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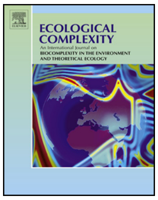

Original Research Article

On crop vector-borne diseases. Impact of virus lifespan and contact rate on the traveling-wave speed of infective fronts

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ABSTRACT

Diseases, in particular, vector-borne diseases are very important issues in crop protection. However, despite their impact on food safety, very few mathematical models have been developed in order to improve control strategies. Motivated by existing literature, we begin by considering a temporal model of vector-borne diseases in (annual) crops. Using appropriate mathematical methods, we show the existence of threshold parameters and discuss several control strategies based on the model. Then, the model is modified to include a spatial component in order to take into account that vectors are moving. We study both theoretically and numerically the related system and other subsystems that are easier to handle using the theory of monotone dynamical systems. We show that traveling wave solutions may exist, with traveling wave speed dependent on the virus lifespan and the contact rate between the pest and the crop. Finally, we discuss the consequences in terms of control strategies.

In the next decade, with the increase in world population and the reduction of lands dedicated to crops, compounded with climate change, there is a challenge to sustain and/or increase food production. Even now in many places around the world, food security is an important issue. It is well known that one quarter of the total crop production is lost because of pests and diseases. Despite many programs and studies to improve on food security, these losses have increased mainly because of the emergence of new diseases or new pests and also because of increasing climatic events. This work focuses on understanding vector-borne diseases in plants with the aim of improving on control strategies.

Like humans and animals, plants have to deal with viruses and/or obligate parasites. However, plant viruses have difficulties to overcome and there are some transmission restrictions due to plant immobility. Contrary to humans or animals, there is no plant-to-plant contact, at least in standard crops, and the wall made of cellulose and pectin that surround all plant cells limit the entries and exits of viruses. To circumvent these obstacles, plant viruses have developed different strategies to transfer efficiently from one host to another. In this case, plant viruses need some *outside partners* or some transport devices that allow an efficient transmission to new hosts. Such devices are usually called vectors, and are found among parasiti fungi, root nematodes and plant-feeding arthropods, particularly insects.

To be efficient in virus transmission, these vectors are able to break the cellulose and pectin barriers using their feeding organs, usually the stylet, and then move frequently from plant to plant. Thus any organism that may feed on an infected plant and travel between plants can potentially transport the virus and thus transmit it to healthy plants. In some sense, plant vectors are involved in the same way mosquitoes are involved in the transmission of diseases such as Malaria (Ross, 1911), Dengue or Chikungunya (Dumont et al., 2008; Dumont and Chiroleu, 2010). However, in the plant kingdom, transmission mechanisms are more complex.

Indeed, a very important difference between animal viruses and plant viruses lie in the transmission process. For animal/human viruses, no mechanical or direct transmission is possible. For example, an extrinsic incubation period is necessary such that an infected mosquito becomes infective, i.e., to be able to infect susceptible humans. For plant, virus transmission characteristics are different and depend on the interaction between the virus and the vector (Nault, 2003; Gray and Banerjee, 1999). Mechanical and biological transmissions are considered to be the main way for viruses transmission by arthropod vectors. However theses terms are not always clear and do not represent efficiently the mechanism of insect transmission of plant-infecting viruses.

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Following (Gray and Banerjee, 1999), it is necessary to consider different types of transmission mechanisms described by time events. Three main transmission modes have been defined:

- the non-persistent mode, with viruses acquired within seconds, and not retained for more than a few hours by their vectors.
- the semi-persistent mode, with viruses acquired within minutes and retained for several hours.
- the persistent mode if they remain in the vector for the rest of its life. In that case the acquisition and inoculation times, as well as the latent periods are of days.

An additional classification has been considered by biologists. They distinguish viruses that remain *outside* the vectors, from those traversing the intestine via the body lumen to the salivary glands. The first type of viruses enter the category of non circulative viruses that have a more superficial and transient relationship with the vector. Transmissible virus particles attach only to the exterior mouthpieces of the insect from which they are released into a new host. In the animal kingdom, this kind of transmission is also called mechanical transmission and is important in the epidemiology of many animal diseases. In particular, many Diptera species are responsible for mechanical transmission. The second type of plant viruses are called circulative viruses and they may be inoculated with the saliva into a new host plant. A circulative virus can further be classified as circulative non propagative or circulative propagative, if, in addition, the virus replicates within the vector. In general, non circulative viruses are non-persistent or semi-persistent, while circulative viruses are semi-persistent or persistent.

Altogether plant viruses strongly depend on vectors for their transmission and survival. As a result modeling has to take into account the vector population and the type of virus. Moreover, it seems natural to consider vector control as an efficient method to reduce the epidemiological risk.

Aphids and whiteflies are known to transmit more than 500 non-persistent, semi-persistent or persistent viruses, (Brault et al., 2010; Navas-Castillon et al., 2011; Fereres and Raccah, 2015; Jones, 2003). Among them, around 300 are non-persistent viruses. That is why, in particular, aphid-borne non-persistent diseases are the most damaging around the world. In addition to that, most of the impacted crops or plants are not suitable for the reproduction or even the survival of aphids.

Indeed, once landed on a plant, aphids first probe the prospective food source by short, only seconds lasting intracellular punctures in epidermis and mesophyll cells that do not even kill the punctured cells. After these exploratory punctures and they judge the plant as suited, the aphids insert their proboscis-like mouthpieces (stylets) into the phloem and feed from its sap for time spans that may exceed several hours. Depending on the tissues they infect, plant viruses can be acquired by aphids during either or only one of the two puncture phases. For example, Luteoviruses are only acquired from the vascular tissues, whereas Cauliflower mosaic virus (CaMV) is acquired from both vascular and no-vascular tissues (Palacios et al., 2002). CaMV is one of the most studied non-persistent virus. Here, we list some examples of non-persistent plant viruses for which aphids are the principal vectors:

- the Potato virus Y causes the most important aphid-borne virus diseases in potato crops.
- the Cucumber mosaic virus (CMV) was first found on cucumber, but it can infect a wide varieties of plants, including vegetables. It can be transmitted by aphids (between 60 and 80 species), but also by humans and seeds.
- Tomato chlorosis virus (ToCV) is a non-circulative-transmitted crinivirus which can be transmitted by whiteflies such as *Bemisia tabacci*, (Fereres et al., 2016).

According to Fereres et al. (2016), plants infected by viruses like CMV or ToCV produce volatiles that attract aphids or whiteflies. This is called the *Host Manipulation Hypothesis* (Blanc and Michalakis, 2016; Ingwell et al., 2012). However, for circulative virus, we may also have the *Vector Manipulation Hypothesis* (Blanc and Michalakis, 2016; Ingwell et al., 2012). This is a strategy by plant pathogens to enhance their spread to new hosts through their effects on mobile vectors, inducing, for instance, a migratory behavior (Blanc and Michalakis, 2016). Thus, virus transmission can be rather complex. That is why a good knowledge on Host-Vector-Virus interactions is necessary in order to develop appropriate vector control or crop protection strategies. It is important to note that non-persistent viruses are related to annual crops.

For decades, mathematical epidemiology has mainly focused on human diseases (Anderson and May, 1991) and vector borne diseases, like Malaria (Ross, 1911; Macdonald, 1957), Dengue or Chikungunya (Dumont et al., 2008; Dumont and Chiroleu, 2010), using various mathematical theories (Anderson and May, 1991), with some great successes or achievements. One of the greatest achievement is the so-called *Mosquito Theorem*, proved by Ross (1911), who, using a mathematical model, was able to show that reducing the anopheles population is necessary (but not sufficient!) to lower the epidemiological risk. This theorem is more or less still used today for many vector-borne diseases. Another great achievement is the famous basic reproduction number $\mathcal{R}_0$, a threshold parameter related to some parameters of the model and aggregating important informations related to the dynamics of the disease, (Anderson and May, 1991; Diekmann et al., 1990). In general, when $\mathcal{R}_0 < 1$, the disease is supposed to die out, while the disease becomes endemic when $\mathcal{R}_0 > 1$.

It is clear that for human and animal diseases, mathematical models have been helpful to better understand complex systems and improve health control strategies. However, from a modeling point of view, compared to human vector-borne diseases, plant or crop vector-borne diseases have been poorly studied though they use a similar compartmental approach leading to almost the same kind of equations. There are, however, some additional changes depending on the type of virus, vectors and the relationship between the virus and the vector.

The aim of this study is to extend the model studied in Anguelov et al. (2012b) by taking into account different control strategies (like sanitary harvest and/or the use of Barrier plants), and vector displacement. In Section 1, we recall the temporal model, consider and study some control strategies like sanitary harvest or barrier plants. Then, in Section 2, we build an ODE-PDE Model in order to take into account that vectors can move while plants are stationary. In Section 3, we consider a simplified version to show the existence of traveling wave solutions, with a speed dependent on the virus lifespan or the daily contact rate between vectors and plants. Finally, in Section 4, we present simulations to illustrate the theoretical results. The paper ends with a discussion and further possible ways of investigations both mathematically and experimentally.

1. The temporal vector-borne plant disease model

We begin with the model developed in Anguelov et al. (2012b), that is summarized in the following compartmental diagram (Fig. 1):

The plant population is divided into four epidemiological states: H_p, the healthy plants, L_p, the infected but not infectious plants, I_p, the infected plants, and R_p, the recovered plants. The insect population is divided into two epidemiological states: S_v, the susceptible vectors and I_v, the infectious vectors. We assume that

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