



## *Bemisia tabaci*-mediated facilitation in diversity of begomoviruses: Evidence from recent molecular studies

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### ABSTRACT

Begomoviruses are considered as one of the most notorious plant viruses worldwide, which cause substantial economic losses to various field crops. Management of begomoviruses has become a challenge due to the continuous evolution and the emergence of new strains. *Bemisia tabaci* is globally known to be the key vector of begomoviruses, having relatively high reproductivity, fast dispersal ability, high survival rate due to its polyphagous nature and high resistance to various groups of insecticides. Continuous transmission of begomoviruses by the vector has led to the development and spread of epidemics of various diseases worldwide. In this review, we have critically analyzed the various dynamics which facilitate the diversity of begomoviruses through their vector. The interaction of begomovirus-whitefly leads to continuous research activities regarding management of both virus and its vector, thus opening exciting new horizons to formulate potential control strategies to ensure a disease-free cropping environment.

### 1. Introduction

The genus *Begomovirus* (*Geminiviridae*) embeds more than 320 species [1,2] and is considered to be the most diverse and destructive group of viruses worldwide [3]. They cause various diseases to dicotyledonous crops in temperate and tropical zones of the world [4]. The viral genome of most of the begomoviruses consists of two components, i.e., DNA-A & DNA-B, each sizing about 2.6–2.8 kb [5], where DNA-B is dependent upon the DNA-A for its replication; while both strands play an equal role in causing infections to the host (Fig. 1a) [6]. Approximately, 133 species belong to the monopartite genome (Old world; OW) are more prominent in Indian, Asian, African and Japanese regions, while bipartite (New world; NW) genome viruses prevail in American regions [7,8]. DNA-A is responsible for replication inside the nucleus via two fundamental steps (ssDNA to dsDNA conversion and rolling circle amplification) [9] and followed by the encapsidation process

where DNA-B systemically regulates symptom production in the host cells [6,10]. Both DNAs (DNA-A and DNA-B) of bipartite begomoviruses have the same size except common region, which consists of a predicted stem-loop structure with TAATATTAC sequenced nucleotide and many other regulatory elements [6]. The loopy structure also has multiple repeats of 6–12 nt sequences which act as binding sites for replication-associated protein [11]. Recent research findings further exhibited about the association of two satellite molecule classes named Alpha and Beta satellites, respectively, with classical begomoviruses which have led towards the emergence of begomovirus disease complexes in most parts of the world (Fig. 1b).

Begomoviruses are the agents which cause various economically serious diseases worldwide, thus lead to considerable losses in many countries [12,13]. For example, in China, severe losses have been recorded in recent years via begomovirus diseases to various notable crops such as tobacco, squash, tomato and papaya [14,15]. Other

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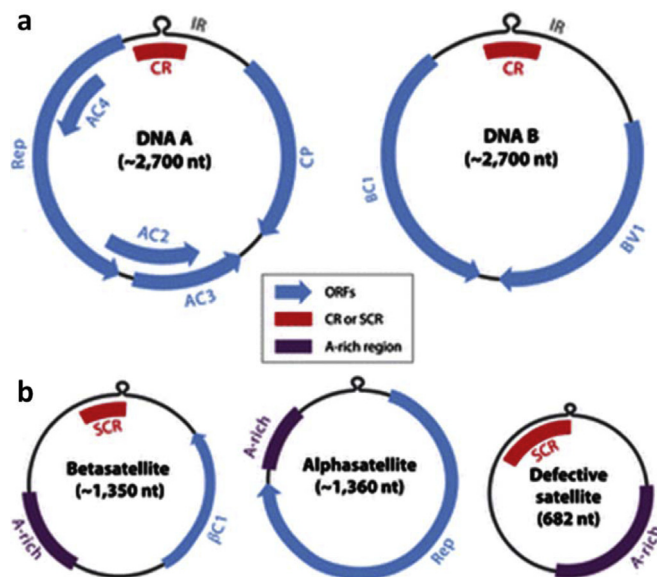


Fig. 1. Structure of begomoviruses and their associated satellites.

examples include cotton leaf curl disease multiple epidemics in Pakistan [16] and cassava mosaic disease (CMD) epidemics in Africa [17].

Whiteflies are small Hemipterans belonging to family Aleyrodidae. They typically feed on the undersides of plant leaves. Up till now, more than 1550 whitefly species have been described [18–20]. Among them the prominent pest species which continuously pose threat to agricultural crops, are *Aleurocanthus woglumi* (citrus blackfly), *Aleyrodes proletella* (cabbage whitefly), *Bemisia tabaci* (silverleaf whitefly) and *Trialeurodes vaporariorum* (greenhouse whitefly) [21]. Worldwide, whitefly is one of the most disastrous pests of economically important plants including vegetables, ornamentals and household plants worldwide [22–25].

Although it is thought that whiteflies directly cause crop losses through sap sucking but actually the indirect damage caused by whitefly is more serious concern. For example, they secrete large quantity of honeydew which supports the growth of sooty mold [26]. Moreover, they inject their saliva inside the phloem of the plant which decreases the overall turgor pressure, is considered as more harmful than the growth of the fungus [27,28]. Apart from all this, the most important aspect is the transmission of many virus diseases through whitefly. It transmits several economically important groups of viruses including begomoviruses, which cause great yield losses in tropical and subtropical regions [13,29–31]. The polyphagous feeding behavior of whitefly gives ample opportunities to acquire and transmit begomoviruses to new hosts [32] (Fig. 2). Although the transmission of begomoviruses is a complicated process, sucking mouthparts of whitefly allow it to acquire and further transfer the begomoviruses [33]. Whitefly transmits begomoviruses in a circulative persistent manner [34]. The virus has to cross several barriers and checkpoints successfully while interacting with various receptors and other whitefly proteins. However, the bulk of the virus remains associated with the insect midgut and the filter chamber [35]. In these tissues, viral genomes may be transcribed and may replicate [36]. The whitefly plays an essential role in the dispersal of begomoviruses to the nearest agro-ecological zones, further spreading them for long distances through trade activities [37]. The reason regarding the evolution of begomoviruses and emergence of new strains can be the existence of other viruses, various hosts, new vector species, changing environmental conditions and varying agricultural practices [38]. So, here we reviewed the characteristics of *B. tabaci* which make them favorites for the biodiversity of begomoviruses. We further discussed how the vector helps or contributes to the emergence of new virus strains.

## 2. What characters make *Bemisia tabaci* an important begomovirus vector?

*Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is considered as a cryptic species complex [39], embedding more than 35 cryptic species [2,40], which are morphologically indistinguishable but are reproductively isolated [41,42]. Worldwide, *B. tabaci* is considered as one of the most invasive and disastrous pests of economically important crops, including vegetables, ornamentals and household plants [29,43]. The pests are involved in causing damage to crops in multiple manners, i.e., via direct feeding upon the plant tissues, further secreting honeydews thus inviting fungal growth upon damaged tissues and through active transmission of begomoviruses [44,45]. Furthermore, begomovirus epidemic breakout in various regions of the world is exhibited due to higher populations and abundance of *B. tabaci* biotype B and Q [37,45]. On the other hand, the situation became worst as the biotype Q is now considered as resistant to most of the commercially available insecticides such as pyriproxyfen and neonicotinoid, thus making management of *B. tabaci* and begomoviruses difficult worldwide [46].

This rapid distribution of various *B. tabaci* cryptic species into new areas (Australia, China, Mexico, Turkey, USA and Pakistan) has been evident when referring to recent publications [43,47,48]. Researchers have explained the phenomena of competition [49,50] among the *B. tabaci* complex members that leads to rapid displacement of one or more members from a particular ecological zone [51,52]. These kinds of sudden displacement and invasion of species further complicate the virus-vector management strategies, thus pushing scientists to find new potential control methods [40].

*B. tabaci* have a high reproduction rate, faster dispersal ability, polyphagous nature thus facilitating their existence in large populations and adaptation into various agro-ecological zones worldwide [53]. They further embed the ability of alteration in the host plant defense mechanisms through small RNAs [54]. Moreover, the mouthparts of *B. tabaci*, i.e., piercing-sucking allow them to feed upon large plant area. Approximately, 500 species from 74 different families of whitefly feed upon cultivated, non-cultivated, household and ornamental plants [55]. The vector plays enough roles in detoxification, metabolism and alteration in various plant metabolites [56–58]. Another character that makes *B. tabaci* a successful vector for begomoviruses transmission is its feeding nature, i.e., a phloem-feeding insect which does not like to probe extensively before feeding thus favoring the active transmission of begomoviruses [59]. The combination of the newly adapted begomoviruses which are transferred through newly identified *B. tabaci* cryptic species enhances the rapid and dynamic paradigm shifts that ultimately lead towards the epidemic prevalence of various diseases.

## 3. How *Bemisia tabaci* spreads begomoviruses worldwide?

Global dispersal of begomoviruses is facilitated by *B. tabaci* along with the other factors such as the trade of different host plant materials. This has led towards the identification of several begomoviruses in new areas where they were not previously reported (Table 1). Such trade activities also contribute to the diversification and spread of *B. tabaci*. As *B. tabaci* can acquire many different types of viruses from several host plants and can transfer them into single or multiple hosts, so this phenomenon enables transportation of begomoviruses to long distances [60]. This long-distance transport of begomoviruses is supported via a large number of virus-infected symptomless plants thus avoiding the quarantine measures successfully [61]. When the phytophagous *B. tabaci* feed upon these plants, it not only enables the host plants infection but also ensures the wide distribution of begomoviruses. If these trade activities are maximized upon a single location, it can result in the sudden emergence of a new begomovirus strain via their quick acquisition, fast transmission into the host. Persistent type of transmission of begomoviruses via *B. tabaci* further facilitates global transportation and dispersal of a virus within juvenile, pupal, or adult stages of the vector

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