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The Current Status of Begomovirus Research in India: Solemn Threat to Crop Production

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A B S T R A C T

Begomoviruses being the largest genera of Geminiviridae cause significant economical losses in a wide variety of crops in several tropical and subtropical regions of India and a major threats to food security. Begomoviruses are transmitted by the whitefly (Bemisia tabaci) in a circulative persistent manner. Begomoviruses as of their small genomes (ssDNA) and limited coding capacities, rely heavily on host machineries for infection. They interact with a wide range of plant proteins and process them to support viral DNA replication, gene expression, movement, and to neutralize host defenses. Many of these interactions have antagonistic effect on the growth of crops, resulting in symptoms that include stunting, vein clearing, curling, leaf deformation and loss in fruit quality and production. The main research studies focused on Begomoviruses are: identification, molecular characterization, sequence analysis, DNA replication, infectivity, phylogeny, functions of viral proteins, virus-host interaction, transgenic resistance, promoter analysis and virus based gene silencing vectors. This review presents current status of begomovirus research in India and future areas that need to be explored.

Introduction

Begomoviruses are emergent pathogen widely distributed in tropical, subtropical and temperate regions worldwide and are a serious threat to diverse economically important crops (Castillo *et al.*, 2011; Varma *et al.*, 2011). The genus *begomovirus* is the largest among seven genera viz. *Becurtovirus*, *Begomovirus*, *Curtovirus*, *Eragrovirus*, *Mastrevirus*, *Topocuvirus* and *Turncurtovirus* classified in family *Geminiviridae* (Brown *et al.*, 2015; Varsani *et al.*, 2014). *Begomoviruses* are small ssDNA viruses transmitted in a circulative persistent manner by the whitefly (Czosnek, 2007).

Begomoviruses have either a monopartite (single DNA) or a bipartite (two DNA components: DNA-A and DNA-B) genome organization, infecting mostly dicotyledonous plants. The DNA-A of bipartite and the single component of monopartite *begomoviruses* contain five (sometimes six) Open Reading Frames (ORFs), one (AV1) or two (AV1 and AV2) in the viral sense (V-sense) strand and four (AC1 to AC4) in the complementary sense (C-sense) strand. Both the DNA-A and

DNA-B are approximately 2.8 kb in size. The DNA-B contains two ORFs (BV1 and BC1, in V-sense and C-sense strand, respectively). In DNA-A, AV1 codes for coat protein (CP), the AV2 for a protein of unclear function, AC1 for a replication associated protein (Rep) and AC2 for a transcriptional activator (TrAP).The protein encoded by AC3 is the replication enhancer (Ren) and the protein encoded by AC4 functions as a suppressor of RNA silencing. In DNA-B, the BV1 codes for a nuclear shuttle protein (NSP) and the BC1 for a movement protein (MP), required for intracellular and intercellular movement of the viral DNA respectively. The non-coding region (called Intergenic region-IR, approximately 500 bp) contains the origin of replication, where the viral Rep protein binds for initiating rolling circle replication. A part of this region is conserved between the two DNA components of bipartite *begomoviruses*. The IR also harbours the promoter/ regulatory elements for expression of the viral genes in both V-sense and C-sense strand.

Monopartite *begomoviruses* are often associated with satellite DNAs, about 1.4 kb in size. Two types of satellite DNAs are known: the alpha satellites and beta satellites. The alpha satellites encode their own replication-associated protein whereas, the beta satellites do not code for any replication associated proteins but carry a single ORF (βC1), encoding a multifunctional protein. Both the alpha and beta satellites are dependent upon the helper virus for replication and, in many cases, attenuate the symptoms produced by it (Idris *et al.*, 2011).

All *begomoviruses* encode a coat protein (CP) in which all the genomic and satellite molecules are present. The CP acts as the coat of the virus particles and is essential for virus transmission from diseased to healthy plants by *B. tabaci*. The CP is therefore an essential component of *begomovirus* survival and has been used widely to characterize and establish the relationships of many *begomoviruses* (Harrison *et al.,* 2002).

Plants use a combination of transcriptional gene silencing and post transcriptional gene silencing as defense against *begmovirus* infection. Viral infections in plants trigger the defense responses by degradation of the invading viral RNA into small fragments (siRNA), phenomenon known as RNA-interference (RNAi). Therefore successful viral infection results only upon suppression of this defense response by specific viral proteins, known as RNAi suppressors. RNAi suppressor activities have been discovered in several begomoviral gene products (Voinnet, 2005).

Genetic resistance against plant viruses, if available in the germplasm, is considered to be one of the most efficient ways to control viral infections for example it is appraised during research studies that out of 26 collections of pumpkin, seven namely, LC-1, LC-2, LC-3, LC-4, LC-5, LC-6 and LC-9 were highly resistant to viruses (Sharma *et al.*, 2012, 2013). The genes conferring such resistance can be transferred to cultivated varieties by breeding. Against *begomoviruses*, very few resistance genes are known, the most important of them being the Ty series of genes available in wild tomato (*Solanum chilense*) against *Tomato yellow leaf curl virus* (TYLCV). Transgenic resistance against *begomoviruses* has been achieved in a number of plants using a variety of strategies.

The strategies which includes expressing proteins of viral origin (CP, Rep and its derivatives and TrAP), expressing nonviral proteins having an anti-viral effect (toxic protein dianthin, antibodies raised against viral CP), DNA interference involving defective viral DNAs and RNAi against viral transcripts (Vanderschuren *et al.,* 2007).

Earlier emerging threat of *begomoviruses* on crop yield has been extensively addressed (Varma and Malathi, 2003). The extent of yield loss caused by some begmoviruses has been estimated to be as high as 100 per cent (Dasgupta *et al.,* 2003; Borah and Dasgupta, 2012). *Bhendi yellow vein mosaic virus* reported to cause up to 96 per cent loss in yield (Pun and Doraiswamy, 1999). Yield losses in blackgram, mungbean and soybean have been estimated to be approximately $300 million per year (Varma and Malathi, 2003).

Presently in India a large number of *begomoviruses* have been identified which infecting the various crops. Researchers in India are recently focusing on the molecular interactions between *begomoviruses* and their hosts with the objective to gain insight on the molecular cross-talk, which might throw light on newer and hitherto unexplored aspects of their biology and reveal novel approaches for their management.

Considering the importance of *begomoviruses* in India, the salient research achievements related to *begomoviruses*, have been reviewed here. The review describes our current knowledge of how *begomoviruses* interact with their plant hosts, functional consequences of these interactions and the possible directions in which future efforts could be channeled to manage diseases caused by begomoviruses.

Begomovirus research in India

Begomoviruses have been reported from different groups of crops in India. Extensive research work has been done on these viruses such as sequence analysis, phylogeny, infectivity, virus host interaction, functions of viral proteins; virus derived transgenic resistance and associated satellites. The review brings together the research work performed in India, focusing on the above aspects, described in the alphabetical order of their major hosts below.

Bhindi

Bhendi yellow vein mosaic disease was first reported from Mumbai in India by Kulkarni. In India, distinctive monopartite *begomoviruses* such as *Bhendi yellow vein Madurai virus* (BYVMV), *Bhendi yellow vein Bhubaneswar virus* (BYVBhV), *Bhendi yellow vein Maharashtra virus* (BYVMaV) and *Okra enation leaf curl virus* (OELCuV) have been reported (Fauquet *et al.,* 2008; Brown *et al.,* 2012; Venkataravanappa *et al.,* 2012b, 2013a,b). Besides these, *Bhendi yellow vein Delhi virus* (BYVDV), a new bipartite *begomovirus* species, was recently found to be associated with YVMD on okra (Venkataravanappa *et al.,* 2012a). Inoculation of bhindi plants with cloned BYVMV DNA, a monopartite *begomovirus*, produced mild symptoms; typical vein yellowing symptoms were produced only in association with the cognate beta satellite (Jose and Usha, 2003), possibly due to the silencing suppression activity of the βC1, reported later (Gopal *et al.,* 2007). The CP showed nuclear localization, whereas the βC1 localized to the cell periphery (Kumar *et al.,* 2006).

Brinjal

Brinjal is also found to be infected with a variant of the *Tomato leaf curl New Delhi virus* (Tolcvnd). The researchers identified cloned and sequenced the complete DNA-A and DNA-B genomic components of the causative virus (Pratap *et al.,* 2011).

Cassava

Cassava mosaic disease (CMD) had been reported in India in 1966. *Indian cassava mosaic virus* (ICMV) and *Sri Lankan cassava*

mosaic virus (SLCMV) cause Cassava Mosaic Disease (CMD) in India (Saunders *et al.,* 2002; Hong *et al.,* 1993; Patil *et al.,* 2005). Later, in a biodiversity study, while ICMV was found restricted to only certain regions, SLCMV was found to be rather widespread in southern India. In addition, based on PCR-RFLP from multiple samples, it was concluded that these isolates showed high diversity (Patil *et al.,* 2005; Rothenstein *et al.,* 2006). Phylogenetic analysis of several CMD-affected cassava samples revealed recombination among the population of cassava infecting *begomoviruses* in India (Rothenstein *et al.,* 2006). Virus free cassava, generated by meristem tip culture, was used to study the whitefly transmissibility of the viruses in cassava. Using cassava adapted whiteflies; symptoms appeared in 85 per cent of the plants after 25th day of inoculation (Duraisamy *et al.,* 2012).

Chilli

In India, chilli has been reported to be infected by several *begomoviruses* namely *Chilli leaf curl virus* (ChiLCV), *Tomato leaf curl New Delhi virus* (ToLCNDV) and *Tomato leaf curl Jodhpur virus* (Khan *et al.,* 2006; Senanayake *et al.,* 2007). The presence of a *begomovirus* was confirmed by PCR while the BLAST search of GenBank revealed close similarity of the sequence with the *Chilli leaf curl virus*-(Pakistan:Multan) (ChiLCuV-[Pk:Mul]; AF336806) (Shih *et al.,* 2003). In India, *Tomato leaf curl New Delhi virus* (ToLCNDV) was shown to be associated with chilli leaf curl disease occurring in Lucknow with a diverse group of beta satellites found in crops and weeds (Khan *et al.,* 2006; Kumar *et al.,* 2015).

Cotton

The first outbreak of CLCuD in the Indian subcontinent, the '*Multan epidemic*' occurred in Multan, Punjab province of Pakistan during the 1990s. Production of cotton is severely constrained by cotton leaf curl disease (CLCuD), which is considered as the most complex and economically important disease of cotton (Zubair *et al.,* 2017; Naveen *et al.,* 2017; Sattar *et al.,* 2017).The etiological viral agents associated with this disease are collectively known as CLCuD associated *begomoviruses* (CABs) belongs to the genus *Begomovirus* (Sattar *et al.,* 2017; Zerbini *et al.,* 2017; Brown *et al.,* 2015). The genome of the CABs predominantly consists of a monopartite circular ssDNA (Sattar *et al.,* 2017; Brown *et al.,* 2015) frequently associated with non-viral, single stranded circular satellite DNA molecules together presenting as an infection complex (Sattar *et al.,* 2013,2017; Briddon *et al.,* 2006).

Monopartite *begomoviruses* associated with a beta satellite (Kirthi *et al.,* 2002). At least four *begomoviruses* are associated with this disease in India, namely, *Cotton leaf curl Rajasthan virus* (CLCuRV), *Cotton leaf curl Multan virus* (CLCuMuV), *Cotton leaf curl Kokhran virus* (CLCuKV) and *Tomato leaf curl Bangalore virus* (Ahuja *et al.,* 2007). The CP gene sequence of another Indian isolate, *Cotton leaf curl virus*-Hissar 2, was reported from Haryana, India, which showed 97.3 per cent amino acid sequence identity with *Pakistan cotton leaf curl virus* (Sharma *et al.,* 2005). A recent work has identified two new isolates, CLCuV-SG01 and CLCuVSG02 from Rajasthan, which are reportedly recombinants with other *begomoviruses* (Kumar *et al.,* 2010). A recombinant CP of a *cotton leaf curl virus* strain was observed to have non-specific ssDNA binding activity, which demonstrates a possible role of the protein in virus assembly and nuclear transport; this property being possibly conferred by a conserved C2H2-type zinc finger motif (Priyadarshini and Savithri, 2009).

Cucurbits

Natural infection of *begomoviruses* on cucurbitaceous crops have also been reported from India (Muniyappa *et al.,* 2003; Varma and Malathi, 2003; Sohrab *et al.,* 2003,2006; Mandal *et al.,* 2004; Singh, 2005; Tiwari *et al.,* 2011) which revealed that *begomoviruses* are emerging as a major constraint to cultivation of cucurbitaceous crops in India. Author reported more than 98 per cent samples were found to be infected with *Begomovirus* (Nagendran *et al.,* 2017). Chlorotic curly stunt disease of bottle gourd from Delhi and adjoining state of Haryana was reported to caused by a *begomovirus* on the basis of whitefly transmission and sequence identity of coat protein (CP) and replication initiator protein(Rep) genes (Sohrab *et al.,* 2010).

Legumes

Yellow mosaic disease (YMD) in legumes such as blackgram (*Vigna mungo*) and mungbean (*V. radiata*) was first reported by Nariani. It is a major constraint in the productivity of legumes across the Indian subcontinent (Varma and Malathi, 2003). This disease affects the majority of legume crops viz. mungbean, blackgram, pigeonpea, soybean, mothbean and common bean, while causes huge loss of blackgram, mungbean and soybean together (Varma and Malathi, 2003).

Four species of *begomoviruses* have been reported to cause YMD of legumes in India (Qazi *et al.,* 2007). *Mungbean yellow mosaic India virus* (MYMIV) and *Mungbean yellow mosaic virus* (MYMV) are prevalent and the *Dolichos yellow mosaic virus* and *Horsegram yellow mosaic virus*, occur rarely (Fauquet and Stanley, 2003; Maruthi *et al.,* 2006). A bipartite *begomovirus* isolate causing YMD in blackgram produced differential symptom in different leguminous hosts and had DNA-A, a variant of MYMV, and DNA-B, a variant of MYMIV (Haq *et al.,* 2011).

Begomoviral DNA replication is interesting and therefore to understand the properties of Rep and its interacting partners have been the focus of several studies. The Rep of blackgram infecting MYMIV-Bg was found to bind to the intergenic region in a specific manner. The protein also undergoes ATP-regulated cleavage and conformational change (Pant *et al.,* 2001). The Rep of MYMIV also acts as a replicative helicase in viral replication and works as a large oligomer, needs less than six nucleotides to function and translocates in 3′-5′ direction (Choudhury *et al.,* 2006). Another host factor, RAD54 (a known recombination/repair protein) has also been identified to be an essential interacting partner of Rep of MYMIV. The interacting domain of RAD54 was identified which enhances the enzymatic activities of MYMIV-Rep (Kaliappan *et al.,* 2012).

Transgenes (CP, Rep, Rep-antisense, truncated Rep, NSP and MP) were evaluated by agroinoculation in transgenic tobacco (*N. tabacum*) to attain resistance against mungbean infecting *begomoviruses*. Transgenic plant harbouring the the antisense-Rep ORF showed inhibition of viral DNA accumulation (Shivaprasad *et al.,* 2006).

Papaya

The CP, Rep and the IR of the genome of a *begomovirus* causing severe leaf curl in papaya plants were amplified, cloned and sequenced. The viral isolate was found to share 89.9 per cent homology with ICMV and was named as *Papaya leaf curl virus-India* (PLCV-India). Analyses of the N-terminal 70 amino acid of the CP of the virus showed its relatedness to *begomoviruses* from the Old World (Saxena *et al.,* 1998). Small fragments

(siRNAs) were designed using computational tools, could possibly be used to confer resistance against *begomovirus* infecting papaya (Saxena *et al.,* 2011).

Potato

A *begomovirus* causing a severe disease of potato was observed in India (Usharani *et al.,* 2004). The nucleotide sequence data indicate that the cause is a virus closely related to *Tomato leaf curl New Delhi virus* (ToLCNDV) (Gawande *et al.,* 2007).

Tomato

Tomato leaf curl disease (ToLCD) is a common disease of tomato all over India. ToLCD was first reported in northern India by Vasudeva and Sam Raj. Symptoms of ToLCD include leaf curling, vein clearing and stunting, which can often lead to sterility. Tomato leaf curl is becoming a serious concern due to involvement of six different species of *begomovirus*, *viz*., *Tomato leaf curl Bangalore virus* (ToLCBV), *Tomato leaf curl Bangladesh virus* (ToLCBDV), *Tomato leaf curl Gujarat virus* (ToLCGV) *Tomato leaf curl Karnataka virus* (ToLCKV), *Tomato leaf curl NewDelhi virus* (ToLCNDV), and *Tomato leaf curl Sri Lanka virus* (ToLCVSLV) (Fauquet *et al.,* 2003). In general, the population of *Tomato leaf curl viruses* (ToLCVs) in India is highly diverse, which was shown after analysis of the CP sequence from 29 infected tomato samples across India. Five clusters (with less than 88% similarity among them) were observed among the population; while four of them represented the known tomato leaf curl viruses, one cluster showed more similarity (89%) with *Croton yellow vein mosaic virus* (Reddy *et al.,* 2005).

Potential recombination sites among the DNA-A components of the strains/species of ToLCVs from Bangalore were mapped in an early study (Kirthi *et al.,* 2002). There has been report of a distinct bipartite *begomovirus* from a temperate region (Palampur), which is possibly a natural pseudo recombinant (Kumar *et al.,* 2008). Possible recombination has also been reported in two monopartite *begomoviruses*, one from New Delhi (ToLCV-CTM) and another from Kerala ToLCV-K3/K5 (Pandey *et al.,* 2010). It was demonstrated that changes in DNA-A virion-sense mRNA structure or translation affect viral replication (Padidam *et al.,* 1996).

There have been several efforts to confer resistance against the tomato leaf curl viruses in India using different strategies. Transgenic tomato lines harbouring the CP of ToLCNDV-[India: Lucknow] were generated, which showed durable resistance against the virus (Raj *et al.,* 2005). Transgenics carrying antisense sequence of Rep gene was shown to recover from ToLCD (Praveen *et al.,* 2005a, b). In a biosafety analysis, the above transgenics were shown to be non-toxic to mice (Singh *et al.,* 2009), thereby making the product easily acceptable to consumers. Virus-induced gene silencing (VIGS) vector are useful tools for the study of gene functions in plants. It was also shown that a mutation in the AC3 (a putative silencing suppressor) can increase the silencing efficiency several folds (Pandey *et al.,* 2009). Genetic resistance against geminiviruses is known in some crops which can act as sources of resistance, and as subjects for study of plant–pathogen interaction. ToLCNDV-resistant cultivar H-88-78-1 has been found to differentially express 106 transcripts in response to viral infection, eight of which were induced more than fourfold compared to an un-infected control. They represented proteins participating in defence response, transcription, proteolysis and hormone signalling (Sahu *et al.,* 2010). Such studies will help in the deployment of genes

in developing virus resistance using transgenics and marker assisted selection.

India is an agriculture based country therefore a large number of *begomoviruses* have been reported from the country. Indian weather is very much suitable for the prevalence and survival of white fly. Indian *begomovirus* have an overlapping host range for example tomato-infecting begomoviruses have also been reported in chilli, cotton and mentha. One of the major factors responsible for this overlapping host range could be the polyphagous nature of the vector whitefly and the mixed cropping system prevalent in the country. An expected consequence of this scenario would be recombination which could play an important role for the evolution of new *begomovirus* strains in India and these new strains could be responsible for severe losses in new host varieties. The emergence of a large number of beta satellites and more recently, alpha satellites associated with *begomoviruses* in India is also remarkable. The interdependence of the satellites and their helper *begomoviruses* is thus an area of immense importance for investigation. Thus, there is an urgent need to control *begomovirus* infections in new host varieties. The use of computational and molecular techniques e.g. RNAi could be a potential tools for reducing the prevalence of various *begomovirus* diseases. The reports of success in controlling *begomoviruses* with virus derived and other transgenes are encouraging. Well characterized resistance genes hold a lot of promise in controlling *begomoviruses*. However, as mentioned earlier, only a few such genes have been characterized to a level where they can be used for breeding to develop resistance against *begomovirus* and can be used to intrigues into popular crop varieties. Hence, more research works to be undertaken to search for natural *begomovirus* resistant wild varieties of crop plants against *begomoviruses* and when found, to characterize the resistance traits. The interaction of *begomoviruses* with the vector whiteflies, a crucial step in the spread of *begomoviruses* in the field, also needs to be carefully looked at. These, as well as the exciting developments on plant–virus interactions, promise many more avenues of *begomovirus* control opening up in the near future. These need to be urgently deployed to assure crop protection against the huge losses incurred due to begomoviral infections in India. Results of these techniques should be effectively applied for disease management, crop protection and development of quarantine strategies at state and national level in India.

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