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Pathogen profile

Bacilliform DNA-containing plant viruses in the tropics: commonalities within a genetically diverse group

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SUMMARY

Plant viruses, possessing a bacilliform shape and containing double-stranded DNA, are emerging as important pathogens in a number of agricultural and horticultural crops in the tropics. They have been reported from a large number of countries in African and Asian continents, as well as from islands from the Pacific region. The viruses, belonging to two genera, *Badnavirus* and *Tungrovirus*, within the family *Caulimoviridae*, have genomes displaying a common plan, yet are highly variable, sometimes even between isolates of the same virus. In this article, we summarize the current knowledge with a view to revealing the common features embedded within the genetic diversity of this group of viruses.

Taxonomy: Virus; order Unassigned; family *Caulimoviridae*; genera *Badnavirus* and *Tungrovirus*; species Banana streak viruses, *Bougainvillea spectabilis chlorotic vein banding virus*, *Cacao swollen shoot virus*, *Citrus yellow mosaic badnavirus*, Dioscorea bacilliform viruses, *Rice tungro bacilliform virus*, Sugarcane bacilliform viruses and *Taro bacilliform virus*.

Microbiological properties: Bacilliform in shape; length, 60–900 nm; width, 35–50 nm; circular double-stranded DNA of approximately 7.5 kbp with one or more single-stranded discontinuities.

Host range: Each virus generally limited to its own host, including banana, bougainvillea, black pepper, cacao, citrus species, *Dioscorea alata*, rice, sugarcane and taro.

Disease symptoms: Foliar streaking in banana and sugarcane, swelling of shoots in cacao, yellow mosaic in leaves and stems in citrus, brown spot in the tubers in yam and yellow–orange discoloration and stunting in rice.

Useful websites: http://www.dpvweb.net.

INTRODUCTION

Viruses belonging to the Genera *Badnavirus* and *Tungrovirus* are emerging as important pathogens of various crops in the tropics. Both genera form part of the family *Caulimoviridae*, whose members have a double-stranded DNA (dsDNA) genome of 7.5–8.0 kb displaying features suggestive of a reverse transcription-based replication step, namely a highly conserved initiator transfer RNA ($tRNA^{met}$) binding site, together with a gene arrangement [coat protein (CP)–protease–reverse transcriptase (RT)/ribonucleaseH (RNaseH)] resembling the *gag–pol–env* pattern of animal retroviruses. According to the latest release of the International Committee on the Taxonomy of Viruses (ICTV) (2011), within the family *Caulimoviridae*, genus *Badnavirus* has the largest number of species (25), the majority of which (19) are found in the tropics. Genus *Tungrovirus* has a single species, *Rice tungro bacilliform virus* (RTBV), which resembles badnaviruses in having a dsDNA and bacilliform shape, but differs in the genome organization [an extra open reading frame (ORF)] and vector transmission (by leafhopper, as opposed to mealybugs in the case of badnaviruses).

Over the past few years, reports of the analysis of nucleotide sequences of the members of these two viral genera have been accumulating steadily. This review attempts to synthesize the above information, focusing mainly on the badnaviruses found in the tropics (Table 1), and attempts to find commonalities within the diversity exhibited in their genomes. As these viruses are emerging as important pathogens of agricultural and horticultural crops in the tropics, their common features may point towards new strategies for their management.

DIVERSITY, DISTRIBUTION AND HOST RANGE

Badnaviruses have been reported from across all tropical regions of the African, American and Asian continents, and in the Pacific Islands (Fig. 1). They are regarded as a highly diverse and heterogeneous group of viruses (Al-Kaff and Covey, 1994; Geering *et al*., 2000; Harper *et al*., 2004, 2005; Jaufeerally-Fakim *et al*., 2006; Kenyon *et al*., 2008; Lockhart and Olszewski, 1993). They share relatively low nucleotide identities, even within the same genus, when compared with other virus genera. The number of ORFs also varies from virus to virus; whereas most contain three ORFs (*Sugarcane bacilliform virus*, SCBV), some may have four (*Taro*

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Table 1 Hosts, vectors and genomic information on badnaviruses and tungrovirus.

Name	Genome size (kb)	Number of ORFs	Host(s)	Mode of transmission	Country(ies) reported from	Accession numbers of complete sequences	Reference(s)
Banana streak virus	7.4	4	Banana	Aphid, mealybug (*Dysmicoccus brevipes*, *Planococcus citri* and *P. ficus*), pink sugarcane mealybug (*Saccharicoccus sacchari*), pineapple mealybug (*D. brevipes*)	Uganda, Australia, Vietnam, Nigeria, India	NC_008018, DQ859899, NC_007003, NC_003381, DQ451009, NC_007002, DQ092436, AF214005, AY493509, AY750155	Geering *et al*. (2005); Harper and Hull, (1998); Lockhart and Jones, (2000); Lheureux *et al*. (2007)
Bougainvillea vein banding-associated badnavirus	8.8	4	*Bougainvillea spectabilis*	–	Brazil, Taiwan, India	NC_011592, EU034539	Baranwal *et al*. (2010); Rivas *et al*. (2005)
Cacao swollen shoot virus	7.1	5	*Theobroma cacao*	Mealybug (*P. citri*, *Ferrisia virgata* and *P. njalensis*)	Togo, Ghana, Ivory Coast, Nigeria	NC_001574, AJ609019, AJ781003, AJ609020, JN606110, L14546, AJ534983, AJ608931	Hagen *et al* (1993); Kouakou *et al*. (2012); Muller and Sackey (2005); Quainoo *et al*. (2008)
Citrus yellow mosaic badnavirus	7.5	6	Citrus (sweet orange, Rangpur lime, acid lime, pummelo)	Mealybug (*P. citri*)	India	NC_003382, DQ875213, JN006806, JN006805, AF347695, FJ617224, EU489744, EU489745, EU708316, EU708317, EU884191	Borah *et al*. (2009); Huang and Hartung (2001); Johnson *et al*. (2012)
Pineapple bacilliform comosus virus and *Pineapple bacilliform erectifolius virus*	7.6	3	Pineapple	Mealybug (*D. brevipes*)	Australia	NC_014648, GQ398110, GU121676	Gambley *et al*. (2008)
Piper yellow mottle virus	–	–	*Piper nigrum*	Mealybug (*F. virgata*, *P. citri*) and black pepper lace bug (*Diconocoris distanti*). Also by grafting	Brazil, Malaysia, Thailand, Philippines, Sri Lanka, India	Complete sequences are not available	Bhat *et al*. (2003); Lockhart *et al*. (1997)
Rice tungro bacilliform virus	8.0 (South-East Asian), 7.9 (South Asian)	4	*Oryza sativa*	Green leafhopper (*Nephotettix virescens*, *N. cincticeps*, *Resilia dorsalis*)	Bangladesh, India, Indonesia, Malaysia, Philippines, Vietnam	JX255736, NC_001914, HQ385226, FN377814, AF113831, AF113830, AF113832, AF220561, AF076470, M65026, X57924, D10774, AJ314596, JX255736	Banerjee *et al*. (2012); Cabauatan *et al*. (1999); Hay *et al*. (1991); Kano *et al*. (1992); Marmey *et al*. (1999); Mathur and Dasgupta (2007, 2013); Nath *et al*. (2002); Qu *et al*. (1991); Sharma and Dasgupta (2012)
Sugarcane bacilliform virus	7.6	3	Sugarcane *Saccharum officinarum*, *S. barberi*, *S. sinense*, *S. robustum* and *Saccharum* L. interspecific hybrids	–	Morocco, USA, India	NC_008017, NC_003031, AJ277091, NC_013455, FJ824814, FJ439817, FJ824813, M89923	Bouhida *et al*. (1993); Lockhart and Autrey (1988); Muller *et al*. (2011)
Taro bacilliform virus	7.5	4	Taro (*Colocasia esculenta*)	Mealybug	Pacific Island countries	NC_004450, AF357836	Yang *et al*. (2003)
Dioscorea bacilliform virus	7.3	3	*D. cayenensis*, *D. bulbifera*, *D. japonica*	–	Caribbean, Ivory Coast, Japan, France, Benin, Ghana, Togo, Nigeria	NC_009010, DQ822074, DQ822073	Seal and Muller (2007)

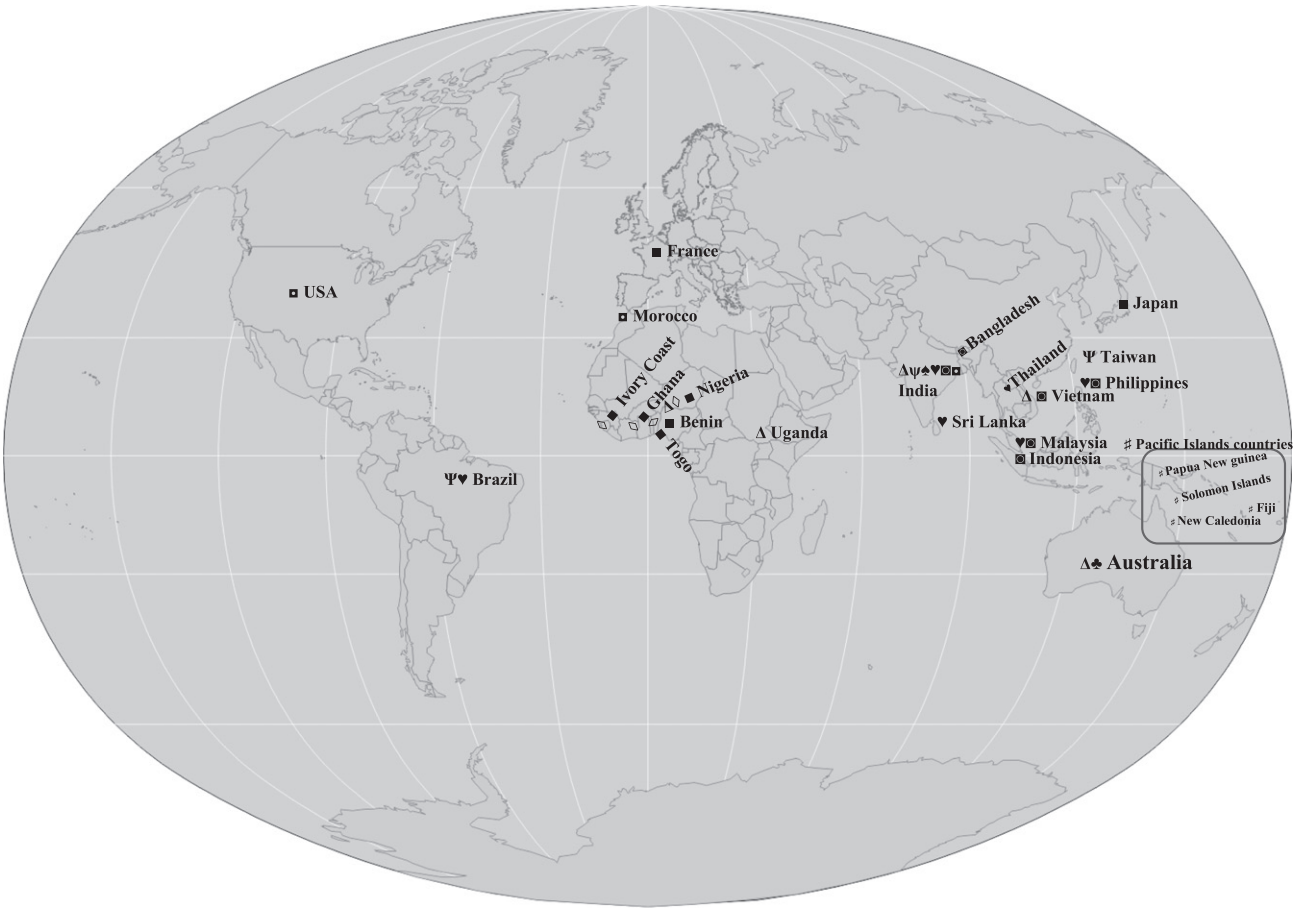

Fig. 1 Occurrence of badnaviruses and tungrovirus across the tropical regions of the world. Symbols given for each virus are as follows: Δ, *Banana streak virus*; ψ, *Bougainvillea vein banding-associated badnavirus*; ◊, *Cacao swollen shoot virus*; ♠, *Citrus yellow mosaic badnavirus*; ♣, *Pineapple bacilliform comosus virus* and *Pineapple bacilliform erectifolius virus*; ♥, *Piper yellow mottle virus*; ◙, *Rice tungro bacilliform virus*; ◘, *Sugarcane bacilliform virus*; ♯, *Taro bacilliform virus*; ■, *Dioscorea bacilliform virus*.

bacilliform virus, TaBV), five (*Cacao swollen shoot virus*, CSSV), six (*Citrus yellow mosaic badnavirus*, CMBV) or seven (*Dracaena sanderiana badnavirus*) ORFs.

One of the most well-studied badnavirus groups is that infecting banana: Banana streak viruses (BSVs). Viral leaf streak of banana was first described in Ivory Coast, Africa in 1968 (Lassoudiere, 1974), and the causal agent, BSV, was identified in Morocco in 1985 (Lockhart, 1986). Countries affected by this disease include Malaysia, China, Indonesia, India, Philippines, Vietnam, Thailand, Sri Lanka and Australia (Jones and Lockhart, 1993; Vuylsteke *et al*., 1996). In Africa, BSVs from Uganda were found to show a very high degree of variability, possibly as a result of a series of introductions of banana into Uganda, each with a different complement of infecting viruses (Tushmereirwe *et al*., 1996). Initially, four isolates of BSV, namely BSV-RD (from cultivar Red Decca), BSV-Cav (from cultivar Williams), BSV-Mys (from cultivar Mysore) and BSV-GF (from cultivar Goldfinger), were described by Lockhart and Olszewski (1993) based on DNA hybridization analysis. Two more isolates, BSV-OL (from cultivar Obino l'Ewai; Harper *et al*., 1999) and, more recently, BSV-IM (Geering *et al*., 2011) have been reported.

Variation in the nucleotide sequences of BSV isolates is considerable. For example, Geering *et al*. (2000) observed 21.8%–33.6% sequence differences in the RT/RNaseH coding regions of three BSV isolates in Australia. In another report, 140 partial sequences of the RT/RNaseH region (representing 49 infected banana samples) were reported to belong to as many as 15 different species (Harper *et al*., 2005). Interestingly two isolates of BSV cloned from southern India showed 99% and 97% identity to BSV-OL in the RT/RNaseH domain (Cherian *et al*., 2004).

SCBV is another group of relatively well-studied badnaviruses, widely reported from a number of species of sugarcane (*Saccharum officinarum*, *S. barberi*, *S. sinense*, *S. robustum* and *Saccharum* L. interspecific hybrids). It was first reported in 1985 (Rodriguez-Lema *et al*., 1985) and was later purified in 1988 (Lockhart and Autrey, 1988). SCBVs have since been found to be distributed throughout all major sugarcane-growing regions worldwide causing considerable yield reductions in some varieties

(Autrey *et al*., 1995; Comstock and Lockhart, 1990; Lockhart and Autrey, 1988; Viswanathan *et al*., 1996). The first complete sequence of SCBV-Mor (from Morocco; NC_008017) was reported in 1993 (Bouhida *et al*., 1993). Presently, there is one more complete SCBV sequence in the database, known as SCBV-IM (isolate Ireng Maleng, from Australia; NC_003031). Although separated by a large geographical distance, SCBV-IM was found to share quite high sequence identities with SCBV-Mor (with amino acid sequence identities of 91.4%, 83.8% and 85.3% in ORF I, II and III, respectively). However, all SCBVs were more closely related to each other than to other badnaviruses within their ORF III amino acid sequence. The significant serological heterogeneity (Autrey *et al*., 1995) and sequence variability reported in SCBVs (Braithwaite *et al*., 1995; Smith *et al*., 1996) suggest that the viral populations are complex and variable, even within the group, a view further supported by reports by Geijskes *et al*. (2002) and Muller *et al*. (2011). The latter group reported three more complete sequences of SCBV, presumably representing a new species, *Sugarcane bacilliform Guadeloupe A virus*/*Sugarcane bacilliform Guadeloupe D virus*. The variability has been exemplified further in the latest ICTV report, in which SCBV-Mor and SCBV-IM have been described as two different species (Fauquet *et al*., 2005).

SCBV is an exception among the badnaviruses with its special ability to infect plants of two different families. SCBV-Mor has been found to infect banana (Musaceae), and rice (Bouhida *et al*., 1993), *Sorghum halepense* and *Brachiaria extensa* (Frison and Putter, 1993), all three of the family Poaceae, through agroinoculation (cloned viral DNA in a binary plasmid introduced into the plant through *Agrobacterium*). Considering the fact that BSV can also multiply in sugarcane, SCBV and BSV are sometimes considered as strains of the same virus (Lockhart and Autrey, 1988).

CMBV, the causative agent for the mosaic disease of citrus, has been reported from a few districts of the state of Andhra Pradesh, India (Ahlawat *et al*., 1996; Dakshinamurti and Reddy, 1975) in at least four important citrus species: sweet orange (Ahlawat *et al*., 1996), pummelo (*C. grandis* L., Osbeck; Ahlawat, 1997; Ahlawat *et al*., 1996), acid lime (*C. aurantifolia*; Johnson *et al*., 2012) and rough lemon (*C. jambhiri*; Johnson *et al*., 2012). The virus is graft transmissible to 13 citrus cultivars. Five complete CMBV sequences from four different hosts [sweet orange, rangpur lime (*Citrus* × *limonia*, Osbeck), acid lime and pummel], all four sequences sharing more than 90% identity to each other (Borah *et al*., 2009; Johnson *et al*., 2012), are available in the database.

The association of a flexuous badnavirus with internal brown spot symptoms was first reported in *Dioscorea alata* and *D. cayenensis-rotundata* in the Caribbean islands (Harrison and Roberts, 1973; Mantelle and Haque, 1979). Thereafter, the virus was partially characterized from *D. alata* (Phillips *et al*., 1999). The complete nucleotide sequence (7.4 kb) of another badnavirus infecting *D. alata*, which is not associated with the internal brown spot, was also reported and was named *Dioscorea alata bacilliform virus* (DaBV; Briddon *et al*., 1999). By immunosorbent electron microscopy, badnavirus-like particles were reported from yam (*D. sansibarensis*), which was later further characterized by sequence analysis of the viral DNA. The sequence shared 61.9% identity with DaBV, and the virus was named *Dioscorea sansibarensis bacilliform virus* (DsBV; Seal and Muller, 2007). A study on 14 yam-infecting DaBV and DsBV isolates from West Africa showed that they shared between 75% and 96% amino acid identities with each other (Eni *et al*., 2008).

TaBV is restricted to its host and is widespread throughout the Pacific Island countries (Yang *et al*., 2003). Analysis of the putative RT/RNaseH regions from 22 TaBV isolates collected from Fiji, French Polynesia, New Caledonia, Papua New Guinea, Samoa, Solomon Islands and Vanuatu showed a variability of 22.9% and 13.6% at the nucleotide and amino acid levels, respectively. The diversity was higher within the CP coding region (30.7% and 19.5% at the nucleotide and amino acid levels, respectively) in 13 of the 22 isolates mentioned above. Among all the isolates, those from the Solomon Islands showed the greatest variability, whereas those from New Caledonia and Papua New Guinea were the least variable (Yang *et al*., 2003).

CSSV was first reported on cocoa in West Africa and Nigeria in 1936 and 1944, respectively (Adegbola, 1971; Murray, 1945), but it was not until 1993 that the complete nucleotide sequence was reported (Hagen *et al*., 1993). Subsequently, five new isolates have been sequenced (sharing a maximum of 29.4% identity), two from Togo and three from Ghana (Muller and Sackey, 2005).

Bougainvillea spectabilis chlorotic vein banding virus (BsCVBV), listed as *Bougainvillea chlorotic vein banding virus* by the ICTV, infecting *Bougainvillea spectabilis* Willd, was reported for the first time from Brazil (Rivas *et al*., 2005). The same authors also generated a partial sequence (465 bp) of the viral DNA. Simultaneously, another badnavirus from Taiwan was also reported to cause mottling, chlorosis and vein banding in bougainvillea; the partial (676 bp) sequence of the latter shared 82% identity to the former (Tsai *et al*., 2005). Two new isolates of BsCVBV were partially characterized from southern and northern India (Baranwal *et al*., 2010). A polymerase chain reaction (PCR)-amplified 600-bp fragment from the RT/RNaseH region from both viruses showed more than 70% identity to BsCVBV.

There are several reports of badnaviruses associated with plant diseases in the tropics, whose identities are still unclear. For example, two badnaviruses, *Pineapple bacilliform comosus virus* (PBCoV) and *Pineapple bacilliform erectifolius virus* (PBErV), and an endogenous badnavirus (*Endogenous pineapple pararetrovirus-1*, ePPRV-1) were suspected to be involved in Pineapple mealybug wilt disease from partial sequence analyses (Gambley *et al*., 2008). However, there is no information regarding the complete genome sequence and infectivity of the isolated viruses in their natural and/or experimental hosts. Some other reports of the occurrence of badnaviruses associated with disease

symptoms include *Piper yellow mottle virus* (PYMV), reported from Brazil, Malaysia, Thailand, Philippines, Sri Lanka (Duarte *et al*., 2001; Lockhart *et al*., 1997) and India (Bhat *et al*., 2003), and a badnavirus-like sequence amplified from *Yucca elephantipes* from Costa Rica and Guatemala (Clover *et al*., 2003).

In the genus *Tungrovirus*, RTBV infection, together with *Rice tungro spherical virus* (RTSV; genus *Waikavirus*; family *Secoviridae*), causes rice tungro disease. At present, 12 complete sequences of RTBV are available in the database, eight of which are from South-East Asia and four from India. The genome sequences fall into two distinct groups, the South Asian and South-East Asian groups, sharing approximately 75% sequence identity, the nucleotide identities within a group being about 95% (Fan *et al*., 1996; Mathur and Dasgupta, 2007, 2013; Nath *et al*., 2002).

DISEASE INCIDENCE AND ECONOMIC LOSSES

Diseases caused by badnaviruses are widespread in tropical regions of the world. The symptoms are mostly expressed in the aerial parts of the plants and yield losses in crop plants caused by badnavirus infections can reach 90% (for example, in BSV; Dahal *et al*., 2000; Daniells *et al*., 2001; Lassoudiere, 1974). CMBV is one of the major factors of citrus decline (Aparna *et al*., 2002), which can sometimes lead to total failure of production from large citrus plantations by causing the premature death of plants (Ahlawat *et al*., 1996). Trees affected by CMBV produce significantly fewer and poorer quality fruits containing less juice and ascorbic acid (Ahlawat *et al*., 1996). Cacao swollen shoot disease causes serious crop losses in many cacao-growing areas of West Africa (Thresh, 1991). CSSV and Phytophthora pod-rot are the two most important diseases of cacao in Nigeria (Adejumo, 2005). Thresh (1959) reported that large areas in Nigeria (approximately 70 000 ha) had to be abandoned because of devastation by CSSV. Although SCBV is known to occur in all sugarcane-growing regions of the world, details regarding the extent of yield losses caused by the virus are not available (Autrey *et al*., 1995). The virus was detected in around 50% of samples of *S. officinarum* L. clones in the USA (Comstock and Lockhart, 1990), and in the majority of samples from Morocco and Hawaii (Lockhart and Autrey, 1988).

In certain parts of the province of Kerala in India, up to 100% incidence of pepper mosaic disease, which is associated with PYMV, has been reported in black pepper plantations (Bhat *et al*., 2003), and causes considerable seed yield losses (Sivaraman *et al*., 2002). Similarly, the presence of badnaviruses in yam in the South Pacific islands poses serious implications for the international movement of yam germplasm (Kenyon *et al*., 2001).

Rice tungro disease, caused by the tungrovirus species RTBV (Azzam and Chancellor, 2002), is one of the most devastating viral diseases affecting food production in the world, and is the most important viral disease of rice in South and South-East Asia (Hull, 1996). The annual loss caused by rice tungro disease has been estimated to be in excess of $US10^9$ (Herdt, 1991). In India, although losses in rice production caused by the disease have been estimated to be about 1% at the national level, the figure could be substantial in specific regions of the country and may result in grave food shortages (Muralidharan *et al*., 2003).

SYMPTOMS

Various types and degrees of symptoms, ranging from mild leaf distortion to death, have been reported to be associated with badnavirus infection. The severity and types of symptoms also depend on the species as well as the developmental stage of the host. Most of the badnaviruses, however, cause some kind of malformation in the foliage, or parts thereof. Symptoms of badnaviruses may also vary depending on the virus strains/isolates. For example, BSV isolates differ widely in their symptoms, varying from faint broken chlorotic lines to the necrosis of emerging leaves. There are, nevertheless, extreme cases of total and/or premature death of plants in badnavirus infections, such as BSVs (Geering *et al*., 2005), TaBV (Jackson, 1978; Rodoni *et al*., 1994), CSSV (Longworth, 1963), SCBVs (Viswanathan *et al*., 1996), etc. However, sometimes, certain badnaviruses may also produce symptomless infection, for example, SCBV and CSSV on certain sugarcane and cacao varieties (Geijskes *et al*., 2002; Muller *et al*., 2001). Virus-specific symptoms are sometimes observed during the infection of certain badnaviruses, such as irregularly shaped outgrowths on the petioles in infections of TaBV (Jackson, 1978; Rodoni *et al*., 1994).

Several badnaviruses are also known to produce symptoms in plant parts in addition to the foliage. Examples of such viruses include BSVs producing streak symptoms in the pseudostem, which vary in colour from yellow to brown to black (Lockhart, 1986), DaBV causing discoloration of the flesh of the yam tuber (described as 'internal brown spot'; Harrison and Roberts, 1973) and some CSSV isolates inducing swelling on shoots (Longworth, 1963) and roots (Muller and Sackey, 2005; Posnette, 1947). In addition to chlorotic speckles starting at the leaf tip, plants infected with viruses, such as SCBV, display various other symptoms, such as stunted growth in severely infected plants, poor or no tillering, reduction in internodal elongation, bunchy top, etc. (Viswanathan *et al*., 1996). Symptoms of CMBV in citrus plants include mosaic on various parts of the plant, including the leaves, branches, fruits, etc., and irregular yellow or bright green patches against a dark green background and yellow flecking along the veins.

In rice tungro disease, RTBV is the symptom determinant and produces stunting and yellow–orange foliar coloration in tungro-affected patches in rice fields. As a result of the existence of RTBV and RTSV together under natural conditions, and the mechanical transmission of RTBV alone not being successful, it was difficult,

until recently, to assign symptoms to the individual viruses. However, this issue has been resolved with agroinoculation, showing that plants infected with RTBV only display mild stunting and yellowing symptoms, whereas the symptoms are accentuated on dual infection with RTBV and RTSV (Dasgupta *et al*., 1991).

TRANSMISSION

Although several biotic agents are known to be involved in the transmission of badnaviruses, they do not multiply in vectors and there is no trans-ovarial transmission. All life stages of vectors can acquire and transmit the virus (ICTV description; http://ictvdb.bio-mirror.cn/ICTVdB). Vectors include mealybugs, leafhoppers, aphids and nematodes. Some badnaviruses are transmitted mechanically and by dodder.

Fourteen species of mealybugs of the family Pseudococcidae (order Hemiptera; Roivainen, 1976) transmit badnaviruses in a semipersistent manner. One of the earliest reports on the mealybug transmission of badnaviruses was in TaBV (Brunt *et al*., 1990; Gollifer *et al*., 1977; James *et al*., 1973). Experiments with specific species of mealybug showed that, although certain badnaviruses are transmitted by multiple species, others are more specific with regard to the species of mealybug vector. For example, CSSV is transmitted by mealybug species *Planococcus citri*, *Ferrisia virgata* and *P. njalensis* (Dufour, 1988), but CMBV is known to be transmitted only by *P. citri* (Reddy and Ahlawat, 1997). Mealybug transmission of PYMV [transmitted by *P. citri* (De Silva *et al*., 2002) and *F. virgata* (Bhat *et al*., 2003)] and BSV-OL, BSV-Mys and BSV-GF (by *P. citri* and *P. ficus*) (Geering *et al*., 2005; Meyer *et al*., 2008) has been reported. SCBV and DaBV are transmitted by *S. sacchari* (Lockhart and Autrey, 1988) and *P. citri* (Kenyon *et al*., 2008), respectively.

The rice tungro virus complex is transmitted by various species of green leafhopper (GLH; *Nephotettix virescens*, *N. cincticeps* and *Resilia dorsalis*) in a semipersistent manner (Hibino *et al*., 1979). Although the transmission of RTBV is dependent on the presence of RTSV, the nature of the 'helper factor' is unknown. Evidence suggests that the helper factor is possibly not physically a part of RTSV, but a diffusible entity, synthesized by the rice plant in response to infection (Hibino and Cabauatan, 1987).

CMBV could be transmitted experimentally by *Myzus persicae* Sulz and *Aphis craccivora* Koch in a nonpersistent manner (Ahlawat *et al*., 1985). Similarly, PYMV has been shown to be transmitted by lace bug vectors (*Diconocoris distanti*; De Silva *et al*., 2002). Soil-inhabiting nematodes have been reported as active transmitting agents of CSSV (Afolami, 1980; Lana and Adegbola, 1977). There are, however, no other reports to date of any other badnavirus or tungrovirus being transmitted by nematodes.

Some badnaviruses show mechanical transmissibility of various degrees to natural and experimental hosts, such as CMBV to citrus (Ahlawat *et al*., 1996; Aparna *et al*., 2002) and several noncitrus species (Aparna *et al*., 2002; Pant and Ahlawat, 1997), an uncharacterized black pepper-associated badnavirus onto healthy pepper (Bhat *et al*., 2003), DaBV to several *Dioscorea* species (Kenyon *et al*., 2008), etc. However, efforts to mechanically transmit PYMV to healthy hosts (De Silva *et al*., 2002) and BsCVBV to several experimental hosts (Rivas *et al*., 2005) have failed.

PYMV was transmitted by grafting to a healthy host (De Silva *et al*., 2002). The graft transmission of an uncharacterized badnavirus in black pepper plants showed typical symptoms of pepper yellow mottle disease (Bhat *et al*., 2003). Vegetative propagation is the major mode of transmission of BSVs (Harper *et al*., 2004). CMBV has been demonstrated to be graft and dodder transmissible to at least 13 citrus cultivars (Ahlawat *et al*., 1996). Indeed, the major mode of dissemination of CMBV is believed to be through the infected rootstocks of rangpur lime during grafting (Baranwal *et al*., 2005).

GENOME ORGANIZATION AND GENE FUNCTIONS

All members of the family *Caulimoviridae* replicate their DNA genomes by reverse transcribing their more-than-genome-length terminally redundant transcript. This step has prompted the coining of the name 'pararetrovirus', based on their similarity to RNA-containing retroviruses. The proposed mechanism of pararetroviral replication (Hohn *et al*., 1985; Pfeiffer and Hohn, 1983) involves the production of a more-than-genome-length terminally redundant transcript by host DNA-dependent RNA polymerase. The transcript serves as a template for both the translation of viral proteins and reverse transcription for replication of the genome. The ubiquitous $tRNA^{met}$ serves as the primer for the reverse transcription (Boeke and Corces, 1989), and the opposite strand is primed from a purine-rich region (Franck *et al*., 1980; Hull *et al*., 1986; Richards *et al*., 1981; Verver *et al*., 1987). The reverse transcription is polymerized by the virally encoded RT, and the positive strand by the same enzyme and the virally encoded RNaseH. The use of RT in the replication of badnaviruses may be the reason for the high degree of sequence variation in badnaviral genomes (Harper and Hull, 1998). The dsDNA genome of badnaviruses has two or more site-specific discontinuities, one in each strand marking the tRNA binding site, the DNA existing primarily in an open circular form (Lot *et al*., 1991; Medberry *et al*., 1990).

The genome of badnaviruses is approximately 7.5 kb in length, which typically contains three ORFs. Whereas ORFs I and II code for proteins with a molecular mass of approximately 10 kDa, ORF III codes for a much larger polyprotein (approximately 250 kDa), which is post-translationally cleaved into smaller functional units by the viral aspartic protease (AP, encoded by the same ORF) to produce proteins required for virus movement, assembly and replication (Hohn and Futterer, 1997). Peptide motifs have been

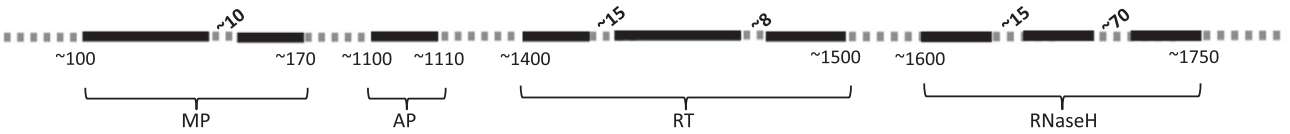

Fig. 2 Arrangement of motifs present within open reading frame (ORF) III polyprotein. Bold continuous lines indicate the motifs and broken lines indicate the gaps. The numbers above the lines indicate the approximate lengths of nonhomologous amino acid residues, and those below the lines indicate the approximate start and end positions. AP, aspartic protease; MP, movement protein; RNaseH, ribonucleaseH; RT, reverse transcriptase.

identified within the viral proteins, which have limited consensus sequences across badnaviruses (Fig. 2). This general arrangement has been observed in TaBV (Yang *et al*., 2003), SCBVs (Bouhida *et al*., 1993), CSSV (Hagen *et al*., 1993), BSVs (Harper and Hull, 1998) and CMBV (Borah *et al*., 2009; Huang and Hartung, 2001; Johnson *et al*., 2012). However, several badnaviruses have additional ORFs, often overlapping the above three. For example, in TaBV, a fourth ORF (ORF IV) has been reported, coding for a putative protein of 13 kDa (Yang *et al*., 2003). In CSSV, two extra ORFs (ORF X, 3 kDa; ORF IV, 14 kDa; overlapping ORF III) have been reported; ORF X was found to be diverse among different isolates (Hagen *et al*., 1993). Similarly, six ORFs have been reported in CMBV (Borah *et al*., 2009; Huang and Hartung, 2001; Johnson *et al*., 2012). The locations of ORF IV of TaBV and CMBV and ORF X of CSSV are similar (Fig. 3).

Attempts to determine the functions of badnaviral ORFs have been reported mainly from CSSV. The carboxyl terminus of ORF II (132 amino acids) of CSSV is rich in lysine and proline, and also contains alanine residues, a composition somewhat similar to the histone-like proteins. Partially purified full-length and C-terminal truncated versions of the CSSV ORF II proteins were able to interact with CSSV and other dsDNAs and with CSSV and other single-stranded RNA (ssRNA) transcripts in a sequence-nonspecific manner (Churchill and Travers, 1991). ORF II contains a 'coiled-coil' self-interaction domain to form a tetramer and a short, basic domain in the C-terminus, providing sequence nonspecific ssRNA and dsDNA binding properties (Jacquot *et al*., 1996, 1997; Stavolone *et al*., 2001). This binding activity was progressively lost as the C-terminus was gradually deleted (Churchill and Travers, 1991). In the cytoplasm, this protein could condense the CSSV DNA genome to permit the assembly of the bacilliform nucleocapsid. The CSSV ORF II-derived protein has been proposed to be involved in viral DNA replication, viral RNA transport and protection (Jacquot *et al*., 1996). ORF III of CSSV encodes a polyprotein of 211 kDa which can be divided into three regions: region 1 coding for a putative viral movement protein, region 2 for a putative protein involved in cell-to-cell spread and region 3 for the viral capsid protein. Region 3 contains the consensus sequences for viral aspartate protease, RT and RNaseH (Hagen *et al*., 1993).

ORF I and ORF II of BSVs potentially encode two proteins of approximately 21 and 15 kDa, respectively. ORF III encodes a polyprotein of 208 kDa with functional motifs similar to other badnaviruses (Harper and Hull, 1998). Among BSV isolates, BSV-Mys is exceptional with a nonconventional start codon for its ORF I (Geering *et al*., 2005), a feature also observed in the tungrovirus species RTBV. Recently, ORF I of BSV-Cav from China was also found to have a non-AUG start codon. The intergenic region (IR) of the isolate contains a large stem-loop, which was presumed to contribute towards the proposed ribosome shunt in the virus (Zhuang *et al*., 2011), a feature common in all members of the family *Caulimoviridae*.

ORF III of CMBV codes for a 226-kDa polypeptide and ORFs IV and V completely, and ORF VI partially, overlap ORF III (Borah *et al*., 2009; Huang and Hartung, 2001). The length of the IR varies from 600 to 731 bp and contains sequences such as the plant $tRNA^{met}$ binding site and a TATAA consensus. Part of the 5′ untranslated region (nucleotide residues 122–231) contains short ORFs (sORFs) which can form stem-loop structures bringing one sORF and the start codon of ORF I within five to ten nucleotides of each other, thereby possibly facilitating the translation of the latter by the ribosome shunt mechanism (Johnson *et al*., 2012). By computational analysis, the ORF II protein is predicted to have a nucleic acid binding and transposase-like activity. Computational analyses also suggest that ORF IV is a component of the viral core complex, ORF V has a transcriptional regulator activity and ORF VI has a membrane localization function (Borah *et al*., 2009). In SCBV-Mor, an additional intercellular transport domain was predicted in ORF III (Bouhida *et al*., 1993).

The only member of the genus tungrovirus, RTBV, has two site-specific discontinuities in its genome, one on each strand of the circular dsDNA genome (Bao and Hull, 1992), which are the result of reverse transcription-based DNA replication (Bao and Hull, 1994). The RTBV genome has four ORFs, the functions of a majority of which have not yet been completely elucidated. The first three ORFs partially overlap one another (Hay *et al*., 1991), whereas the fourth ORF is separated by an IR and is expressed from a spliced RNA (Futterer *et al*., 1994). The ORF II-encoded protein has predicted nucleic acid binding (Jacquot *et al*., 1997) and CP binding domains at its C-terminus (Herzog *et al*., 2000). The ORF III-derived polyprotein is cleaved to generate four putative functional proteins, namely a movement protein, a CP, a protease and a RT/RNaseH (Hay *et al*., 1991). The CP has been localized between the amino acid residues 477 and 791 of the ORF III-derived polyprotein (P194; Marmey *et al*., 1999). The viral protease, which cleaves P194, is associated with virions and is responsible for the formation of the capsid protein from the

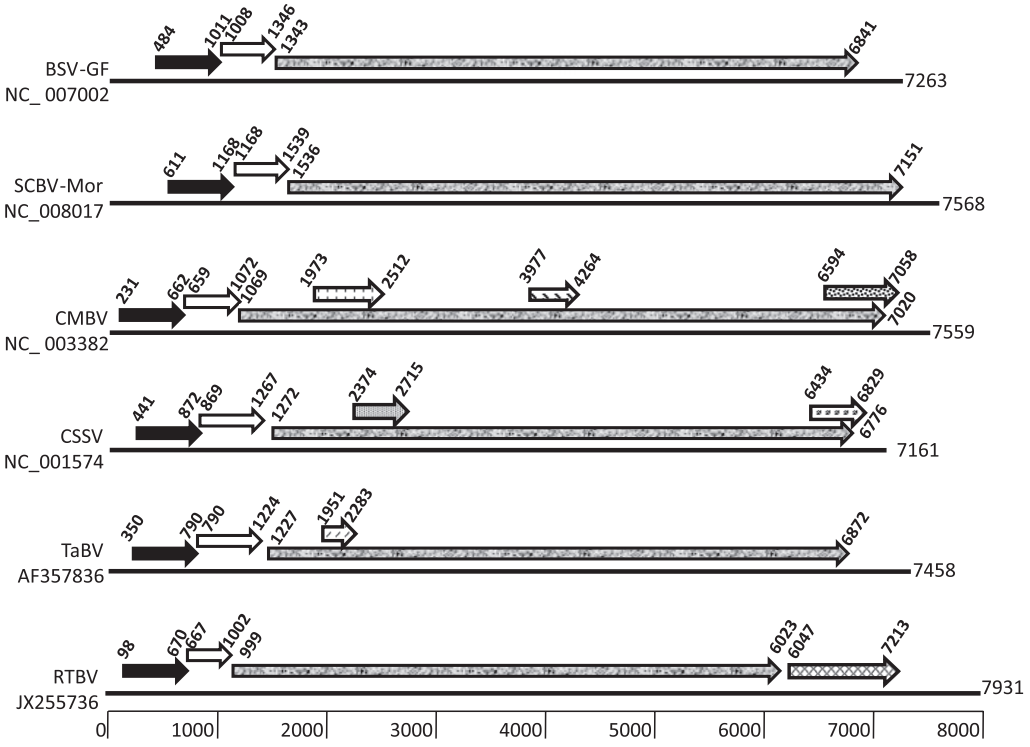

Fig. 3 Organization of open reading frames (ORFs) in badnaviruses and tungrovirus. The homologous ORFs (arrows) are shaded in the same pattern, and their nucleotide positions along the genome are also indicated. The name of the virus and the National Center for Biotechnology Information (NCBI) accession number used for the analysis are shown on the left-hand side, and the lengths of the genomes in nucleotides are indicated on the right-hand side. The approximate nucleotide positions are scaled at the bottom. BSV-GF, *Banana streak virus* cultivar Goldfinger; CMBV, *Citrus yellow mosaic badnavirus*; CSSV, *Cacao swollen shoot virus*; RTBV, *Rice tungro bacilliform virus*; SCBV-Mor, *Sugarcane bacilliform virus* from Morocco; TaBV, *Taro bacilliform virus*.

polyprotein (Marmey *et al*., 2005). Between the end of ORF IV and the beginning of ORF I, an IR harbours the single RTBV promoter, the polyadenylation signal, several sORFs (coding for 2–34 amino acids) and the splice donor site (Qu *et al*., 1991).

GENOME INTEGRATION AND EVOLUTIONARY PATHWAY

Genome sequencing efforts of various plants have revealed sequences resembling portions of integrated plant pararetroviruses (Harper *et al*., 1999; Jakowitsch *et al*., 1999; Lockhart and Jones, 2000; Richert-Pöggeler and Shepherd, 1997; Staginnus and Richert-Pöggeler, 2006). These integrated sequences, also called endogenous pararetroviruses (EPRVs), have been identified in the nuclear genomes of petunia, tobacco, potato, rice and tomato (Budiman *et al*., 2000; Gregor *et al*., 2004; Hansen *et al*., 2005; Jakowitsch *et al*., 1999; Kunii *et al*., 2004; Lockhart and Jones, 2000; Mao *et al*., 2000; Richert-Pöggeler *et al*., 2003). It has been shown recently that some EPRVs have the potential to produce functional viruses (Provost and Iskra-Caruana, 2006). The search for integrated BSV sequences producing episomal viral infection was promoted by the observation that several hybrids containing *Musa acuminata* (with A genome) and *M. balbisiana* (with B genome) genomes have a propensity to produce BSV infection after micropropagation (even when virus-free source plants were used as explants), especially in AAAB tetraploids. Every banana species examined to date contains two different classes of integrated BSV DNAs: the first class consists of partial sequences (Geering *et al*., 2005; Ndowora *et al*., 1999) and the second class consists of multiple tandem copies of complete BSV genomes, interrupted by host genomic sequences, each complete copy having a similar, if not identical, structure (Geering *et al*., 2005). The latter class of integrated sequences is the source of BSV infections arising in tissue culture (Harper *et al*., 1999; Ndowora *et al*., 1999) mentioned above. Fluorescence *in situ* hybridization has revealed that integration occurs at two loci, one being approximately 150 kb and the other approximately 50 kb (Harper *et al*., 1999).

Although the exact mechanism of the integrated BSV sequences causing infection has not been elucidated, a speculative model can be suggested from the observed repeat structures (Ndowora *et al*., 1999). Because the ends of the BSV array harbour a pair of direct duplications and the region of rearranged BSV sequences of the array is also flanked by a pair of direct duplications, it is possible that an infectious genome is produced by recombination among these repeats. If this is the case, recombination between

the repeats can delete the inserted endogenous sequences. A second recombination event between the terminal repeats can produce the free episomal circular BSV genome. As tissue culture is known to stimulate chromosomal aberrations probably involving recombination (Phillips *et al*., 1994), this model is consistent with tissue culture being a causal factor in the induction of infections from endogenous integrated EPRVs. An alternative model involving a recombination removing the inserted sequences, followed by transcription of the resulting integrated BSV genome, and reverse transcription of the transcript, has also been proposed (Ndowora *et al*., 1999).

It has been proposed that the integrated sequences confer a selective advantage to the plant by contributing towards plant virus resistance through the induction of transcriptional or post-transcriptional gene silencing of homologous sequences of the invading virus (Hull *et al*., 2000). Supporting this hypothesis, Mette *et al*. (2002) showed that a reporter gene cloned under a tobacco EPRV promoter sequence was expressed in stably transformed Arabidopsis, but silenced in allotetraploid tobacco containing integrated sequences.

In order to determine the evolutionary pathway of integration of BSV DNA, Geering *et al*. (2005) sequenced such integrated DNA from several species and cultivars of banana. However, no commonality was observed between the sequences amplified from *M. acuminata* and *M. balbisiana*, suggesting that integration occurred following their speciation. The analysis of nucleotide substitution rates suggested that the integrated sequences evolved under a high degree of selective constraint, and that each distinct sequence resulted from an independent integration event (Geering *et al*., 2005).

The ability of some endogenous sequences of BSV to induce infections was demonstrated by Gayral *et al*. (2008). Subsequently, the distribution, insertion site polymorphism and evolution of integrated sequences of BSV-GF and BSV-IM were studied in 60 wild banana genotypes, and it was suggested that both BSV species integrated approximately 640 000 years ago. The analyses also indicated that the integrated sequences of these two isolates had experienced different selective pressures and therefore showed distinct patterns of rearrangement. In another study involving sequence analysis, at least 27 independent integration events were identified (Gayral *et al*., 2010).

A sequence showing approximately 50% nucleotide identity to TaBV in the RT/RNaseH coding region was detected in many virus-free taro samples. This indicated a possibility of host genome integration of badnavirus infecting taro (Yang *et al*., 2003). A nonencapsidated caulimovirus sequence was amplified from pineapple, which was probably derived from an endogenous virus (Gambley *et al*., 2008).

Integrated RTBV-like sequences have been reported from the rice genome. These sequences do not represent any intact ORF and are generally rearranged versions of the RTBV genome. Interestingly, rice varieties carrying low copy numbers of these sequences show high susceptibility to RTBV (Kunii *et al*., 2004). More recently, these EPRVs in rice have been found preferably in AT dinucleotide repeats, indicating a possible preference for such sites during integration (Liu *et al*., 2012).

MANAGEMENT

No serious attempts have been made for the management of badnaviruses. Conventional control measures (chemical, cultural and physical) against the vectors are often the only methods used. However, they are not effective in those cases in which the transmission is not well understood and/or occurs by more than one means, as well as in the case of the occurrence of integrated virus genomes. A major handicap in the development of control strategies against badnaviruses is the absence of comprehensive information on vectors or other modes of transmission, on the relationship between different strains, and their virulence and distribution.

With regard to nonconventional measures of management of badnaviruses, reports exist only on BSVs. BSV was eradicated from banana (cv. Williams BSJ, ITC.0579, AAA, Cavendish subgroup) through cryopreservation. Cryoprotective treatment resulted in 87% BSV-free plants from meristematic lumps (Helliot *et al*., 2002, 2003). Later, the same group reported that three antiviral compounds [adefovir, tenofovir and 9-(2-phosphonomethoxyethyl)-2,6-diaminopurine] efficiently eradicated the episomal form of BSV from banana; up to 90% of plants regenerated from the meristems of BSV-infected plants were found to be virus free following a 6-month treatment with 10 μg/mL of any of the above compounds (Helliot *et al*., 2003).

Attempts to obtain resistance against rice tungro disease using classical breeding have not been durable (Dahal *et al*., 1990; Khush *et al*., 2004), mainly because of the absence of well-characterized resistance genes in the rice germplasm (Azzam and Chancellor, 2002). Several attempts have been reported to obtain resistance against rice tungro disease by targeting RTBV, RTSV or GLH. Transgenic approaches against RTBV include the overexpression of two rice transcription factors, RF2a and RF2b (sequestered by the RTBV promoter during infection), leading to the amelioration of the shortage of these transcription factors (proposed to cause symptoms on RTBV infection), resulting in resistance (Dai *et al*., 2008). Similarly, although an earlier attempt to obtain CP-mediated resistance against RTBV (Philippines isolate) produced disappointing results (Azzam *et al*., 1999), a later report using the CP gene derived from an Indian isolate of RTBV provided tolerance against the virus (Ganesan *et al*., 2009). Transgenic rice plants designed to express dsRNA corresponding to ORF IV of RTBV have been developed using RNA interference technology. These plants accumulate small RNAs against the RTBV transcript, indicating an effective RNA interference, and show a modest

resistance against RTBV (Tyagi *et al*., 2008). This gene construct has now been diversified to two popular rice varieties by backcross breeding, effectively enhancing their value by adding the virus tolerance character (Roy *et al*., 2012).

CONCLUSIONS

The extreme heterogeneity of badnaviral and, to a lesser extent, tungroviral nucleotide sequences (Al-Kaff and Covey, 1994; Geering *et al*., 2000; Harper *et al*., 2004, 2005; Jaufeerally-Fakim *et al*., 2006; Kenyon *et al*., 2008; Lockhart and Olszewski, 1993; Nath *et al*., 2002) seems to suggest that this group of viruses, although ancient in origin, adapted so early and deeply to their respective hosts that most of the ancestral genes have been shed and new ones have been acquired for adaptation to lives restricted by the host. An extreme example is RTBV, which has been reported from only one species of rice (*Oryza sativa*), but between isolates from two rice-growing regions of the world (South Asia and South-East Asia) shows less than 70% overall sequence identity (Banerjee *et al*., 2012; Mathur and Dasgupta, 2013; Nath *et al*., 2002). Probably another consequence of the above heterogeneity is the varying numbers of ORFs in badnaviruses, all within their rather narrow genomic size range. Although most badnaviruses have three ORFs, some can have up to seven. Outside the common, rather short motifs of ORF III (CP, protease, RT/RNaseH), no regions share any significant homologies within the group. For example, CSSV, the closest relative of CMBV, shares only a maximum of 66.5% nucleotide sequence identity, even within ORF III, the most conserved ORF.

One of the major problems faced by badnaviral researchers is the lack of infectious clones for most members. Infectivity has been demonstrated only for CMBV (Huang and Hartung, 2001) amongst the tropical badnaviruses, and for RTBV (Dasgupta *et al*., 1991). Neither badnaviruses nor the badnaviral DNA can be mechanically inoculated onto the respective hosts, and hence agroinoculation has been the only successful method for the re-introduction of cloned badnaviral genomes back to the host plant. Although the reason behind this lack of infectivity has not yet been addressed, it is probably because of the limitation and, possibly, adaptation of the virus particles to the vascular tissue of the host plant into which the vector delivers the viruses. Such possible adaptation, if any, should form the subject of active research in future.

Although information on the possible functions of some badnaviral and tungroviral ORFs exists, generalizations cannot be made on the possible functions of the corresponding ORFs of other badnaviruses for which such information is not available. The lack of infectious clones has also severely handicapped efforts to determine gene functions and their roles in pathogenesis by site-directed mutagenesis, an approach which otherwise can be very fruitful. Moreover, the high degree of variability makes the detection and taxonomic designation of badnaviruses difficult, as exemplified by BSVs (Lheureux *et al*., 2007).

A majority of tropical badnaviruses infect plants which are vegetatively propagated. Hence, their importance as pathogens transmitted by infected plant propagules is an important consideration for quarantine purposes. Methods of detection of badnaviruses need to be made much more robust because of the atypical symptoms produced and the dependence of the results on the method used in sample preparation (Borah *et al*., 2008). More understanding of the molecular biology of the badnaviruses is therefore needed to achieve the ultimate goal of producing efficient and workable management strategies for the important diseases that they cause.

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