - d_2\tau_2} \int_0^t b(g(t-\theta), A(t-\theta))A(t-\theta)e^{d_3(t-\theta)}d\theta + A(0)e^{-d_3 t} \right) \\
&\le e^{-d_1\tau_1 - d_2\tau_2} \int_0^t b(\limsup_{t\to+\infty} g(t-\theta), 0) \limsup_{t\to+\infty} A(t-\theta)e^{d_3(t-\theta)}d\theta \\
&\le \left(e^{-d_1\tau_1 - d_2\tau_2} b(K, 0) \limsup_{t\to+\infty} A(t-\theta) \right) \left(\limsup_{t\to+\infty} \int_0^t e^{d_3(t-\theta)}d\theta \right) \\
&\le \frac{b(K, 0)}{e^{d_1\tau_1 + d_2\tau_2}} \limsup_{t\to+\infty} A(t) \left(\limsup_{t\to+\infty} \int_0^t e^{d_3(t-\theta)}d\theta \right) \\
&= \frac{b(K, 0)}{e^{d_1\tau_1 + d_2\tau_2}} \limsup_{t\to+\infty} A(t) \left(\frac{1}{d_3} \limsup_{t\to+\infty}(1 - e^{-d_3 t}) \right) \\
&= \mathcal{R}_0 \limsup_{t\to+\infty} A(t).
\end{aligned}
$$

In order to ensure

$$
\limsup_{t\to+\infty} A(t) \le \mathcal{R}_0 \limsup_{t\to+\infty} A(t),
$$

it is proven that

$$
\limsup_{t\to+\infty} A(t) = 0.
$$

∎

Summarizing the above theorems (i.e. Theorem 3.3.3 and Theorem 3.3.4), we have proven the following theorem.

Theorem 3.3.5 *The insect-free equilibrium is globally asymptotically stable when $\mathcal{R}_0 < 1$. It becomes unstable when $\mathcal{R}_0 > 1$.*

Remark 3.3.1 *Rewrite $\mathcal{R}_0$ as*

$$\mathcal{R}_0 = \underbrace{b(K,0)}_{\substack{\text{per capita birth rate} \\ \text{of leafhoppers}}} \quad \underbrace{\frac{1}{d_3}}_{\text{expected life time of adult leafhoppers}} \quad \underbrace{e^{-(d_1\tau_1+d_2\tau_2)}}_{\substack{\text{survival probability of adult leafhoppers} \\ \text{during hatching and maturation periods}}} .$$

Based on the meaning of the parameters involved, one can see the biological meaning of $\mathcal{R}_0$, which is the average number of new adults reproduced by one adult in its lifetime.

Remark 3.3.2 *In [15], the authors argue that, empirically, it is more efficient to apply insecticide in the nymph stage. Based on our model, this argument can be mathematically proven. The idea is to obtain the new $\mathcal{R}_0$, as explained below.*

Assume that the insecticide is applied during the nymph stage, then system (3.12) becomes

$$\begin{cases} \frac{dE(t)}{dt} = -d_1 E(t) + b(g(t), A(t))A(t) - b(g(t-\tau_1), A(t-\tau_1))A(t-\tau_1)e^{-d_1\tau_1} \\ \frac{dN(t)}{dt} = -d_2 N(t) + b(g(t-\tau_1), A(t-\tau_1))A(t-\tau_1)e^{-d_1\tau_1} - \sigma N(t) \\ \qquad\quad - b(g(t-\tau_1-\tau_2), A(t-\tau_1-\tau_2))A(t-\tau_1-\tau_2)e^{-d_1\tau_1-d_2\tau_2} \\ \frac{dA(t)}{dt} = -d_3 A(t) + b(g(t-\tau_1-\tau_2), A(t-\tau_1-\tau_2))A(t-\tau_1-\tau_2)e^{-d_1\tau_1-d_2\tau_2} \\ \frac{dg(t)}{dt} = G(g(t))g(t) - h_1(g(t), A(t))A(t) - h_2(g(t), N(t))N(t) \end{cases} , \qquad (3.11)$$

where the σ is the death rate of nymphs due to the insecticide.

The new reproduction number is denoted as $\mathcal{R}_{0N}$, where N is the subscript that denotes that the insecticide is applied in the nymph stage:

$$\mathcal{R}_{0N} = \frac{b(K,0)}{d_3 e^{d_1\tau_1+(d_2+\sigma)\tau_2}}.$$

If the insecticide is used in the egg stage or the adult stage, we can get the new reproduction numbers, respectively:

$$\mathcal{R}_{0E} = \frac{b(K,0)}{d_3 e^{(d_1+\sigma)\tau_1+d_2\tau_2}},$$

$$\mathcal{R}_{0A} = \frac{b(K,0)}{(d_3+\sigma)e^{d_1\tau_1+d_2\tau_2}}.$$

As functions of σ, among the above three insecticide mediated reproduction numbers, R_{0N} decreases the fastest as σ increases, due to the fact that $\tau_2 > \tau_1$.

3.4   Analysis of two Specific Models

When $\mathcal{R}_0 > 1$, the insect-free equilibrium loses its stability, and a positive equilibrium appears. However, further information can not be drawn from the general model. Therefore, in this section, we choose some particular functions of b, h_1, h_2 and G that satisfy all the assumptions in Section §3.2 to further our analysis of the system. To continue the analysis, we investigate two special cases based on the monotonicity of the birth rate $b(g, A)A$ with respect to the adult population A.

3.4.1   Case 1

In this case, we consider a scenario that the birth rate of leafhoppers, $b(A, g)A$, is an increasing function with respect to the adult population A. This goal can be realized by choosing the Beverton-Holt function [7]

$$b(A(t), g(t)) = \frac{mg(t)}{1 + ng(t)} \frac{p}{q + A(t)}.$$

Moreover, based on the literature [7], we choose

$$h_1(g(t), A(t)) = f_1 A(t), \quad h_2(g(t), N(t)) = f_2 N(t),$$

$$G(g(t)) = r\left(1 - \frac{g(t)}{K}\right).$$

where p/q is the proliferation rate of leafhoppers; $mg(t)/(1 + ng(t))$, which is an increasing function with respect to the crop biomass $g(t)$, represents the influence of food resources on the reproduction ability of leafhoppers; f_1 and f_2 are the crop-attack rates of nymphs and adults, respectively; $G(g(t))$ is the logistic function, with r being intrinsic growth rate, and K being carrying capacity.

With the above assumptions, the population dynamics are then described by the following system of delay differential equations:

$$\begin{cases} \frac{dE(t)}{dt} = -d_1 E(t) + \frac{mg(t)}{1+ng(t)} \frac{p}{q+A(t)} A(t) - \frac{mg(t-\tau_1)}{1+ng(t-\tau_1)} \frac{p}{q+A(t-\tau_1)} A(t - \tau_1)e^{-d_1\tau_1} \\ \frac{dN(t)}{dt} = -d_2 N(t) + \frac{mg(t-\tau_1)}{1+ng(t-\tau_1)} \frac{p}{q+A(t-\tau_1)} A(t - \tau_1)e^{-d_1\tau_1} \\ \qquad\quad - \frac{mg(t-\tau_1-\tau_2)}{1+ng(t-\tau_1-\tau_2)} \frac{p}{q+A(t-\tau_1-\tau_2)} A(t - \tau_1 - \tau_2)e^{-d_1\tau_1-d_2\tau_2} \\ \frac{dA(t)}{dt} = -d_3 A(t) + \frac{mg(t-\tau_1-\tau_2)}{1+ng(t-\tau_1-\tau_2)} \frac{p}{q+A(t-\tau_1-\tau_2)} A(t - \tau_1 - \tau_2)e^{-d_1\tau_1-d_2\tau_2} \\ \frac{dg(t)}{dt} = r\left(1 - \frac{g(t)}{K}\right)g(t) - f_1 g(t)A(t) - f_2 g(t)N(t) \end{cases} \qquad (3.12)$$

In the following sections, we discuss the stability of the equilibria.

Equilibria

The qualitative behaviours of the trivial equilibrium $E_0 = (0, 0, 0, 0, 0, 0)$ and $E_1 = (0, 0, 0, K, 0, 0)$ follow the general model. E_0 is always unstable. E_1 is globally asymptotically stable when

$$\mathcal{R}_0 = \frac{mK}{(1 + nK)} \frac{p}{qd_3 e^{d_1\tau_1 + d_2\tau_2}} < 1.$$

It becomes unstable when $\mathcal{R}_0 > 1$. Thus, we consider a possible positive equilibrium of (3.12), which should be of the form $E_2 = (E^*, N^*, A^*, g^*)$ with the components satisfying the following system of nonlinear equations:

$$\begin{cases} E^* = (1 - e^{-d_1\tau_1})\frac{mg^*}{(1+ng^*)d_1}\frac{p}{q+A^*}A^* \\ N^* = (e^{-d_1\tau_1} - e^{-d_1\tau_1 - d_2\tau_2})\frac{mg^*}{(1+ng^*)d_2}\frac{p}{q+A^*}A^* = \frac{d_3}{d_2}(e^{d_2\tau_1 - 1})A^* \\ A^* = \frac{p}{d_3 e^{d_1\tau_1 + d_2\tau_2}}\frac{mg^*}{1+ng^*} - q \\ g^* = K - \frac{Kf_1}{r}A^* - \frac{Kf_2}{r}N^* \end{cases}, \tag{3.13}$$

To start with, we need to prove the existence of a unique positive equilibrium provided $\mathcal{R}_0 > 1$, that is, (3.13) has a positive solution when $\mathcal{R}_0 > 1$.

Theorem 3.4.1 *If $\mathcal{R}_0 > 1$, (3.13) has a unique positive solution.*

Proof. To prove the existence of the positive equilibrium, it suffices to show that $A^*, g^* > 0$.

Since A^*, g^* follow the equation system

$$\begin{cases} -d_3 + \frac{mg^*}{1+ng^*}\frac{p}{q+A^*}e^{-d_1\tau_1 - d_2\tau_2} = 0 \\ K - \frac{Kf_1}{r}A^* - \frac{Kf_2}{r}\frac{d_3}{d_2}(e^{d_2\tau_2} - 1)A^* = g^* \end{cases}. \tag{3.14}$$

Substituting g^* into the first equation of system (3.14) gives rise to:

$$\frac{mK - m\frac{Kf_1}{r}A^* - m\frac{Kf_2}{r}\frac{d_3}{d_2}(e^{d_2\tau_2 - 1})A^*}{1 + nK - n\frac{Kf_1}{r}A^* - n\frac{Kf_2}{r}\frac{d_3}{d_2}(e^{d_2\tau_2 - 1})A^*}\frac{p}{q + A^*} = \frac{mKp}{(1 + nK)q\mathcal{R}_0}. \tag{3.15}$$

In equation (3.15), if $A^* = 0$, then the left-hand side of the equation equals $mKp/(1 + nK)q$, which is larger than $mKp/((1 + nK)q\mathcal{R}_0)$, provided $\mathcal{R}_0 > 1$. And if A^* is sufficiently large,

then the left-hand side of equation (3.15) approaches to zero, which is smaller than $mKp/((1 + nK)q\mathcal{R}_0)$. Since the left-hand side of equation (3.15) is a continuous and strictly decreasing function with respect to A^*, there exists a unique positive value of A^* that satisfies the equation (3.14).

Similarly, we can prove the existence, uniqueness and positivity of g^*. Hence, the existence and uniqueness of the positive equilibrium have been proven. ∎

The following theorem addresses the local asymptotical stability of the positive equilibrium.

Theorem 3.4.2 *The positive equilibrium E_2, if exists, is locally asymptotically stable when $d_2 = d_3$, $f_1 = f_2$, and $1 < \mathcal{R}_0 < \mathcal{R}^*$, where $\mathcal{R}^* \in (1, +\infty)$ is some constant.*

Proof. Before giving the analysis, we state the relations between $\mathcal{R}_0$ and g^* and A^*. Based on equation (3.14), we find that if $\mathcal{R}_0 \to 1$, $g^* \to K$, and $A^* \to 0$. In this theorem, to prove the local asymptotic stability, we will assume that $\mathcal{R}_0$ is bigger than one but very close to one; therefore, g^* is close to K, and A^* is close to zero. Also, in this theorem, we assume that τ_1 and τ_2 increase in a range that will ensure the existence of the positive equilibrium.

The characteristic equation of the linearized system at the positive equilibrium (E^*, N^*, A^*, g^*) is given by

$$|\lambda I - J_1 - J_2 e^{-\lambda \tau_1} - J_3 e^{-\lambda(\tau_1 + \tau_2)}| = 0,$$

where

$$J_1 = \begin{pmatrix} -d_1 & * & * & * \\ 0 & -d_2 & 0 & 0 \\ 0 & 0 & -d_3 & 0 \\ 0 & -f_2 g^* & -f_1 g^* & -\frac{rg^*}{K} \end{pmatrix},$$

$$J_2 = \begin{pmatrix} 0 & * & * & * \\ 0 & 0 & \frac{mg^*}{1+ng^*} \frac{q}{q+A^*} e^{-d_1 \tau_1} & \frac{m}{(1+ng^*)^2} \frac{pA^*}{q+A^*} e^{-d_1 \tau_1} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

$$J_3 = \begin{pmatrix} 0 & * & * & * \\ 0 & 0 & \frac{mg^*}{1+ng^*}\frac{q}{q+A^*}(-e^{-d_1\tau_1-d_2\tau_2}) & \frac{m}{(1+ng^*)^2}\frac{pA^*}{q+A^*}(-e^{-d_1\tau_1-d_2\tau_2}) \\ 0 & 0 & \frac{mg^*}{1+ng^*}\frac{q}{q+A^*}e^{-d_1\tau_1-d_2\tau_2} & \frac{m}{(1+ng^*)^2}\frac{pA^*}{q+A^*}e^{-d_1\tau_1-d_2\tau_2} \\ 0 & 0 & 0 & 0 \end{pmatrix}.$$

A simple calculation gives

$$|\lambda I - J_1 - J_2 e^{-\lambda\tau_1} - J_3 e^{-\lambda(\tau_1+\tau_2)}|$$
$$= (\lambda + d_1)\Bigg[(\lambda + d_2)\Bigg(\Big(\lambda + d_3 - \frac{d_3 q}{q + A^*}e^{-\lambda(\tau_1+\tau_2)}\Big)\Big(\lambda + \frac{rg^*}{K}\Big) + f_1\frac{1}{1+ng^*}d_3 A^* e^{-\lambda(\tau_1+\tau_2)}\Bigg)$$
$$+ f_2(\lambda + d_3)\frac{1}{1+ng^*}d_3 A^* \Big(e^{-\lambda\tau_1}e^{d_2\tau_2} - e^{-\lambda(\tau_1+\tau_2)}\Big)\Bigg],$$

since

$$\frac{mg^*}{1+ng^*}\frac{q}{q+A^*} = d_3 e^{d_1\tau_1+d_2\tau_2}.$$

Under the assumptions that $d_2 = d_3$ and $f_1 = f_2$, we obtain

$$|\lambda I - J_1 - J_2 e^{-\lambda\tau_1} - J_3 e^{-\lambda(\tau_1+\tau_2)}| = (\lambda + d_1)(\lambda + d_2)$$
$$\Bigg(\Big(\lambda + d_3 - \frac{d_3 q}{q + A^*}e^{-\lambda(\tau_1+\tau_2)}\Big)\Big(\lambda + \frac{rg^*}{K}\Big) + f_1\frac{1}{1+ng^*}d_3 A^* e^{d_2\tau_2-\lambda\tau_1}\Bigg)$$
$$= (\lambda + d_1)(\lambda + d_2)S(\lambda),$$

where

$$S(\lambda) = \Big(\lambda + d_3 - \frac{d_3 q}{q + A^*}e^{-\lambda(\tau_1+\tau_2)}\Big)\Big(\lambda + \frac{rg^*}{K}\Big) + f_1\frac{1}{1+ng^*}d_3 A^* e^{d_2\tau_2-\lambda\tau_1}. \qquad (3.16)$$

Therefore, the local stability of the positive equilibrium is determined by the roots of $S(\lambda)$. We will show that the other eigenvalues have negative real parts when $\mathcal{R}_0$ is larger than one but not very big.

When $\tau_1 = \tau_2 = 0$, equation (3.16) reduces to

$$
\begin{aligned}
S(\lambda) &= \left(\lambda + d_3 - \frac{d_3 q}{q + A^*}\right)\left(\lambda + \frac{rg^*}{K}\right) + f_1 \frac{1}{1 + ng^*} d_3 A^* \\
&= \lambda^2 + \left(\frac{rg^*}{K} + \frac{d_3 A^*}{q + A^*}\right)\lambda + \frac{rg^*}{K}\frac{d_3 A^*}{q + A^*} + f_1 A^* \frac{d_3}{1 + ng^*},
\end{aligned}
\tag{3.17}
$$

the roots of which have negative real parts since

$$
\frac{rg^*}{K} + \frac{d_3 A^*}{q + A^*} > 0,
$$
$$
\frac{rg^*}{K}\frac{d_3 A^*}{q + A^*} + f_1 A^* \frac{d_3}{1 + ng^*} > 0.
$$

Note that all roots of equation (3.16) depend continuously on τ_1 and τ_2. Therefore, as the delays increase, the roots of equation (3.16) can only enter the right-half in the complex plane by crossing the imaginary axis. Let $\lambda = iw$ with $w > 0$ be a pure imaginary root of equation (3.16), then

$$
S(\lambda) = \left(iw + d_3 - \frac{d_3 q}{q + A^*}e^{-iw(\tau_1 + \tau_2)}\right)\left(iw + \frac{rg^*}{K}\right) + f_1 \frac{1}{1 + ng^*} d_3 A^* e^{d_2 \tau_2 - iw\tau_1} = 0.
$$

Taking moduli in the above equation and grouping in terms of the powers of w give

$$
w^4 + \left(d_3^2 + \frac{r^2 g^{*2}}{K^2}\right)w^2 + \frac{d_3^2 r^2 g^{*2}}{K^2} = A^2 w^2 + B^2 + C^2 - 2ACw\sin(w\tau_2) - 2BC\cos(w\tau_2), \tag{3.18}
$$

where

$$
\begin{cases}
A = d_3(1 - \frac{q}{q+A^*}) \\
B = d_3(1 - \frac{q}{q+A^*})\frac{rg^*}{K} \\
C = f_1 A^* e^{d_3 \tau_2}\frac{d_3}{1+ng^*}
\end{cases}.
$$

Let

$$
S(w) = w^4 + \left(d_3^2 + \frac{r^2 g^{*2}}{K^2}\right)w^2 + \frac{d_3^2 r^2 g^{*2}}{K^2} - A^2 w^2 - B^2 - C^2 + 2ACw\sin(w\tau_2) + 2BC\cos(w\tau_2). \tag{3.19}
$$

As stated before, we assume $\mathcal{R}_0 > 1$ but is very close to one, which means $A^* \to 0$, $g^* \to K$;

therefore, A, B, and $C \to 0$. Along with the fact that $d_3^2 + (rg^*/K)^2 > A^2$, we have

$$S(w) > 0.$$

Therefore, there exists a constant $\mathcal{R}^* > 1$, such that, if $1 < \mathcal{R}_0 < \mathcal{R}^*$, $S(w)$ is always positive, which means that $S(w)$ has no positive roots. In other words, E_2 is locally asymptotically stable. ∎

Moreover, we can prove that the positive equilibrium is indeed globally attractive under certain conditions [2].

Theorem 3.4.3 *The positive equilibrium is globally attractive when*

$$\frac{Kf_1q}{r}(\mathcal{R}_0 - 1) + \frac{Kf_2}{r}\frac{mK}{1+nK}\frac{p(\mathcal{R}_0 - 1)}{\mathcal{R}_0}\left(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}\right) < \frac{(K+nK^2)(\mathcal{R}_0 - 1)}{\mathcal{R}_0 + nK(\mathcal{R}_0 - 1)}.$$

This condition is satisfied when $1 < \mathcal{R}_0 < \mathcal{R}^{**}$, where $\mathcal{R}^{**} \in (1, +\infty)$ is some constant, and when

$$\frac{f_1q}{r} - \frac{f_2p}{r}\frac{mK}{1+nK}\left(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}\right) < 1 + nK.$$

Proof. First of all, we will prove the last statement of Theorem 3.4.3. Let

$$p_1(\mathcal{R}_0) = \frac{Kf_1q}{r}(\mathcal{R}_0 - 1) + \frac{Kf_2}{r}\frac{mK}{1+nK}\frac{p(\mathcal{R}_0 - 1)}{\mathcal{R}_0}\left(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}\right),$$

$$p_2(\mathcal{R}_0) = \frac{(K+nK^2)(\mathcal{R}_0 - 1)}{\mathcal{R}_0 + nK(\mathcal{R}_0 - 1)}.$$

Therefore, $p_1(1) = p_2(1) = 0$. By taking the derivatives of p and q with respect to $\mathcal{R}_0$ at $\mathcal{R}_0 = 1$, we obtain

$$p'(1) = \frac{Kf_1q}{r} - \frac{Kf_2p}{r}\frac{mK}{1+nK}\left(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}\right),$$

$$q'(1) = K + nK^2.$$

If $p'(1) < q'(1)$, it ensures that in some neighborhood of $\mathcal{R}_0 = 1$, $p_1(\mathcal{R}_0) < p_2(\mathcal{R}_0) < K$, which means, there exists a constant $\mathcal{R}^{**} > 1$, the condition in Theorem 3.4.3 is satisfied when $1 < \mathcal{R}_0 < \mathcal{R}^{**}$.

Since the equation for $E(t)$ in (3.12) is decoupled with the rest equations, to prove the global attractivity of the positive equilibrium, which is $\lim_{t\to+\infty}(E(t), N(t), A(t), g(t))=(E^*, N^*, A^*, g^*)$,

it is sufficient to show that $\lim_{t \to +\infty}(N(t), A(t), g(t)) = (N^*, A^*, g^*)$. Let us denote

$$\bar{g} := \limsup_{t \to +\infty} g(t), \quad \bar{A} := \limsup_{t \to +\infty} A(t), \quad \bar{N} := \limsup_{t \to +\infty} N(t),$$

$$\underline{g} := \liminf_{t \to +\infty} g(t), \quad \underline{A} := \liminf_{t \to +\infty} A(t), \quad \underline{N} := \liminf_{t \to +\infty} N(t).$$

We have to prove that $\bar{g} = \underline{g} = g^*$, $\bar{A} = \underline{A} = A^*$, and $\bar{N} = \underline{N} = N^*$.

We proceed by constructing the sequences $\bar{g}_n, \bar{A}_n, \bar{N}_n$ of upper bounds

$$\bar{g} \leq \bar{g}_n, \bar{A} \leq \bar{A}_n, \bar{N} \leq \bar{N}_n,$$

which are strictly decreasing, and the sequences $\underline{g}_n, \underline{A}_n, \underline{N}_n$ of lower bounds

$$\underline{g} \geq \underline{g}_n, \underline{A} \geq \underline{A}_n, \underline{N} \geq \underline{N}_n,$$

which are strictly increasing, satisfying

$$
\begin{aligned}
\lim_{n \to +\infty} \underline{g}_n &= g^* = \lim_{n \to +\infty} \bar{g}_n, \\
\lim_{n \to +\infty} \underline{A}_n &= A^* = \lim_{n \to +\infty} \bar{A}_n, \\
\lim_{n \to +\infty} \underline{N}_n &= N^* = \lim_{n \to +\infty} \bar{N}_n.
\end{aligned}
\tag{3.20}
$$

Since $n \to +\infty$ implies that $t \to +\infty$, if relations (3.20) hold, then

$$\lim_{t \to +\infty}(N(t), A(t), g(t)) = (N^*, A^*, g^*).$$

In order to construct the above sequences, we start with

$$\limsup_{t \to +\infty} g(t) \leq K := \bar{g}_1.$$

From the third equation in system (3.12) and the fact that the birth rate of leafhoppers is an

increasing function with respect to adult population $A(t)$, it follows

$$\limsup_{t\to+\infty} A(t) \le \lim_{t\to+\infty} A(0)e^{-d_3 t}$$

$$+ e^{-d_1\tau_1-d_2\tau_2} \int_0^t \frac{m\limsup_{t\to+\infty} g(t-\theta)}{1+n\limsup_{t\to+\infty} g(t-\theta)} \frac{p\limsup_{t\to+\infty} A(t-\theta)}{q+\limsup_{t\to+\infty} A(t-\theta)} e^{d_3(t-\theta)} d\theta$$

$$= e^{-d_1\tau_1-d_2\tau_2} \int_0^t \frac{mK}{1+nK} \frac{p\limsup_{t\to+\infty} A(t)}{q+\limsup_{t\to+\infty} A(t)} e^{d_3(t-\theta)} d\theta.$$

Canceling $\limsup_{t\to+\infty} A(t)$, it is immediately obtained that

$$\bar{A} \le q(\mathcal{R}_0 - 1) := \bar{A}_1.$$

From the second equation in system (3.12), we define $\bar{N}_1$ to be:

$$\bar{N}_1 = \frac{mK}{(1+nK)d_2} \frac{p\bar{A}_1}{q+\bar{A}_1} (e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}).$$

Then from the first equation in system (3.12),

$$\frac{dg}{dt} = rg \left(1 - \frac{g}{K} - \frac{f_1}{r}A - \frac{f_2}{r}N\right),$$

which is a logistic equation. Based on the property of the logistic equation, and the comparison principle, we obtain that

$$\underline{g}_1 = K - \frac{Kf_1}{r}\bar{A}_1 - \frac{Kf_2}{r}\bar{N}_1.$$

The third equation and fourth equation in system (3.12) give

$$\underline{A}_1 = \frac{m\underline{g}_1}{1+n\underline{g}_1} \frac{p}{d_3 e^{d_1\tau_1+d_2\tau_2}} - q,$$

$$\underline{N}_1 = \frac{m\underline{g}_1}{1+n\underline{g}_1} \frac{p\underline{A}_1}{(q+\underline{A}_1)d_2} (e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}).$$

Moving back to the first equation in system (3.12), it follows that, when t is sufficiently

large, for any positive value δ

$$\frac{dg}{dt} = g\left(r - \frac{r}{K}g - f_1 A - f_2 N\right)$$
$$\leq (K + \delta)\left(r - \frac{r}{K}g - f_1 A - f_2 N\right);$$

we define

$$\bar{g}_2 = K - \frac{Kf_1}{r}\underline{A}_1 - \frac{Kf_2}{r}\underline{N}_1.$$

By iterating the above procedure, we obtain six sequences $\{\bar{g}_n\}$, $\{\underline{g}_n\}$, $\{\bar{A}_n\}$, $\{\underline{A}_n\}$, $\{\bar{N}_n\}$ and $\{\underline{N}_n\}$, $n \in \mathbb{N}$, with elements

$$\begin{cases} \bar{g}_n = K - \frac{Kf_1}{r}\underline{A}_{n-1} - \frac{Kf_2}{r}\underline{N}_{n-1} & n \geq 2 \\ \underline{g}_n = K - \frac{Kf_1}{r}\bar{A}_n - \frac{Kf_2}{r}\bar{N}_n & n \geq 1 \end{cases}, \tag{3.21}$$

where $\bar{g}_1 = 1$. And for $n \geq 1$,

$$\begin{cases} \bar{A}_n = \frac{m\bar{g}_n}{1+n\bar{g}_n}\frac{p}{d_3 e^{d_1\tau_1+d_2\tau_2}} - q \\ \underline{A}_n = \frac{m\underline{g}_n}{1+n\underline{g}_n}\frac{p}{d_3 e^{d_1\tau_1+d_2\tau_2}} - q \end{cases}, \tag{3.22}$$

$$\begin{cases} \bar{N}_n = \frac{m\bar{g}_n}{1+n\bar{g}_n}\frac{p\bar{A}_n}{(q+\bar{A}_n)d_2}(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}) \\ \underline{N}_n = \frac{m\underline{g}_n}{1+n\underline{g}_n}\frac{p\underline{A}_n}{(q+\underline{A}_n)d_2}(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}) \end{cases}, \tag{3.23}$$

Notice that

$$\begin{cases} \underline{g}_1 = K - \frac{Kf_1 q}{r}(\mathcal{R}_0 - 1) - \frac{Kf_2}{r}\frac{mK}{1+nK}\frac{p(\mathcal{R}_0-1)}{\mathcal{R}_0}\left(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}\right) > 0 \\ \underline{A}_1 = \frac{m\underline{g}_1}{1+n\underline{g}_1}\frac{p}{d_3 e^{d_1\tau_1+d_2\tau_2}} - q > 0 \end{cases}, \tag{3.24}$$

since

$$\frac{Kf_1 q}{r}(\mathcal{R}_0 - 1) + \frac{Kf_2}{r}\frac{mK}{1+nK}\frac{p(\mathcal{R}_0 - 1)}{\mathcal{R}_0}\left(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}\right) < \frac{(K + nK^2)(\mathcal{R}_0 - 1)}{\mathcal{R}_0 + nK(\mathcal{R}_0 - 1)} < K.$$

One can easily obtain that $\{\bar{g}_n\}$, $\{\bar{A}_n\}$, and $\{\bar{N}_n\}$, $n \in \mathbb{N}$, are strictly decreasing, and $\{\underline{g}_n\}$, $\{\underline{A}_n\}$, and $\{\underline{N}_n\}$, $n \in \mathbb{N}$, are strictly increasing.

For the sequence $\{\bar{g}_n\}$, since it is decreasing and bounded, there exists $\lim_{t\to+\infty} \bar{g}_n$. For the

sake of simplicity, we define

$$\bar{A}_n = \frac{m\bar{g}_n}{1 + n\bar{g}_n} \frac{p}{d_3 e^{d_1\tau_1 + d_2\tau_2}} - q = X(\bar{g}_n).$$

Based on equations (3.21), (3.22), and (3.23), we are able to get a recurrence relation for $\bar{g}_n$:

$$\bar{g}_{n+1} = K - \frac{Kf_1}{r} \left(\frac{m\left(K - \frac{Kf_1}{r}X(\bar{g}_n) - \frac{Kf_2}{r}\frac{m\bar{g}_n}{1+n\bar{g}_n}\frac{pX(\bar{g}_n)}{d_2(q+X(\bar{g}_n))}(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2})\right)}{1 + n\left(K - \frac{Kf_1}{r}X(\bar{g}_n) - \frac{Kf_2}{r}\frac{m\bar{g}_n}{1+n\bar{g}_n}\frac{pX(\bar{g}_n)}{d_2(q+X(\bar{g}_n))}(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2})\right)} \frac{p}{d_3 e^{d_1\tau_1+d_2\tau_2}} - q \right)$$

$$- \frac{Kf_2}{rd_2} \left(\frac{pm\left(K - \frac{Kf_1}{r}X(\bar{g}_n) - \frac{Kf_2}{r}\frac{m\bar{g}_n}{1+n\bar{g}_n}\frac{pX(\bar{g}_n)}{d_2(q+X(\bar{g}_n))}(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2})\right)}{1 + n\left(K - \frac{Kf_1}{r}X(\bar{g}_n) - \frac{Kf_2}{r}\frac{m\bar{g}_n}{1+n\bar{g}_n}\frac{pX(\bar{g}_n)}{d_2(q+X(\bar{g}_n))}(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2})\right)} - qd_3 e^{d_1\tau_1+d_2\tau_2} \right)$$

$$\times (e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}).$$

$$(3.25)$$

It is natural to try $\lim_{n\to+\infty} \bar{g}_n = g^*$; then

$$\lim_{n\to+\infty} X(\bar{g}_n) = \lim_{n\to+\infty} \frac{m\bar{g}_n}{1 + n\bar{g}_n} \frac{p}{d_3 e^{d_1\tau_1+d_2\tau_2}} - q = A^*, \tag{3.26}$$

$$\lim_{n\to+\infty} \frac{m\bar{g}_n}{1 + n\bar{g}_n} \frac{pX(\bar{g}_n)}{d_2(q + X(\bar{g}_n))}(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}) = \frac{d_3}{d_2}(e^{d_2\tau_2} - 1)A^* = N^*, \tag{3.27}$$

and

$$K - \frac{Kf_1}{r}g^* - \frac{Kf_2}{r}N^* = g^*. \tag{3.28}$$

By taking the limits on both sides of equation (3.25) and using relations (3.26), (3.27) and (3.28), we have

$$g^* = K - \frac{Kf_1}{r} \left(\frac{m\left(K - \frac{Kf_1}{r}g^* - \frac{Kf_2}{r}N^*\right)}{1 + n\left(K - \frac{Kf_1}{r}g^* - \frac{Kf_2}{r}N^*\right)} \frac{p}{d_3 e^{d_1\tau_1+d_2\tau_2}} - q \right)$$

$$- \frac{Kf_2}{rd_2} \left(\frac{pm\left(K - \frac{Kf_1}{r}g^* - \frac{Kf_2}{r}N^*\right)}{1 + n\left(K - \frac{Kf_1}{r}g^* - \frac{Kf_2}{r}N^*\right)} - qd_3 e^{d_1\tau_1+d_2\tau_2} \right)(e^{-d_1\tau_1} - e^{-d_1\tau_1-d_2\tau_2}) \tag{3.29}$$

$$= K - \frac{Kf_1}{r} \left(\frac{mg^*}{1 + ng^*} \frac{p}{d_3 e^{d_1\tau_1+d_2\tau_2}} - q \right) - \frac{Kf_2}{r}\frac{d_3}{d_2}(e^{d_2\tau_2} - 1)A^*$$

$$= K - \frac{Kf_1}{r}A^* - \frac{Kf_2}{r}N^*,$$

which is immediately satisfied. Therefore,

$$\lim_{n \to +\infty} \bar{g}_n = g^*.$$

Similarly,

$$\lim_{n \to +\infty} \underline{g}_n = g^*,$$

$$\lim_{n \to +\infty} \bar{A}_n = \lim_{n \to +\infty} \underline{A}_n = A^*,$$

$$\lim_{n \to +\infty} \bar{N}_n = \lim_{n \to +\infty} \underline{N}_n = N^*.$$

Therefore, we obtain

$$\bar{g} = \underline{g} = g^*,$$

$$\bar{A} = \underline{A} = A^*,$$

$$\bar{N} = \underline{N} = N^*.$$

Hence, we have proven the global attractivity of the positive equilibrium. ∎

Summarizing Theorem 3.4.2 and Theorem 3.4.3, we obtain the following theorem.

Theorem 3.4.4 *The positive equilibrium is globally asymptotically stable when* $1 < \mathcal{R}_0 < \min\{\mathcal{R}^*, \mathcal{R}^{**}\}$, $f_1 = f_2$, $d_2 = d_3$, *and*

$$\frac{f_1 q}{r} - \frac{f_2 p}{r} \frac{mK}{1 + nK} \left(e^{-d_1 \tau_1} - e^{-d_1 \tau_1 - d_2 \tau_2} \right) < 1 + nK.$$

Numerical simulation

In this sub-section, we present some numerical simulations to verify the theoretical results.

1. When $\mathcal{R}_0 < 1$, the insect-free equilibrium is globally asymptotically stable, implying that the insect population cannot establish. See Figure 3.1.
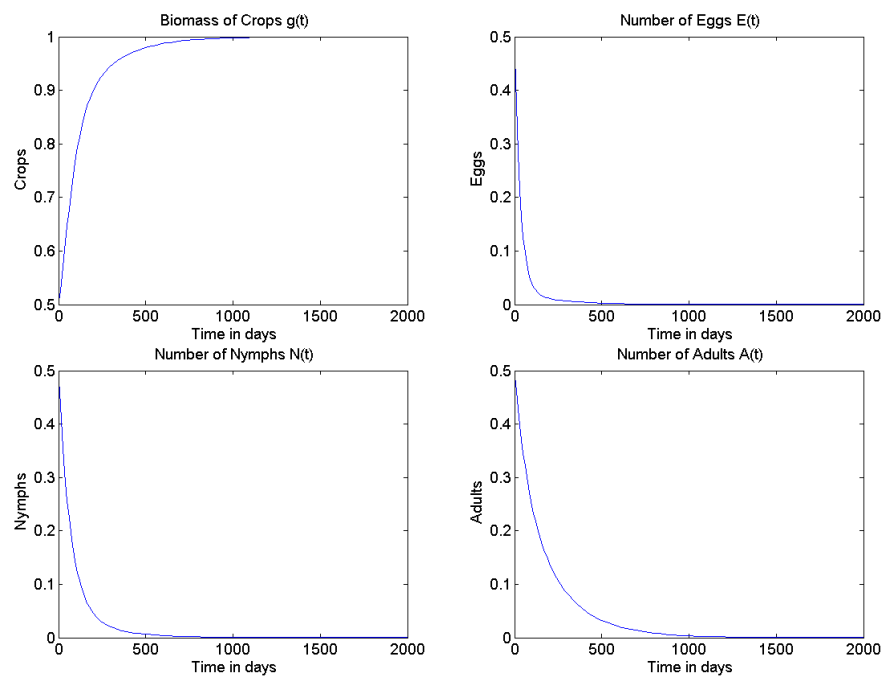
Figure 3.1: The insect population cannot persist. The simulations are done with the following parameter values: $m = 1$, $n = 1$, $f_1 = 0.02$, $f_2 = 0.01$, $p = 0.02$, $q = 1$, $d_1 = 0.03$, $d_2 = 0.015$, $d_3 = 0.01$, $r = 0.01$, $K = 1$, $\tau_1 = 10$, and $\tau_2 = 20$; and initial conditions: $(g(0), E(0), N(0), A(0)) = (0.5, 0.5, 0.5, 0.5)$.

2. When $\mathcal{R}_0 > 1$, the positive equilibrium is locally asymptotically stable (even when $\mathcal{R}_0$ is very large), meaning the population dynamics of leafhoppers and crops will approach a steady state eventually. See Figure 3.2.
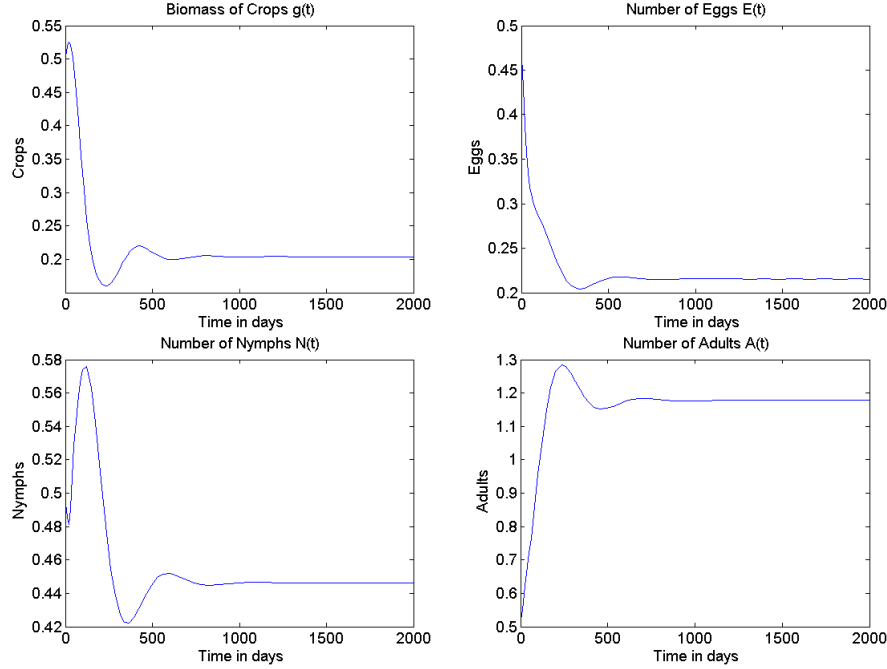

Figure 3.2: The insect population will persist and will approach the positive equilibrium. The simulations are done with the following parameter values: $m = 1$, $n = 1$, $f_1 = 0.02$, $f_2 = 0.01$, $p = 0.2$, $q = 1$, $d_1 = 0.03$, $d_2 = 0.015$, $d_3 = 0.01$, $r = 0.01$, $K = 1$, $\tau_1 = 10$, and $\tau_2 = 20$, and initial conditions: $(g(0), E(0), N(0), A(0)) = (0.5, 0.5, 0.5, 0.5)$.

3.4.2 Case 2

In this case, we investigate a scenario when

$$b(A(t), g(t)) = \frac{mg(t)}{1 + ng(t)} b_0 e^{-cA(t)},$$

where b_0 is the intrinsic birth rate of leafhoppers and c denotes the self-limitation effects within leafhoppers. Here, birth function $b(g, A)$ is the famous Ricker function [7]. h_1, h_2 and G remain the same with those in Case §1. In this situation, $b(A(t), g(t))A(t)$ is no longer an increasing function with respect to the adult population $A(t)$; rather, $b(A(t), g(t))A(t)$ is a bell-shape function with respect to $A(t)$.

In this case, the population dynamics are modeled by the following DDEs:

$$
\begin{cases}
\frac{dE(t)}{dt} = -d_1 E(t) + \frac{mg(t)}{1+ng(t)} b_0 e^{-cA(t)} A(t) - \frac{mg(t-\tau_1)}{1+ng(t-\tau_1)} b_0 e^{-cA(t-\tau_1)} A(t-\tau_1) e^{-d_1 \tau_1} \\
\frac{dN(t)}{dt} = -d_2 N(t) + \frac{mg(t-\tau_1)}{1+ng(t-\tau_1)} b_0 e^{-cA(t-\tau_1)} A(t-\tau_1) e^{-d_1 \tau_1} \\
\qquad\quad - \frac{mg(t-\tau_1-\tau_2)}{1+ng(t-\tau_1-\tau_2)} b_0 e^{-cA(t-\tau_1-\tau_2)} A(t-\tau_1-\tau_2) e^{-d_1\tau_1-d_2\tau_2} \\
\frac{dA(t)}{dt} = -d_3 A(t) + \frac{mg(t-\tau_1-\tau_2)}{1+ng(t-\tau_1-\tau_2)} b_0 e^{-cA(t-\tau_1-\tau_2)} A(t-\tau_1-\tau_2) e^{-d_1\tau_1-d_2\tau_2} \\
\frac{dg(t)}{dt} = r\left(1 - \frac{g(t)}{K}\right) g(t) - f_1 g(t) A(t) - f_2 g(t) N(t)
\end{cases}
\qquad . \qquad (3.30)
$$

As with the general model, the trivial equilibrium E_0 is always unstable. The insect-free equilibrium E_1 is globally asymptotically stable when

$$
\mathcal{R}_0 = \frac{mKb_0}{(1+nK)d_3 e^{d_1\tau_1+d_2\tau_2}} < 1,
$$

and unstable when $\mathcal{R}_0 > 1$. A similar method with Case §1 shows that when $\mathcal{R}_0 > 1$, a positive equilibrium E_2 occurs, and is locally asymptotically stable when $1 < \mathcal{R}_0 < \mathcal{R}_0^*$, where $\mathcal{R}_0^* \in (1, +\infty)$ is some constant. However, the analysis of global behaviours of the positive equilibrium is a challenging question. Instead of giving an analytical analysis, we present some simulation results. And we can see from Figure 3.4, when $\mathcal{R}_0 > 1$ but is smaller than a threshold value, E_2 is locally (even globally) asymptotically stable. However, when $\mathcal{R}_0$ is sufficiently large, unlike Case §1 where E_2 is still asymptotically stable, E_2 loses its stability since periodic solutions take over. This phenomenon indicates the existence of a threshold value of $\mathcal{R}_0$, below which the positive equilibrium is asymptotically stable, and above which the positive equilibrium is no longer asymptotically stable.

Numerical Simulation

The following numerical simulations are given.

1. When $\mathcal{R}_0 < 1$, the insect-free equilibrium is globally asymptotically stable, implying that the insect population cannot establish. See Figure 3.3.
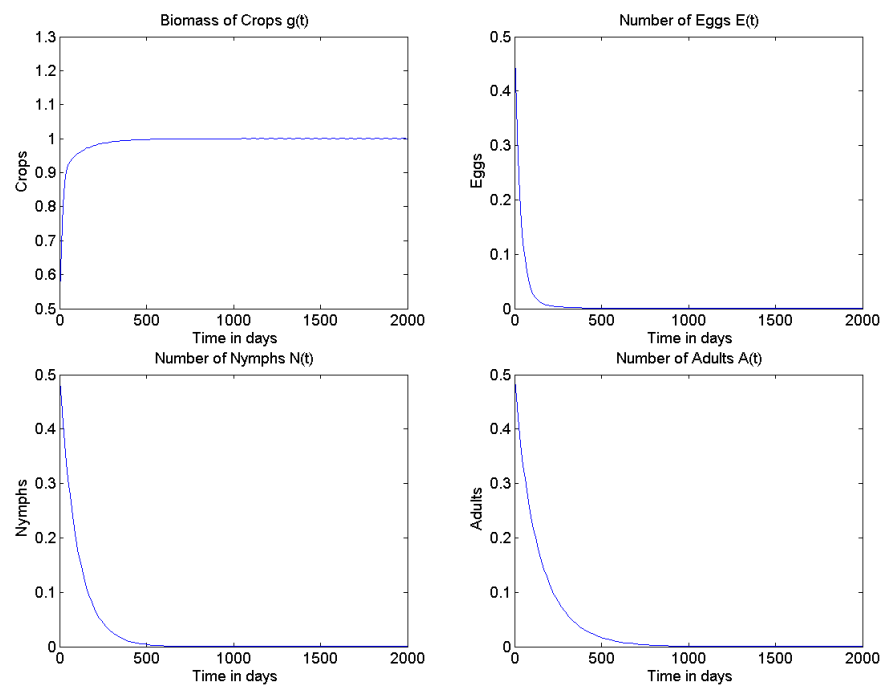
Figure 3.3: The insect population cannot persist. The simulations are done with the following parameter values: $m = 1$, $n = 1$, $f_1 = 0.02$, $f_2 = 0.01$, $c = 1$, $b_0 = 0.08$, $d_1 = 0.03$, $d_2 = 0.015$, $d_3 = 0.01$, $r = 0.01$, $K = 1$, $\tau_1 = 10$, and $\tau_2 = 10$; and initial conditions: $(g(0), E(0), N(0), A(0)) = (0.5, 0.5, 0.5, 0.5)$.

2. When $\mathcal{R}_0 > 1$, but is not very large, then the positive equilibrium is locally asymptotically stable, meaning the population dynamics of leafhoppers and crops will approach a steady state eventually. See Figure 3.4.
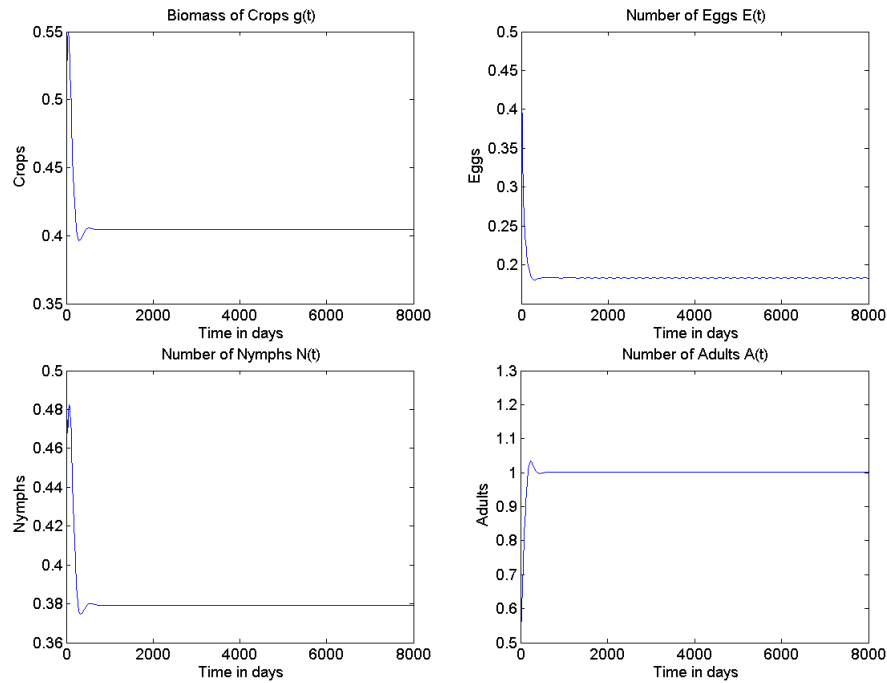

Figure 3.4: The insect population will persist and will approach the positive equilibrium. The simulations are done with the following parameter values: $m = 1$, $n = 1$, $f_1 = 0.02$, $f_2 = 0.01$, $c = 1$, $b_0 = 0.4$, $d_1 = 0.03$, $d_2 = 0.015$, $d_3 = 0.01$, $r = 0.01$, $K = 1$, $\tau_1 = 30$, and $\tau_2 = 40$, and initial conditions: $(g(0), E(0), N(0), A(0)) = (0.5, 0.5, 0.5, 0.5)$.

3. When $\mathcal{R}_0$ is sufficiently large (achieved by decreasing the values of τ_1 and τ_2), the positive equilibrium loses its stability, and oscillatory solutions appear. See Figure 3.5.
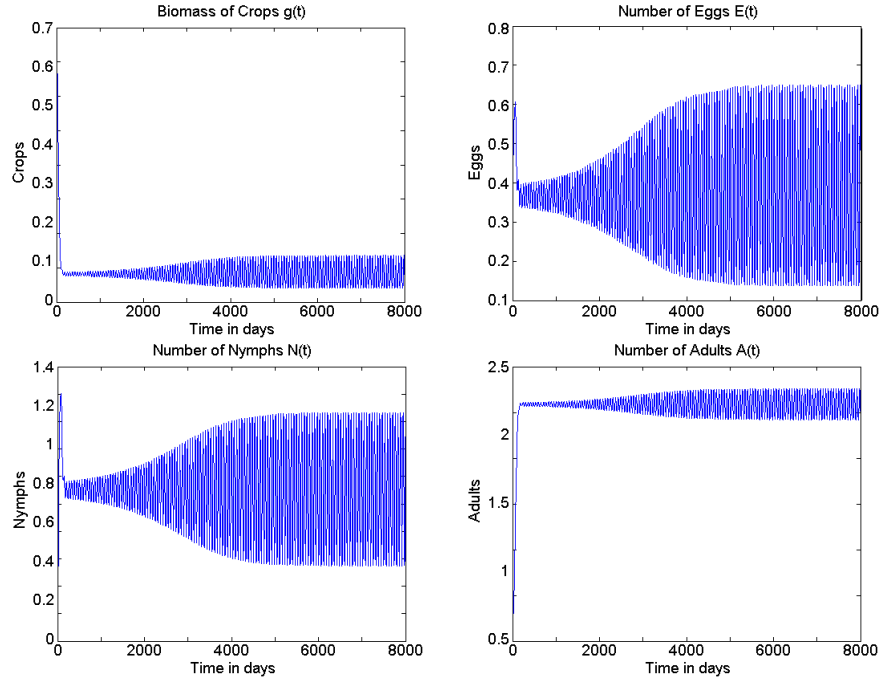

Figure 3.5: Periodic phenomenon appears. The simulations are done with the following parameter values: $m = 1$, $n = 1$, $f_1 = 0.02$, $f_2 = 0.01$, $c = 1$, $b_0 = 0.4$, $d_1 = 0.03$, $d_2 = 0.015$, $d_3 = 0.01$, $r = 0.01$, $K = 1$, $\tau_1 = 10$, and $\tau_2 = 10$; and initial conditions: $(g(0), E(0), N(0), A(0)) = (0.5, 0.5, 0.5, 0.5)$.

3.5 Discussion and Future Work

In this chapter, we construct a delay differential equations system based on the normal age structure to investigate the influence that each life stage of leafhoppers imposes to crops. Our model only applies to a large scale isolated environment, outside of which leafhoppers cannot travel, and inside of which diseases are not involved. Previous models concerning leafhoppers mainly focus on environmental effects, such as temperature and moisture [3, 5, 15]. However, few models have been advanced to study the interactions between leafhoppers and crops, and more specifically, how each life period of the leafhopper affects crops [14]. It is of vital significance to investigate the mutual effects since they would contribute to a better management of the potential damage that might be caused by leafhoppers.

The models we have proposed provide some useful insights. For the general model, we conclude that the trivial equilibrium is always unstable. It is found that the crop biomass grows exponentially at the trivial equilibrium. Besides, the insect-free equilibrium is globally asymptotically stable when $\mathcal{R}_0 < 1$. In other words, if the reproduction ability of leafhoppers is very low (characterized by the basic reproduction number $\mathcal{R}_0$), the leafhopper population will eventually go extinct. When $\mathcal{R}_0 > 1$, the positive equilibrium occurs. To study the qualitative behaviours of this equilibrium, we investigate two special cases based on the monotonicity of the birth rate of leafhoppers. If the birth rate is an increasing function with respect to the adult population, the positive equilibrium is globally asymptotically stable if $\mathcal{R}_0$ is close to one. However, the system exhibits rich dynamics, if we choose the birth rate to be a bell-shape function with respect to the adult population. If $\mathcal{R}_0$ is close to 1, simulations suggest that the positive equilibrium is locally asymptotically stable. The positive equilibrium loses its stability if $\mathcal{R}_0$ is sufficiently large since periodic solutions come into play. Both cases suggest that the insect population will establish.

Simulations have suggested that, for the special case 1, when $\mathcal{R}_0$ is very large, the positive equilibrium remains asymptotically stable, which implies that the conditions in Theorem 3.4.4, which are technical, may be unnecessary for the global stability of the positive equilibrium. However, for the second case, our simulations have captured the oscillatory phenomenon as $\mathcal{R}_0$ grows large. This indicates that the monotonicity of the birth rate of leafhoppers with respect to the adult population plays a very important role in affecting the qualitative behaviours of the system, thus suggesting a study topic on modeling the relation between the birth rate of leafhoppers and adult population.

In this model, the lengths of the hatching and maturation processes determine whether the insect population will thrive or not. Based on the formula of $\mathcal{R}_0$, we find that the increased delays have a negative impact on the establishment of the insect population by deceasing the value of $\mathcal{R}_0$ in an exponential fashion, which is further verified by the simulations. As we choose small values of latencies, simulations show that the population will spread; otherwise, the population will eventually die out. To explain it, if the hatching and maturation periods are very long, much less adult leafhoppers will survive the periods; thus, the population cannot establish.

The model has provided some implications on how to control the pest population. First of all, as suggested by Remark 3.3.2, it is more efficient to control the pest population by applying insecticides that are specific to nymphs. The idea behind this is to get rid of nymphs

as much as possible, which will decease the value of $\mathcal{R}_0$ the fastest. Moreover, the second specific case suggests an oscillatory phenomenon. A thorough analysis would provide people with knowledge of when the leafhopper population reaches the lower peak, and how to manage the insect population so as to keep it low. In addition, it is known that temperature and moisture have great impacts on the lengths of leafhopper hatching and maturation processes [3, 5, 6, 15]. Based on the data records on temperature and moisture, we can get the approximate values of the hatching and maturation lengths [3, 15, 16]. According to the values, we can then estimate whether the leafhoppers will break out, or if so, at what level. The idea is to calculate the value of $\mathcal{R}_0$ to see if $\mathcal{R}_0 > 1$ and how large this value is.

Despite of the results we have obtained, there are some aspects that can be improved in this model. First of all, we have assumed that stage lengths of leafhoppers are all constant and identical. It is biologically more reasonable to consider different and non-constant delays for both hosts and vectors due to the variations of climate and geographic conditions; for example, the hatching length of leafhoppers is greatly affected by temperature and moisture.

Secondly, for Case §1, it is of interest to investigate the global asymptotical stability when $\mathcal{R}_0$ is large, as implied by the simulations. The Lyapunov methods have been very useful; however the construction of an appropriate Lyapunov functional requires substantial efforts.

Moreover, for Case §2, more efforts can be made to find the threshold value of $\mathcal{R}_0$, below which the positive equilibrium is globally asymptotically stable, and above which the positive equilibrium loses its stability. Mathematically, it requires us to prove the existence of a Hopf-bifurcation, which has been suggested by the simulations.

Finally, we can add diseases into the model. To build the model, diagram 3.6 showing the interactions between different stages of leafhoppers will be helpful to understand the process. Here, subscript 1 denotes the susceptible class, and subscript 2 denotes the infectious class.
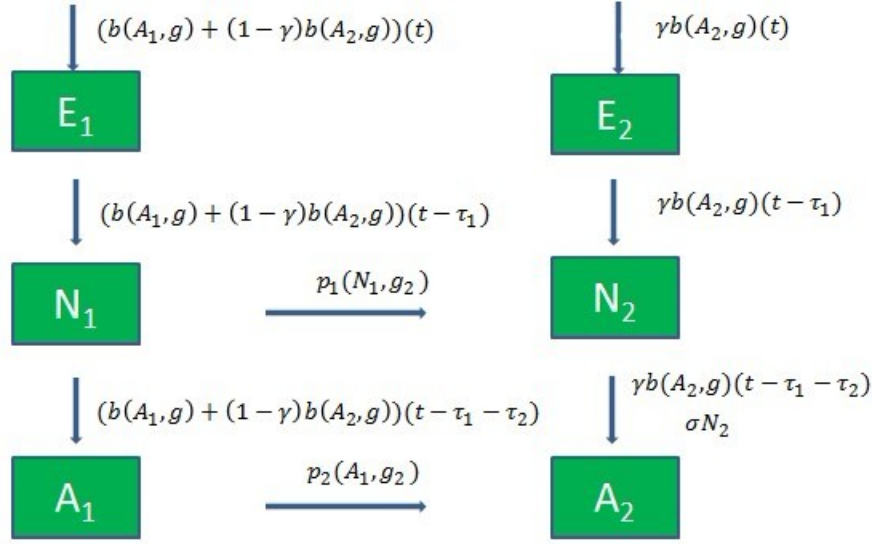
Figure 3.6: How different life stages of leafhoppers transmit diseases.

The general model is as follows:

$$
\begin{cases}
\frac{dE_1(t)}{dt} = b(A_1(t), g(t))A(t) + (1-\gamma)b(A_2(t), g(t))A(t) - b(A_1(t-\tau_1), g(t-\tau_1))A_1(t-\tau_1)e^{-d_{11}\tau_1} \\
\qquad - (1-\gamma)b(A_2(t-\tau_1), g(t-\tau_1))A_2(t-\tau_1)e^{-d_{21}\tau_1} - d_{11}E_1 \\
\frac{dE_2(t)}{dt} = \gamma b(A_2(t), g(t))A_2(t) - \gamma b(A_2(t-\tau_1), g(t-\tau_1))A_2(t-\tau_1)e^{-d_{21}\tau_1} - d_{12}E_2 \\
\frac{dN_1(t)}{dt} = b(A_1(t-\tau_1), g(t-\tau_1))A_1(t-\tau_1)e^{-d_{11}\tau_1} \\
\qquad + (1-\gamma)b(A_2(t-\tau_1), g(t-\tau_1))A_2(t-\tau_1)e^{-d_{21}\tau_1} - p_1(N_1, g_2) \\
\qquad - b(A_1(t-\tau_1-\tau_2), g(t-\tau_1-\tau_2))A_1(t-\tau_1-\tau_2)e^{-d_{11}\tau_1-d_{21}\tau_2} - d_{21}N_1 \\
\qquad - (1-\gamma)b(A_2(t-\tau_1-\tau_2), g(t-\tau_1-\tau_2))A_2(t-\tau_1-\tau_2)e^{-d_{12}\tau_1-d_{22}\tau_2} \\
\frac{dN_2(t)}{dt} = \gamma b(A_2(t-\tau_1), g(t-\tau_1))A_2(t-\tau_1)e^{-d_{21}\tau_1} + p_1(N_1, g_2) - \sigma N_2 - d_{22}N_2 \\
\qquad - \gamma b(A_2(t-\tau_1-\tau_2), g(t-\tau_1-\tau_2))A_2(t-\tau_1-\tau_2)e^{-d_{21}\tau_1-d_{22}\tau_2} \\
\frac{dA_1(t)}{dt} = b(A_1(t-\tau_1-\tau_2), g(t-\tau_1-\tau_2))A_1(t-\tau_1-\tau_2)e^{-d_{12}\tau_1-d_{22}\tau_2} - p_2(A_1, g_2) - d_{31}A_1 \\
\qquad + (1-\gamma)b(A_2(t-\tau_1-\tau_2), g(t-\tau_1-\tau_2))A_2(t-\tau_1-\tau_2)e^{-d_{21}\tau_1-d_{22}\tau_2} \\
\frac{dA_2(t)}{dt} = \gamma b(A_2(t-\tau_1-\tau_2), g(t-\tau_1-\tau_2))A_2(t-\tau_1-\tau_2)e^{-d_{21}\tau_1-d_{22}\tau_2} + p_2(A_1, g_2) \\
\qquad + \sigma N_2 - d_{32}A_2 \\
\frac{dg_1(t)}{dt} = G(g_1(t))g_1(t) - f_1(N(t), g_1(t))N(t) - f_2(A(t), g_1(t))A(t) - p_3(N_2(t), g_1(t)) \\
\qquad - p_4(A_2(t), g_1(t)) \\
\frac{dg_2(t)}{dt} = G(g_2(t))g_2(t) + p_3(N_2(t), g_1(t)) + p_4(A_2(t), g_1(t)) - f_1(N(t), g_2(t))N(t) \\
\qquad - f_2(A(t), g_2(t))A(t) - d_4 g_2(t)
\end{cases}
,
$$

$$(3.31)$$

where $N(t) = N_1(t) + N_2(t)$, $A(t) = A_1(t) + A_2(t)$ and $g(t) = g_1(t) + g_2(t)$; γ is the rate of transovarial transmission, which is the proportion of the infected newborns whose parents are infected; $p_i(x, y)$ $(i = 1, 2, 3, 4)$ are the infection terms.

We retain the function assumptions in Section 3.2 and add some additional assumptions. The infection functions $p_i(x, y)$ $(i = 1, 2, 3, 4)$ follow the rules:

A41) $p_i(x(t), y(t)) \geq 0$ for $x(t), y(t) \geq 0$, $i = 1, 2, 3, 4$.

A42) $p_i(x(t), y(t))$, $i = 1, 2, 3, 4$, are continuously differentiable with

$$\frac{\partial p_i(x, y)}{\partial x} \geq 0, \qquad \frac{\partial p_i(x, y)}{\partial y} \geq 0.$$

A43) $p_i(\cdot, 0) = 0$ and $p_i(0, \cdot) = 0$, $i = 1, 2, 3, 4$.

Well-posedness (i.e. positivity and boundedness) of system (3.31) can be easily proven. Unfortunately, a further analysis of the stability of the equilibria becomes very complicated. However, this model is of great interest to study since it shows that how different life stages of leafhoppers affect the transmission of diseases, facilitating pest management.

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Chapter 4

Summary and Future Work

4.1 Summary

Based on the age structure approaches [1, 3], two different models are proposed focusing on the interactions between leafhoppers and crops. Disease latencies in both leafhoppers and crops and different life periods of leafhoppers are considered.

In Chapter §2, we derive a model that incorporates disease latencies in both leafhoppers and crops. For the general model, the well-posedness of the model is verified and the local stability of the insect-free equilibrium is discussed. To deepen our understanding on the subject, we choose a specific model to analyze. We compute the basic reproduction number $\mathcal{R}_0$, and show that when this number is less than one, the leafhopper population eventually dies out, in the sense that the insect-free equilibrium is globally asymptotically stable; when the reproduction number is greater than one, the insect-free equilibrium is no longer stable. Under this circumstance, the insect population establishes and, moreover, if $\mathcal{R}_1 < 1$, the disease-free equilibrium is locally asymptotically stable. When $\mathcal{R}_1 > 1$, the disease-free equilibrium loses its stability. By employing the persistence theory [2, 4], it is proven that the disease persists and a positive equilibrium appears.

In Chapter §3, we aim to investigate the effects that each life stage of leafhoppers poses on crops. To start with, a general delay differential equations system is proposed. We verify the positivity and boundedness of the system as well as prove the global stability of the insect-free equilibrium when $\mathcal{R}_0 < 1$, which means that leafhoppers eventually goes extinct. When $\mathcal{R}_0 > 1$, the insect-free equilibrium is no longer stable and the positive equilibrium shows up. To further the understanding of the model, we investigate two special cases. If the birth rate

of leafhoppers is an increasing function with respect to the adult population, the population of both leafhoppers and crops approach to a steady state, the positive equilibrium, if $\mathcal{R}_0$ is close to one. Simulations have suggested that the positive equilibrium is still asymptotically stable even if $\mathcal{R}_0$ is large. The system exhibits different behaviours if the birth rate the leafhoppers is a bell-shape function with respect to the adult population. Simulations show that if $\mathcal{R}_0$ is close to one, the positive equilibrium is asymptotically stable. However, the positive equilibrium loses its stability if $\mathcal{R}_0$ grows sufficiently large since periodic solutions take over.

4.2 Future Work

As mentioned in the discussion part of each chapter, there are still some interesting but challenging problems that remain open and are worth exploring in the future.

For the specific model in Chapter §2, we do not obtain the global stability of the disease-free equilibrium and the positive equilibrium. Our simulations seem to suggest that both the disease-free equilibrium and the positive equilibrium are globally asymptotically stable under certain conditions. Therefore, it is interesting to work on the global stability of both equilibria. Moreover, a patch model can be introduced to investigate the disease transmission between different regions.

In Chapter §3, for Case §1, the global asymptotical stability, when $\mathcal{R}_0$ is large, is of interest to investigate. For Case §2, the threshold value of $\mathcal{R}_0$, below which the positive equilibrium is globally asymptotically stable and above which the positive equilibrium loses its stability, needs to be determined. Besides, diseases can be incorporated into the model so that it allows us to investigate how different life stages of leafhoppers transmit diseases.

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Appendix A

Proofs of Theorems

A.1   Proof of the existence and local stability of the positive equilibrium of system (2.30)

To prove the existence of the positive equilibrium, we need to show that

$$
\begin{cases}
\dfrac{mX_{12}+m\frac{\beta\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+m\delta+m\epsilon}{1+nX_{12}+n\frac{\beta\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+n\delta+n\epsilon}be^{-aX_{11}}\left(X_{11}+(1-\alpha_1)\left(\dfrac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta\right)+(1-\gamma_1)\epsilon\right)-d_1X_{11}=0 \\
r\left(1-\dfrac{X_{12}}{K}\right)\left(X_{12}+(1-\alpha_2)\left(\dfrac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta\right)+(1-\gamma_2)\epsilon\right)-\alpha X_{11}X_{12}=0
\end{cases} \tag{A.1}
$$

has positive solutions. To simplify the calculation, let us denote

$$
p_1(\epsilon,\delta)=\frac{\beta\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta+\epsilon,
$$

$$
p_2(\epsilon,\delta)=(1-\alpha_1)\left(\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta\right)+(1-\gamma_1)\epsilon,
$$

$$
p_3(\epsilon,\delta)=(1-\alpha_2)\left(\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta\right)+(1-\gamma_2)\epsilon.
$$

$p_i(\epsilon,\delta)\to 0$ $(i=1,2,3,4)$ as $\epsilon\to 0$ and $\delta\to 0$.

Solving the second equation in system (A.1) for X_{12}, we have

$$
X_{12}=\frac{\sqrt{(r-p_3/K-\alpha X_{11})^2+4r^2}-(p_3/K+\alpha X_{11}-r)}{2r/K}. \tag{A.2}
$$

Substituting equation (A.2) into the first equation of system (A.1), we have

$$\frac{m\frac{\sqrt{(r-p_3/K-\alpha X_{11})^2+4r^2}-(p_3/K+\alpha X_{11}-r)}{2r/K}+mp_1}{1+n\frac{\sqrt{(r-p_3/K-\alpha X_{11})^2+4r^2}-(p_3/K+\alpha X_{11}-r)}{2r/K}+np_1}be^{-aX_{11}}(X_{11}+p_2)-d_1X_{11}=0. \qquad (A.3)$$

When $X_{11}=0$, the left-hand side of equation (A.3) becomes

$$\frac{m\frac{\sqrt{(r-p_3/K)^2+4r^2}-(p_3/K-r)}{2r/K}+mp_1}{1+n\frac{\sqrt{(r-p_3/K)^2+4r^2}-(p_3/K-r)}{2r/K}+np_1}bp_2>0;$$

and when $X_{11}\to\infty$, the left-hand side of equation (A.3) becomes

$$\frac{m\frac{\sqrt{(r-p_3/K-\alpha X_{11})^2+4r^2}-(p_3/K+\alpha X_{11}-r)}{2r/K}+mp_1}{1+n\frac{\sqrt{(r-p_3/K-\alpha X_{11})^2+4r^2}-(p_3/K+\alpha X_{11}-r)}{2r/K}+np_1}be^{-aX_{11}}(X_{11}+p_2)-d_1X_{11}\to-\infty.$$

Therefore, the above two equations suggest positive solutions of equation (A.3), further proving that system (A.1) has positive solutions.

The solution(s) to equation (A.3) depend(s) continuously on ϵ and δ. Based on the fact that equation (A.3) $\to$ equation (2.15) as $\delta, \epsilon \to 0$, and that equation (2.15) has a unique positive solution, if follows that equation (A.3) has a positive solution when δ and ϵ are small.

Linearizing the system at the positive equilibrium, the jacobian matrix is given by

$$J=\begin{pmatrix} \frac{mX_{12}+mp_1(\epsilon,\delta)}{1+nX_{12}+np_1(\epsilon,\delta)}be^{-aX_{11}}(1-a(X_{11}+p_2(\epsilon,\delta)))-d_1 & \frac{mbe^{-aX_{11}}}{(1+nX_{12}+np_1(\epsilon,\delta))^2}(X_{11}+p_2(\epsilon,\delta)) \\ -\alpha X_{12} & r-\frac{2r}{K}X_{12}-\frac{p_2(\epsilon,\delta)}{K}-\alpha X_{11} \end{pmatrix}.$$

As $\epsilon \to 0$ and $\delta \to 0$, $mX_{12}+mp_1(\epsilon,\delta)/(1+nX_{12}+np_1(\epsilon,\delta))be^{-aX_{11}}(1-a(X_{11}+p_2(\epsilon,\delta)))-d_1 \to -ad_{11}X_{11}<0$ and $r-2r/KX_{12}-p_2(\epsilon,\delta)/K-\alpha X_{11} \to -rX_{12}/K<0$. Therefore, there exist small neighborhoods $(0,\epsilon_0)$ of ϵ and $(0,\delta_0)$ of δ, such that if $\epsilon<\epsilon_0$ and $\delta<\delta_0$, the trace of J is negative. Besides, the determinant of J is positive. As a result, the eigenvalues associated with matrix J have negative real parts, which implies the positive equilibrium is locally asymptotically stable when ϵ and δ are small.

A.2 Proof of the existence and global stability of the positive equilibrium of system (2.33)

To prove the existence of the positive equilibrium, we need to show that

$$
\begin{cases}
\dfrac{mX_{22}(t)}{1+nX_{22}(t)}be^{-a\left(X_{21}(t)+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right)} - \beta_1\epsilon - d_1 = 0 \\[4mm]
r\left(1 - \dfrac{X_{22}(t)+\epsilon+\frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2-\alpha_2 r}+\delta}{K}\right) - \beta_2\epsilon - \alpha\left(X_{21}(t)+\epsilon+\dfrac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1-\alpha_1 mKb/(1+nK)}+\delta\right) = 0
\end{cases}
\tag{A.4}
$$

has a positive solution. Denote

$$
q_1(\epsilon, \delta) = \epsilon + \frac{\beta_1\epsilon\bar{S}_1}{d_1 + \bar{d}_1 - \alpha_1 mKb/(1 + nK)} + \delta,
$$

$$
q_2(\epsilon, \delta) = \epsilon + \frac{\beta_2\epsilon\bar{S}_2}{\bar{d}_2 - \alpha_2 r} + \delta.
$$

The second equation of system (A.4) gives

$$
X_{22} = \frac{K}{r}\left(r - \frac{rq_2}{K} - \beta_2\epsilon - \alpha q_2 - \alpha X_{21}\right).
\tag{A.5}
$$

Substituting equation (A.5) into the left-hand side of the first equation in system (A.4) leads to

$$
\frac{m\frac{K}{r}\left(r - \frac{rq_2}{K} - \beta_2\epsilon - \alpha q_2 - \alpha X_{21}\right)}{1 + n\frac{K}{r}\left(r - \frac{rq_2}{K} - \beta_2\epsilon - \alpha q_2 - \alpha X_{21}\right)}be^{-a\left(X_{21}+\epsilon+\frac{\beta_1\epsilon\bar{S}_1}{d_1+\bar{d}_1}+\delta\right)} - \beta_1\epsilon - d_1 = 0.
\tag{A.6}
$$

Following the idea in Theorem 2.4.3, we can show that equation (A.6) has a unique positive solution when $\mathcal{R}_0 > 1$, and ϵ and δ are small.

It follows the proof in Appendix A.1 that when ϵ and δ are sufficiently small, the positive equilibrium is locally asymptotically stable. Furthermore, periodic solutions can be eliminated by using the Bendixson-Dulac theorem. Since

$$
\frac{\partial}{\partial X_{21}}\left(\frac{X'_{21}}{X_{21}X_{22}}\right) + \frac{\partial}{\partial X_{22}}\left(\frac{X'_{22}}{X_{21}X_{22}}\right) < 0,
$$

provided $X_{21} > 0$ and $X_{22} > 0$. As the ODE system is 2-dimensional, the positive equilibrium is globally asymptotically stable provided, $\mathcal{R}_0 > 1$, and ϵ and δ are sufficiently small.

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