



A dynamical model for epidemic outbursts by *begomovirus* population clusters



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ABSTRACT

Begomovirus is a genus of highly destructive plant viruses that belongs to the family *Geminiviridae* and spreads through a single vector, the whitefly *Bemisia tabaci*. Although an old family of organisms, *begomovirus* has recently emerged as a potent threat to large-scale cultivation of crops. It is a threat with a very wide domain of influence and it can infect a very wide range of green plants cultivated for both sustenance and as cash crops.

We introduce a mathematical model that simulates the complex dynamic interaction between *begomovirus* genetics, their adaptability to certain plants, and the availability of those plants to the virus under different cropping patterns. The model captures many empirically observed patterns of *begomovirus* epidemic outbursts, even if the equations do not directly depend on the genetics of *begomovirus* strains, and simply assume the vector to be ubiquitous. The model is formulated as a population dynamic system of differential equations, with nonlinear interactions between plant availability and *begomovirus* dynamic adaptability to different crop species. It also includes spatial diffusion allowing simulations over multiple neighboring regions.

The ability of such a model to reproduce qualitatively correct epidemic structures indicates that the main reason for epidemic outbursts and the global spreading of the disease could be found in the patterns of inter-species interactions, many of which are human-induced. If this is the case, then the key to mitigating *begomovirus* epidemics would be the modification of agricultural practices. In particular, the use of intensive cropping patterns and resistant cultivars triggers aggressive virus adaptability through mutation speed-up. It seems that the only simple recourse would be to develop more diverse and less concentrated cropping patterns, both in cropland extent and in time.

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Author summary

Begomovirus epidemics are a major threat to crop plant cultivation in tropical to temperate climate zones. *Begomovirus*, an aggressive plant virus carried by the whitefly (*Bemisia tabaci*) is able to infect a very wide variety of green-leaved crop plants, from cassava, tomato, tobacco, potato, pepper and cotton to many kinds of pulses. It quickly conquers resistant cultivars by its fast genetic adaptability. Previous research indicates that this is partly due to the fact that *begomoviruses* appear not as a single virus species, but as clusters of virus strains.

We construct a population dynamic model that accounts for the versatility of *begomovirus* populations and demonstrates the emergent patterns of population dynamics that can cause massive virus epidemics. Such epidemics appear mostly on large-scale cultivation areas of a similar set of crop plants under intensive cultivation. The model explains how the combination of intensive farming practices for cash crop farming create an ideal platform for *begomovirus* epidemics through their interplay with the structural properties of *begomovirus* clusters. Alternative cropping patterns are proposed to reduce the impact of massive *begomovirus* epidemics.

1. Introduction

Begomovirus is a genus of highly destructive plant viruses that belongs to the family *Geminiviridae*. Although an old family of organisms, *begomovirus* has recently emerged as a potent threat to large-scale crop cultivation and it can infect a very wide range

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of green plants cultivated for both sustenance and as cash crops in tropical, sub-tropical and ever more frequently also in temperate climates. It is also a very versatile adversary that has been seen to adapt to new, resistant cultivars in a matter of a few years only.

Begomovirus spreads through a single vector, the whitefly *Bemisia tabaci* (Bedford et al., 1994). This minuscule fly is difficult to eradicate by chemical means, because its adults, pupae and nymphs reside mostly on the bottom sides of leaves. Moreover, not only do insecticides or pesticides poorly control the whitefly, but they also damage the plant itself. Whiteflies are capable of using very many different leaved plants, at least 500 in number (Rojas et al., 2005), both crops and weeds, for nutrition. This ability of the polyphagous *B. tabaci* is a consequence of the fact that it uses only the phloem cells in a plant (John, 2012). Phloem cells – the vascular system of a plant – carry nutrients, especially sucrose, within a plant. These cells are rather similar in different plants, although they do possess broad molecular diversity. *B. tabaci* therefore specialize, in their guts mainly, by modifying their ability to adapt to different phloem liquid cell variants in different leaved plants.

An analogous specialization pattern has been observed with the *begomovirus*. Any individual whitefly does not carry just a single strain of the virus, but a whole population – or cluster – of strains. When a whitefly feeds on a plant, it injects its population of *begomovirus* strains into the plant. Those members of the cluster that are able to thrive on that plant will do so, while others will decay (Prasanna et al., 2010; Leke, 2010; Renteria-Canett et al., 2011). Polyphagous whiteflies are classified by their *biotypes*, i.e. local or global clusters of plants, the phloem fluid cells of which a population of whiteflies can suck in. The worldwide spread of the whitefly and global movement of plant materials has further prompted the spreading of *begomovirus* diseases (Rojas et al., 2005; Seal et al., 2006).

Some mathematical models have been introduced to replicate *begomovirus* dynamics. However, they have been either omitting the spatial aspect through their classical formulation as a system of ordinary differential equations (Jeger et al., 2004; Miyai et al., 1986), or they were losing clarity due to deep detail in model definition (Poss, 2011; Sanford and Nelson, 2012). In this article, we present a mathematical model of *begomovirus* population dynamics that accounts for many properties of the virus population. The advantage of our approach is the preserved simplicity of differential equation-based formulation. However, since we move on from the classical, in epidemiology, ordinary differential equations to partial DEs, we gain the ability to include the spatial dimension. Moreover, the system is nonlinear and accounts for time- and space-dependent aggressive genetic adaptability of the virus to known and unknown plants.

With simulations using the model, we demonstrate that recent very aggressive *begomovirus* epidemics in crop pulses on many continents, particularly in India, can potentially be explained by a combination of population dynamics and evolutionary selection processes at local virus cluster level. In particular, the increasing prevalence of single-crop fields, longer growth periods with up to three crops annually, and larger unified cultivation areas all contribute to creating favourable circumstances for both increasingly severe *begomovirus* epidemics and an increasing survival rate of *begomovirus* strands. Through simulations, we also study two alternative cropping patterns, one of which might alleviate the severity of these epidemics.

In Section 2 of this article, the basic biological principles of *begomovirus* epidemics and the mathematical model are introduced. In Section 3 the model simulation results are presented for various scenarios of cropping patterns and interventions. The last section discusses the results of the simulations with the model.

2. Materials and methods

2.1. *Begomovirus* genealogy

Plant-infecting *geminiviruses* belong to the family *Geminiviridae*. *Geminiviruses* are divided into four genera based on genome organization, host range, and insect vector: *Mastrevirus*, *Curtovirus*, *Topocovirus*, and *Begomovirus* (Fauquet and Stanley, 2005). *Geminiviruses* are single-stranded DNA viruses with geminate particle morphology. *Begomovirus* is the largest genus and consists of more than 180 species and several unassigned isolates. *Geminiviruses* belonging to the genus *begomovirus*, are exclusively transmitted by the insect, whitefly (*B. tabaci* Gennadius) and infect dicotyledonous plants only. *Begomoviruses* not only interact with each other in terms of synergism and interference but also interact with their transmission vector and the vast range of host plants where they continue their life cycle.

2.2. Pulses, whiteflies and the *begomovirus* life cycle

2.2.1. Vector transmission

As all *geminiviruses*, which require an insect vector for transmission to other plants, *begomoviruses* rely entirely on their vector, the whitefly *B. tabaci* for plant-plant transmission. The native whiteflies present in a region can affect the *begomovirus* prevalence in that particular region because most biotypes can transmit a range of different *begomoviruses*, but with differing efficiencies depending on virus species to be transmitted and the corresponding whitefly biotype (Bedford et al., 1994; Maruthi et al., 2002). In the latter publication, the authors demonstrated that vector specificity with the “B” biotype of *B. tabaci* could reach 15 *begomoviruses*. This indicates that at least some *begomoviruses* have evolved to be transmitted by specific biotypes. According to De Barro et al. (2005), there is geographical rather than host plant origin relationship between vector *B. tabaci* and the *begomoviruses*. Due to commercial international trading and concomitant insect dispersal, different biotypes of *B. tabaci* are no longer restricted to specific geographic regions.

2.2.2. *Begomovirus* infection

The *begomovirus* infection cycle is known to be started at the instant when a whitefly carrying the virus starts feeding on a host plant recognized by the given *begomovirus* strain. This results in an immediate transmission of viral particles into the vascular system of the host plant. From there, the viral particles are carried to the mesophyll cells where they lose coating, which allows the viral DNA to enter into the host nucleus where viral DNA replication and transcription takes place (Gafni and Epel, 2002). Replicated virions are coated again and are either passed to the next cell of the host plant, or get taken up by another feeding vector and passed to a new host plant. Newly emerging *geminiviruses* are causing severe disease epidemics in cotton, grain, legumes, tomato, and other staple food and cash crops in tropical and subtropical regions (Khan, 2000; Boulton, 2003). Under some circumstances, weeds can be a potential source of primary inoculum and survival of the virus in off seasons. This increases the chances of epiphytotic attack of the disease making disease management difficult. Fig. 1 presents a picture of an infected *Glycine max*.

2.2.3. *Begomovirus* interaction with vector and host plants

Every time a whitefly feeds on a host plant, it picks some particular virus strains to its gut and, therefore, it increases the variety of *begomovirus* population in each next host it feeds on (Czosnek and Ghanim, 2002). Experiments showed no effect on the transmission of already fed Tomato yellow leaf curl virus (TYLCV), when the vector was sequentially fed on Tomato yellow leaf curl Sardinia virus

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