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REVIEW

Banana bunchy top virus and the bunchy top disease

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Abstract *Banana bunchy top virus* (BBTV) is a circular single-stranded (ss) plant DNA virus and the type member of the genus *Babuvirus* in the family *Nanoviridae*. BBTV causes bunchy top disease of banana and plantain. Its integral genome consists of at least six circular ssDNA genome components and is associated with all geographical isolates of BBTV. BBTV is a phloem-limited virus that is transmitted from plant to plant by the aphid vector, and long-distance spread is through the movement of infected plant material. BBTV is an economically important plant pathogen causing substantial damage to banana crops worldwide. In the past 2 decades, with the advent of molecular techniques, the genome of BBTV has been elucidated, and its genetic diversity has been studied extensively. However, the molecular interactions of viral proteins with host metabolites and proteins have not been studied in depth. Protein functions and viral interactions of BBTV are comparable to the other group of single-stranded plant DNA viruses, *Geminiviridae*. However in many other aspects, BBTV is clearly distinct from geminiviruses. Further research is required to better elucidate the virus–host interactions and protein functions of this pathogen.

Keywords BBTV · BBTD · M-Rep · *Pentalonia nigronervosa* · PIO · SEA

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Introduction

Banana bunchy top virus (BBTV) is a plant virus having a circular single-stranded (ss) DNA genome. It causes bunchy top disease of banana and plantain. BBTV has been nominated as among 100 of the "World's Worst" invaders (Lowe et al. 2000) and is one of the oldest known viral diseases. Although the viral nature of bunchy top disease was established in Australia in 1920s by C. J. P. Magee, the virus particles were first isolated in 1990, long after its recognition as a viral disease. BBTV belongs to the family *Nanoviridae*, a small family of plant-infecting, circular ssDNA viruses. *Nanoviridae* has two genera, *Nanovirus* and *Babuvirus*, and a total of nine virus species (Mandal 2010; Vetten et al. 2005). Genus *Babuvirus* initially included only BBTV (Harding et al. 1991), but later *Abaca bunchy top virus* (ABTV) and *Cardamom bushy dwarf virus* (CBDV) were reported as new virus species under this genus (Mandal et al. 2004; Sharman et al. 2008). ABTV mainly infects abaca and cause symptoms similar to those of BBTV in *Musa* spp.; however, it is less prevalent and recognized so far only in the Philippines and Malaysia (Sharman et al. 2008). The genus *Nanovirus*, initially included three species (Chu and Helms 1988; Katul et al. 1997; Sano et al. 1998), but the number has risen to five recently (Grigoras et al. 2009, 2010). *Coconut foliar decay virus* (CFDV) is the only unassigned species in the family *Nanoviridae*.

BBTD caused by BBTV, considered to be the most economically destructive of the viral diseases, can contribute up to 100 % yield reduction and is responsible for a dramatic reduction in cropping area in the Old World. The disease received its name from the bunched appearance of leaves at the top of infected plants. The common name banana is used for all the plants in the family *Musaceae*

that produce fruit. Among the plants in the two genera of family *Musaceae*, edible banana, abaca, plantain and ornamental bananas are the only confirmed hosts of BBTV. Edible bananas are among the world's top 10 food crops (FAOStat 2014) and the fourth most-cultivated fruit in over 130 countries in Africa, Asia, America, Oceania, and the Pacific. So BBTV could potentially have a devastating economic impact.

At present BBTD, is widespread in the Old World, mainly in Asia Pacific regions and to a lesser extent in the African continent. No serological differences have been detected among any isolates using polyclonal or monoclonal antibodies. Sequence diversity (>85 %) is fairly low among BBTV isolates around the world (Banerjee et al. 2014). A phylogenetic analysis of BBTV sequences reveals the presence of two major groups among BBTV isolates: Pacific–Indian Oceans (PIO) group and South-East Asian (SEA) group.

BBTV has a multicomponent genome comprising at least six transcriptionally active circular ssDNA components, each approximately 1 kbp in size (Burns et al. 1994, 1995; Harding et al. 1991, 1993). Each genomic component is individually encapsidated in the isometric virion particles of 18–20 nm diameter. Each icosahedron is composed of 20 triangular faces and 30 edges. Some isolates of BBTV contain additional Rep-encoding DNAs that are capable only of self-replication and behave like satellite molecules.

Although the promoters and transcriptional activity of the viral genome components are well understood, the gene functions and virus–host interactions require further investigation. Master replication (M-Rep) is the best-studied protein of BBTV, and the replication mechanism has similarities to the well-studied mechanism of replication in geminiviruses, another family of plant-infecting ssDNA viruses. Protein functions of BBTV genes are determined based upon similarity with the related geminiviruses. However, each family has its own distinctive features and differs from the other in particle morphology and dimensions, size of genome and number of components, modes of transcription, and species of vector. Three proteins of BBTV are known to suppress gene silencing in model plants. Infectious clones of BBTV for infectivity analysis have not been made yet.

Banana bunchy top disease

Host plants and disease symptoms

BBTV mainly infects species in the genus *Musa* including *M. acuminata*, *M. balbisiana*, *M. coccinea*, *M. jackeyi*, *M. ornata*, *M. textilis* and *M. velutina* (Espino et al. 1993; Furuya et al. 2003; Magee 1927, 1948; Thomas and Dietzgen 1991; Thomas and Iskra-Caruana 2000). BBTV also infects the closely related species *Ensete ventricosum* (Wardlaw 1961). There are a few reports of alternative hosts of this virus outside family *Musaceaei*, but these reports require further confirmation (Geering and Thomas 1997; Hu et al. 1996; Ram and Summanwar 1984).

Depending upon the time of infection and severity of disease, the symptoms may vary in the field. The early symptoms, characteristic dark green streaks on the leaves along the veins, vary in length to create a dot dash appearance called the Morse code pattern (Thomas and Iskra-Caruana 2000). As the infection progresses, leaves at the top of infected plants develop chlorosis along the margins and become narrower, dwarfed, upright and appear to be "bunched" at the top of the plant, thus giving the disease its name (Fig. 1). Symptom severity depends upon the susceptibility of the banana cultivar at the time of infection. Susceptible cultivars infected at a young stage are severely stunted and usually will not fruit, but if fruit is produced, it is likely to be distorted and twisted (Nelson 2004).

Disease history and current epidemiological status

The epidemiology of BBTD is simplified by one insect species as its vector and its limited host range. BBTD is prevalent in a number of Old World countries (36 countries in Africa, Asia, and Oceania), and there are no records of BBTD in the New World except in Hawaii, United States (Amin et al. 2008; Blomme et al. 2013; Conant 1992; Dale 1987; Diekmann and Putter 1996; Jones 2013; Kumar et al. 2008, 2011). The disease was first reported from Fiji in 1889 (Magee 1927; Stover 1972) and then from Taiwan in 1900 (Sun 1961). The origin of the virus in the Fiji epidemic is not clear; however, it is supposed to have been introduced through infected suckers from a country in Oceania (Simmonds 1931). Available records indicate the wide dissemination of BBTD in the Old World along with the movement of planting material by humans, traders and returning soldiers in the early part of the twentieth century (Fahmy 1927; Magee 1927, 1953; Wardlaw 1961). The presence of the virus in many countries from the South Pacific group can be traced back to its introductions within the last century. BBTV has caused some devastating epidemics including one in Australia between 1913 and 1926 that destroyed half of its banana industry. Another epidemic in Pakistan, with disease incidences up to 100 %, by 1992 had destroyed about half of the plantations (Khalid et al. 1993; Soomro et al. 1992). One of the most significant BBTD epidemics was in Tamil Nadu, India that resulted in huge production losses (Kesavamoorthy 1980). New BBTD outbreaks (2007–2010) in different states of

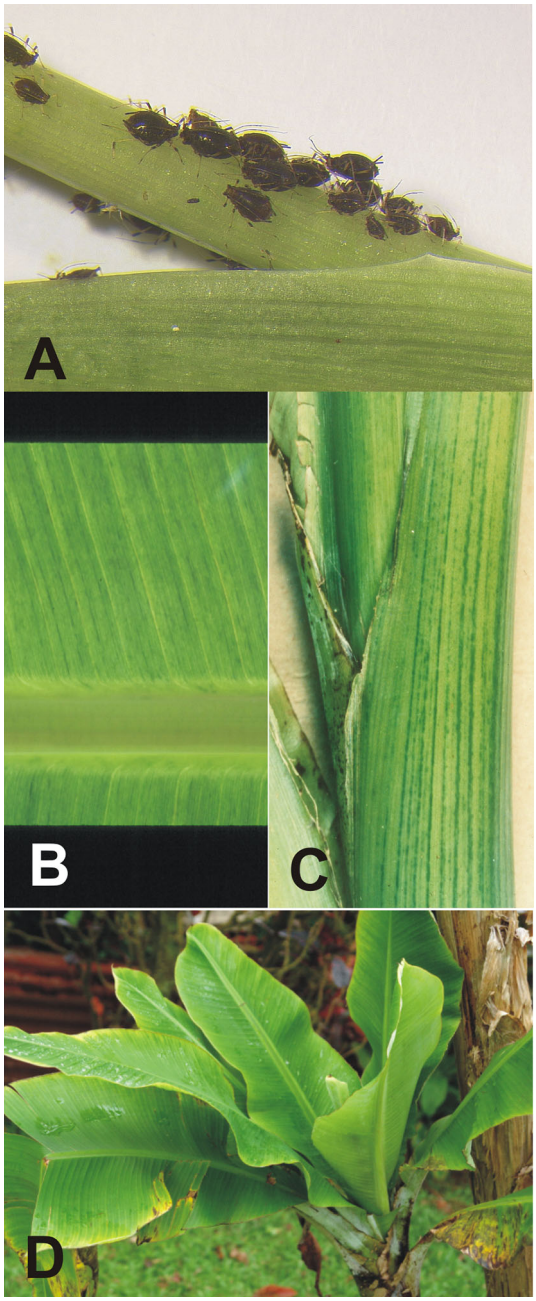

Fig. 1 Insect vector and symptoms of BBTV on banana plants. **a** Colony of banana aphids, *Pentalonia nigronervosa*. **b**, **c** Banana bracts and leaves showing the Morse code symptom. **d** Bunched leaves at top of infected plant (photographs are adopted by online resource maintained by Mr. Scot Nelson, University of Hawaii and the Hawaii Department of Agriculture)

India also caused production losses of US$50 million (Selvarajan and Balasubramanian 2014). At present, the disease is widespread in Asian Pacific region (Australia, China, Guam, India, Pakistan, Sri Lanka, Hawaii, Indonesia, Japan, the Philippines, Taiwan, Tonga, Samoa and Vietnam) and in the African continent (Egypt, Gabon, Angola and Burundi) to a lesser extent (Amin et al. 2008; Banerjee et al. 2014; Dale 1987; Ferreira 1991; Mansoor et al. 2005). It is not yet reported from Central or South America or Western Australia (Diekmann and Putter 1996; Kagy et al. 2001; Kenyon et al. 1997; Thomas and Iskra-Caruana 2000; Thomas et al. 1994). There are many other banana-growing regions, like the Caribbean, Papua New Guinea, Thailand and many countries in Africa and Asia, where BBTV has not been confirmed (Karan et al. 1994; Mandal 2010; Singh 2003). Figure 2 shows the worldwide prevalence of the disease.

Disease transmission and spread

The virus is locally transmitted by the aphid *P. nigronervosa* Coquerel (*Hemiptera: Sternorrhyncha: Aphididae*) in a persistent circulative and non-replicative manner. Long-distance spread is through infected plant material such as suckers and corms for vegetative propagation (Bressan and Watanabe 2011; Hafner et al. 1995; Hu et al. 1996; Magee 1927, 1940; Robson et al. 2007; Watanabe et al. 2013). A short latent period of 20–28 h is required for vector transmission (Anhalt and Almeida 2008). BBTV is not transmitted mechanically or by contact or agriculture implements (Hafner et al. 1995; Thomas et al. 2003).

Disease detection and control

Once established the disease is very difficult to control or eradicate. The universal strategies for controlling BBTV include identifying and destroying virus-infected plants as early as possible, replanting with virus-free plants and controlling aphid-vector populations with the use of insecticides (Dale 1987; Robson et al. 2006). ELISA (using monoclonal and polyclonal antibodies) was one of the first molecular detection techniques for BBTV detection (Thomas and Dietzgen 1991; Wu and Su 1990) and is still successfully used for BBTV diagnostics. Triple antibody sandwich ELISA, plate-trapped antigen ELISA, and double antibody sandwich ELISA have been established for the reliable detection of the virus in field-grown plants, tissue culture plants, and aphids (Geering and Thomas 1996; Selvarajan et al. 2010; Thomas and Dietzgen 1991; Wu and Su 1990). DNA-based diagnostics include nucleic acid spot hybridization, classical and real time PCR (Chen and Hu 2013; Harding et al. 1991; Selvarajan and Balasubramanian 2008; Xie and Hu 1995; Mansoor et al. 2005; Watanabe and Bressan 2013). Recently, loop-mediated isothermal amplification (LAMP), and rolling circle amplification (RCA) have also been used for BBTV diagnostics (Peng et al. 2012; Stainton et al. 2012).

The use of banana plants developed by micropropagation is not only the largest source of virus-free planting material but is also a good control strategy (Kumar et al. 2015).

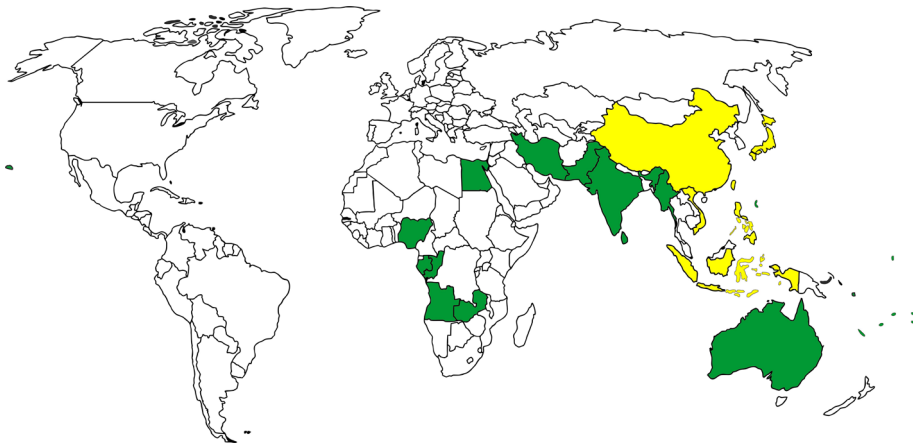

Fig. 2 Worldwide distribution of banana bunchy top disease. *Yellow* represents prevalence of the POI group; *green* shows SEA group of BBTV

Transgenic banana, with resistance against BBTV, has been attempted in Australia, Hawaii and India using pathogen-derived resistance (PDR) approach. PDR strategies including coat protein gene, full-length and truncated rep gene, RNAi vector using rep gene of BBTV have been applied (Borth et al. 2011; Dale and Harding 2003; Elayabalan et al. 2013; Shekhawat et al. 2012). Although efforts in this area are ongoing, such approaches against BBTV have only been successful in laboratory tests, not in glasshouse or field trials (Elayabalan and Kalaimughilan 2013; Horser et al. 2001; Su et al. 2003).

Banana bunchy top virus

Genome organization

The genome of BBTV consists of at least six components, each approximately 1 kb and associated with all geographical isolates (Fig. 3); "at least" is used because a few isolates have additional Rep-coding components (satellite Rep). The minimum infectious genome components required to produce typical symptoms of BBTV has yet to be determined because infectious clones have not been made yet. Initially, the genome components were designated 1 through 6, but different genome components were later assigned names according to their predicted functions (Burns et al. 1995; Harding et al. 1993). The functions were assigned based on their similarity with the genes of geminiviruses with known functions or with other nanovirus genes of known function. These components were named DNA-R [encoding a rolling-circle replication initiator protein (Rep)], DNA-S [encoding the coat protein (CP)], DNA-C [encoding the cell-cycle link protein (Clink)], DNA-M [encoding the movement protein (MP)], DNA-N [encoding the nuclear shuttle protein (NSP)] and DNA-U3 (unknown function) (Harding et al. 1993; Vetten et al. 2005; Wanitchakorn et al. 1997, 2000). The previously used designation of numbers correlates with the new naming system of the components as DNA-R (1), DNA-S (3), DNA-M (4), DNA-C (5), DNA-N (6) and DNA-U3 (2).

The genome components are characterized by the presence of two conserved regions within the intergenic region of each component: the stem loop common region (CR-SL) and the major common region (CR-M). The CR-SL contains a region of 69 nucleotides, which is 62 % identical among all components and incorporates a putative stem loop structure (Burns et al. 1995). The CR-M is located at the 5′ end of the CRSL. The CR-M incorporates a 66 ± 92 nucleotide region, which is 76 % identical between components (Burns et al. 1995). Polyadenylation signal is found to be associated with each gene. All components are monocistronic except for DNA-R. An internal second ORF, DNA-U5, is present in DNA-R (Beetham et al. 1997).

Origin, evolution and diversity of BBTV isolates

The area of origin of BBTV remains unclear; however according to one hypothesis, BBTV originated and evolved in the area of origin of banana; the South and Southeast Asian-Australasian region (Perrier et al. 2011; Stainton et al. 2012). The disease was first reported from Fiji in 1889. There is evidence that the disease was present before the start of the export industry for banana cultivars. Other earlier reports of disease are from Egypt (1901, source unknown), Australia and Sri Lanka (both in 1913, and probably from planting material imported from Fiji).

Individual BBTV component sequences (usually DNA R) were mostly used previously for phylogenetic analysis as there were only a few full length BBTV genome sequences available in data bases. The two groups of BBTV isolates determined on the basis of this sequence comparison were named the South Pacific group and the Asian group (Hu et al. 2007; Karan et al. 1994; Stainton

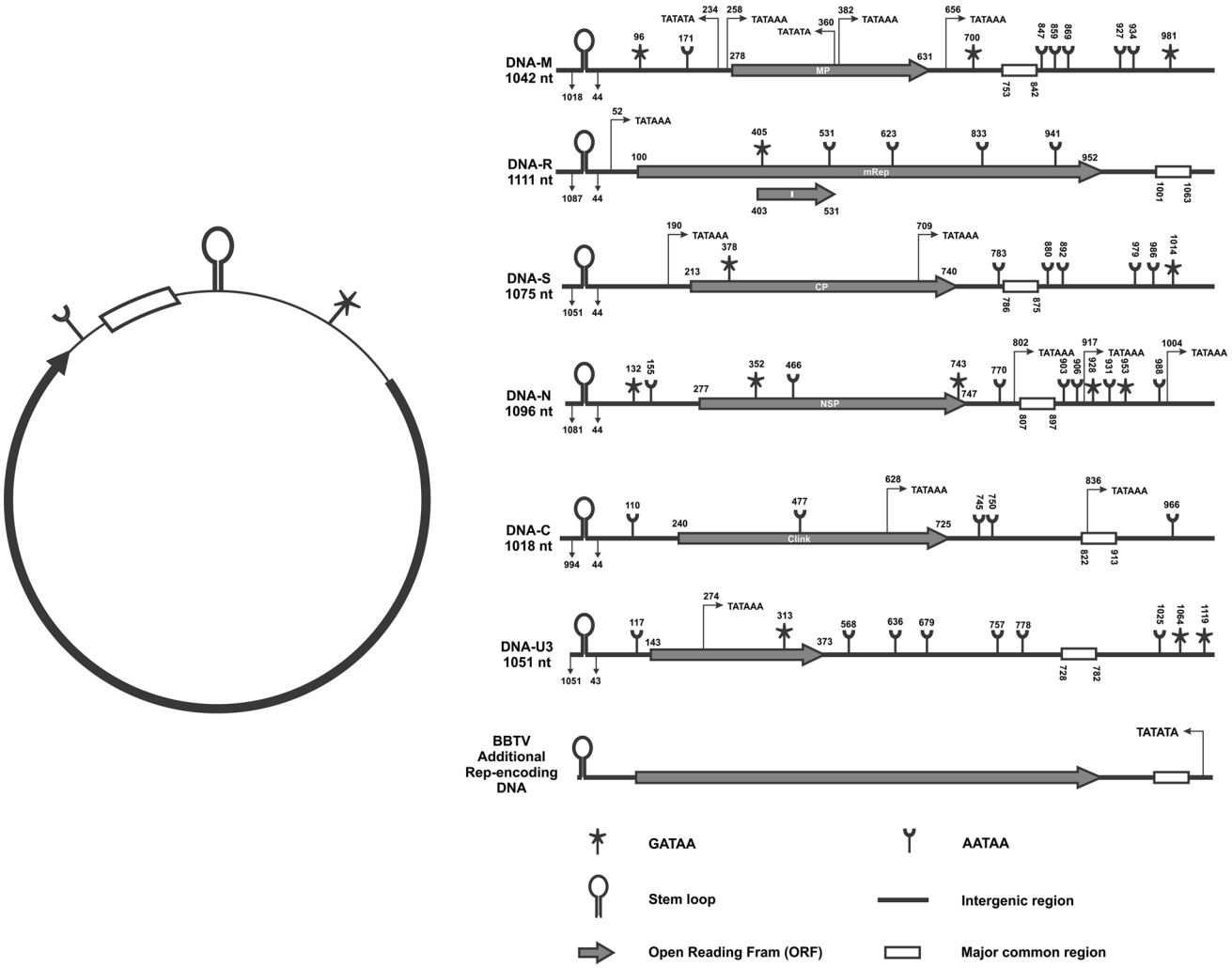

Fig. 3 Genome organization of BBTV. Reconstructed from Amin et al. (2008)

et al. 2012). This grouping has been modified recently to the PIO group (comprising the isolates from Australia, Egypt, Hawaii, India, Myanmar, Pakistan, Sri Lanka and Tonga) and SEA group (comprising the isolates from China, Indonesia, Japan, Philippines, Taiwan and Vietnam) (Yu et al. 2012).

There are two theories of evolution of these two groups of BBTV isolates based on sequence data analysis. According to one theory, the timescales over which these evolutionary groups diverged might span the history of banana cultivation (Perrier et al. 2011). However, the other theory, based upon more sequences and recent studies, proposes that the two main BBTV lineages could have split only hundreds of years ago as an outcome of high basal mutation rate and frequent homologous recombination between different components of the same genome (Hu et al. 2007) and between homologous components in different genomes (Hu et al. 2007; Hyder et al. 2011).

The PIO group (shown in Fig. 2) has a broader distribution over the globe than the SEA group does, and the transport of infected banana material is considered the main reason. Differential adaptation of Asian and South Pacific groups of BBTV isolates is suggested for different banana species, but this hypothesis cannot be proven because of the lack of an infectivity assay system. All available BBTV component sequences were analyzed by Stainton and Coworkers in 2012, who showed that DNA-R is the most conserved component, with more than 88 % sequence identity among the isolates, while DNA-U3 is least conserved with 73 % sequence identity. Rest of the components, i.e., DNA-S, DNA-C, DNA-N and DNA-M, have more than 80 % identity among all isolates.

Because the overall variation in BBTV isolates across the globe is very low (85 %), variation within countries is also low. Genetic diversity of BBTV isolates is low within Pakistan, India, Indonesia, Africa and Oceania (Adegbola

et al. 2013; Amin et al. 2008; Banerjee et al. 2014; Chiaki et al. 2015; Selvarajan et al. 2010; Stainton et al. 2012).

Satellite molecules associated with BBTV

Additional circular ssDNA components have also been found. Rep satellites are associated with a few BBTV isolates and encode additional Rep-like proteins. These molecules are the same size as the rest of the BBTV genome components. Additional Reps encoded by these satellites are suggested to be involved in self replication. Rep satellites have been detected in isolates from the SEA group but not from the PIO group (Amin et al. 2008; Horser et al. 2001). Satellite Reps have a CR-SL, but the stem sequence is not conserved as are the other integral DNA components. Unlike DNA-R, the putative satellites lack the internal ORF, their TATA boxes are at the 5′ end of the stem loop, and they generally lack the CR-M. Satellites Reps differ from M-Rep not only in genome organization but also in their coding sequences (Horser et al. 2001). Interestingly, the amino acid sequences of satellite Reps are actually more closely related phylogenetically to the Reps encoded by nanovirids outside the genus Babuvirus than with M-Rep of BBTV.

These additional components named as DNA-S1, S2, S3, W1, W2 and Y. DNA-S1, S2, W1, W2 and Y were originally found to be associated with Tiawanese isolates, whereas S3 was associated with a Vietnamese isolate of BBTV (Yeh et al. 1994; Wu et al. 1994). Though these molecules are found in databases with these different names, sequence analysis reveals that S2 and W2 are homologous, and Y and W1 are essentially the same molecules (Horser et al. 2001). Similar molecules have been detected by Southern hybridization in isolates from the Philippines, Tonga, and Western Samoa, but not from Australia, Egypt, Fiji, and India.

These satellites have similarity to geminivirus (monopartite begomovirus)-associated Rep-like alpha satellites, which are about half the size of the helper virus and play no role in the etiology of begomovirus-induced diseases. Alpha satellites replicate autonomously, and they encode a nanovirus-like replication-associated protein (Briddon et al. 2004; Mansoor et al. 1999). Although they are not well characterized, it is very likely that, like alpha satellites, the satellites associated with BBTV are responsible for reducing the levels of helper viruses due to competition for host factors involved in DNA replication (Briddon and Stanley 2006). Evidence for this hypothesis comes from studies on the Rep satellites of another nanovirus, FBNYV; the expression of Rep satellites along with all genomic components of the virus substantially reduces the number of symptomatic and severely infected faba bean plants and thus interferes with establishment of disease. Moreover, for many nanovirid infections, additional Rep DNAs were identified often before the master Rep-encoding DNA-R, suggesting that they attain higher concentrations than DNA-R in nanovirid-infected plants. In vitro studies on the activity of the satellite Reps of FBYNV revealed that the Rep satellite has 10 times more origin cleavage and nucleotidyl-transfer activity than does the M-Rep of the virus (Timchenko et al. 2006).

Transcription of viral genes

BBTV replicates via a dsDNA intermediate that also serves as a template for virion sense transcription. Each DNA component with the exception of Rep encodes a single gene in the virion sense that is transcribed during infection. Two mRNAs are transcribed from DNA-R, one mapping to the M-Rep, ORF and the other to a small ORF completely internal to the major ORF in a +2 reading frame (Beetham et al. 1997, 1999; Herrera-Valencia et al. 2007). Promoter regions associated with each of the six integral genome components as well as Rep satellite S1 and S2 have been characterized using transient as well as stable expression of marker genes in both monocot and dicot systems (Dugdale et al. 1998, 2000; Hermann et al. 2001). On the basis of the transient GFP expression in embryogenic cells, DNA-M and DNA-C might encode genes that are expressed early in infection (Chiu et al. 1996; Dugdale et al. 1998, 2000).

Protein functions and virus–host interactions

The functions of all gene products associated with BBTV have been elucidated with the exception of those encoded by DNA-R (U5/small internal ORF) and DNA-U3 (Amin et al. 2011). The protein product of ORF U5 is suggested to have a role in regulating Rep expression, but further evidence is needed for confirmation (Beetham et al. 1997). Primers used for self-priming of BBTV genome components are derived from DNA-5. DNA-R (M-Rep/major ORF) encodes the 33.6 kDa master replication initiation protein (Hafner et al. 1997a; Harding et al. 1993). M-Rep is the best characterized protein of BBTV. The nuclear shuttle protein (NSP, 20-kDa) of BBTV is encoded by DNA-N (Wanitchakorn et al. 2000). DNA-C encodes for a cell-cycle-linked protein, clink (20-kDa). Clink is involved in facilitating viral replication by directing host cell progression into the S-phase by interacting with a wide range of cell-cycle-related proteins (Wanitchakorn et al. 2000). Clink is also reported to be a suppressor of RNA silencing (Amin et al. 2011). DNA-S encodes the coat protein (CP, 19.3 kDa). The coat protein gene of BBTV is highly conserved, with a maximum difference of 3 % at the amino acid level between isolates. The movement protein (MP) has a hydrophobic N terminus and is encoded by DNA-M

(Wanitchakorn et al. 1997). Both CP and MP also act as suppressors of gene silencing (Amin et al. 2011; Niu et al. 2009).

Replication of viral genome

The overall process of BBTV replication is assumed to be much the same with all other nanoviruses and geminiviruses (Harding et al. 1993; Wu et al. 1994; Sano et al. 1998; Timchenko et al. 1999). Like other nanoviruses in BBTV, only one of the Reps is a master Rep (M-Rep) and is capable of triggering replication of genomic components (Timchenko et al. 2000). One of the first events is the synthesis of viral dsDNA with the aid of host DNA polymerases and endogenous primers bound to the genomic DNA (Hafner et al. 1997b). From these dsDNA forms, the host RNA polymerase then transcribes mRNAs encoding the M-Rep and other viral proteins required for virus replication. Viral DNA replication is initiated by the M-Rep protein that interacts with common sequence signals on all the genomic DNAs. Nicking and joining within the conserved nonanucleotide sequence TAT/GTATT-AC by the Rep proteins of BBTV has been demonstrated by in vitro studies (Hafner et al. 1997a; Herrera-Valencia et al. 2007). In the case of the geminiviruses, the Rep proteins interact with cell cycle regulatory proteins (Gronenborn 2004) to enhance the replication of the viral DNAs by the cellular replication machinery. In nanoviruses, this function is fulfilled by Clink and is very likely the same role played by the Clink protein of BBTV. Clink of the nanoviruses has been shown to bind an Rb analogue as well as SKP1, part of the ubiquitin-protein turnover pathway (Aronson et al. 2000; Lageix et al. 2007).

Localization of BBTV in plants and aphid vector

BBTV is a phloem-limited virus. The NSP of BBTV is targeted to the nucleus when expressed alone but, in the presence of MP, is targeted to the cell periphery (Wanitchakorn et al. 2000). The characteristics of the NSP and MP of BBTV are very similar to those of the BV1 (nuclear shuttle) and BC1 (movement) proteins of geminiviruses (Sanderfoot and Lazarowitz 1995; Noueiry et al. 1994). BBTV may utilize a system analogous to that of the geminiviruses where NSP binds with viral DNA to be transported, while the MP transports the NSP–DNA complexes to the cell periphery for intercellular transport. To prevent degradation inside insect vectors, circulative plant viruses including geminiviruses bind to GroEL proteins produced by endosymbiotic bacteria. However, for BBTV a distinct tissue tropism has been proposed in that the virus is translocated from the anterior mid gut to the salivary glands of *Pentalonia nigronervosa* without interacting with GroEL (Bressan and Watanabe 2011; Watanabe et al. 2013).

Suppression of gene silencing

Most plant viruses have evolved suppressor proteins as a counter-defense strategy to counteract host RNA silencing (Chapman et al. 2004). The mechanism of suppression of gene silencing is not well studied in BBTV. However, according to two independent reports involving two different isolates of BBTV, three proteins of BBTV (CP, MP and Clink) have been shown to act as silencing suppressors (Amin et al. 2011; Niu et al. 2009). Both reports confirm the role of the MP as a silencing suppressor. However, for one of the isolates, the second protein reported to be a suppressor is CP, but for the other isolate, it is Clink. Interestingly, both these studies used the same Potato virus X (PVX) delivery system in transgenic *Nicotiana benthamiana* and reported suppression of GFP silencing (Amin et al. 2011; Niu et al. 2009). That this disparity is due to variation in the viral defense pathways in different isolates of BBTV is very unlikely because of the sequence similarity between the isolates used in the two studies. However, the disparity might indicate that viral suppressors evolve rapidly, shifting the main actor from one protein to another one as also reported for the related begomoviruses (Hohn and Vazquez 2011).

Conclusions

BBTV is the most important disease of banana where it is present. Regions of the world where the virus has not been reported but the insect vector is present are at risk of acquiring the disease. Because the virus has a limited host range and no germplasm resistant to the disease is available, the only measure to control the disease is planting disease-free material and killing the aphid vector. Although important progress has been made in understanding the gene function of this virus recently, further research in this area is required to fully understand the role of viral proteins in disease pathogenesis and elucidate host–pathogen interactions. Lack of a system to analyse infectivity is the main hurdle for studies on the interaction between BBTV and its host. A better understanding of virus pathogenesis will improve the likelihood that PDR can be used successfully against BBTV.

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Compliance with ethical standards

Conflict of interest I declare that I have no conflict of interest.

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