Infection, Genetics and Evolution 21 (2014) 83–89

Contents lists available at ScienceDirect

Infection, Genetics and Evolution

journal homepage: www.elsevier.com/locate/meegid

Review

The common evolutionary history of badnaviruses and banana

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ARTICLE INFO

Article history:
Received 9 July 2013
Received in revised form 13 October 2013
Accepted 15 October 2013
Available online 31 October 2013

Keywords:
Badnavirus
Banana streak virus
Co-evolution
Phylogeny
Epidemics
Endogenous viral sequences

ABSTRACT

Recent plant genome sequencing efforts have revealed myriad viral sequences suggesting a cryptic interaction between both partners. Interestingly, no integration step has ever been reported as an obligatory step in the life cycle of plant viruses. Circular dsDNA viruses belonging to the family *Caulimoviridae* are the most abundant among integrated plant viral sequences. In this review, we describe how this hitherto hidden interaction could inform the evolutionary history of both partners badnaviruses and banana plants.

Contents

1. Introduction

Recent analysis of plant genome sequences has revealed that the contribution of viruses to plant evolution is greater than expected, and reports extensive viral colonisation of host plant genomes, named endogenous viral elements (EVE), as the result of an endogenisation process (Feschotte and Gilbert, 2012). This indicates a close interaction between viruses and their host plants, clearly reflecting an impact/effect of co-evolution for both partners. Nowadays, most of plant endogenous viral sequences belong to the family *Caulimoviridae* encompassing plant pararetroviruses. *Caulimoviridae* are open-circular double-stranded DNA (dsDNA) viruses of 7–8.3 kbp, replicating via a reverse transcription step

Abbreviations: EVE, endogenous viral elements; BSV, *Banana streak virus*; eBSV, endogenous *Banana streak virus*; BEV, Banana endogenous virus; BSOLV, Banana streak *Obino l'ewai* virus; BSGFV, Banana streak *Goldfinger* virus; BSIMV, Banana streak *Imové* virus; BSMYV, Banana streak *Mysore* virus; BSVNV, Banana streak *Vietnam* virus; BSCAV, Banana streak *Cavendish* virus; BSPEV, Banana streak Peru virus; BSUAV, Banana streak Uganda A virus; BSUIV, Banana streak Uganda I virus; BSUJV, Banana streak Uganda J virus; BSUKV, Banana streak Uganda K virus; BSULV, Banana streak Uganda L virus; BSUMV, Banana streak Uganda M virus; PKW, pisang klutuk wulung; EAH, east African Highland.

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http://dx.doi.org/10.1016/j.meegid.2013.10.013

(King et al., 2012). In the 1990s, Xiong and Eickbush (1990) established a phylogenetic relationship between the family *Caulimoviridae* and the Ty3-gypsy retroelement belonging to the family *Metaviridae*. Both families share a similar organisation of the POL domain harbouring the reverse transcriptase (RT) and the ribonuclease H (RNaseH) genes but *Caulimoviridae* lack the integrase gene. Consequently, and in contrast to the retroelements, the integration function is excluded from the life cycle of the *Caulimoviridae*. However, following cell infection, one part of the viral replication occurs in the nucleus where the viral DNA genome is transcribed from minichromosomes formed by an association with histones (Hull, 2002; Jacquot et al., 1996). This likely facilitates randomly integrations into the host genome by illegitimate recombination (Holmes, 2011) or during repair of DNA breaks (Gayral et al., 2008) due to the gaps that exist within the open circular viral DNA molecules (Hohn et al., 2008). Such non-active integration within the host genome has been found for five of the six genera constituting the family *Caulimoviridae*; only the genus *Soymovirus* is reported as no integrated so far.

Bousalem et al. (2009) identified a bipolar topology of the family *Caulimoviridae* phylogeny separating the genus *Badnavirus* from the others based on both full length and partial viral genome sequences. Badnaviruses – bacilliform viruses with a genomic organisation consisting of at least three major open reading frames (ORFs)-appeared as the most recent genus in the family *Caulimoviridae*. Badnaviruses today are known for their large biodiversity and are considered as emerging pathogens in tropical countries (Borah et al., 2013; Fargette et al., 2006). Curiously, some species are described as viruses only whereas others also appear to be integrated into the genome of their host plant. Consequently a large number of viral sequences has been generated in recent years, resulting in a lack of clarity of both biodiversity and taxonomy status concerning this genus (Staginnus et al., 2009; Teycheney and Geering, 2010). Interestingly, the family *Caulimoviridae* is currently extended due to its propensity to gather new genera based on *de novo* assembly of numerous endogenous viral sequences generated by the new generation sequencing processes and for which no episomal counterpart are reported so far (D'Hont et al., 2012; Geering et al., 2010); (Geering and Teycheney, unpublished); (Lockhart, unpublished).

In this review, we address the current genetic structure of the genus *Badnavirus* with a view to describing the curious diversity of badnaviruses species infecting banana that have resulted in a very specific process of co-evolution. We describe three kinds of interactions, each likely attesting to one part/picture of the co-evolutionary story of badnaviruses and banana, and propose a potential evolutionary scheme.

2. *Badnavirus* genetic diversity in tropical plants

The genus *Badnavirus* is considered as the most diversified and heterogenous genus within the family *Caulimoviridae*. It currently gathers more than thirty five distinct species showing low nucleotidic sequence identity; the majority of which infect tropical crops. Therefore, it is established by ICTV classification that a threshold of 20% nucleotide divergence in the RT-RNaseH region of ORF3 differentiates two badnavirus species (King et al., 2012). A badnavirus phylogeny was inferred based on alignments of the partial conserved 540bp fragment of the RT/RNase-H region (Fig. 1). The current genetic diversity of badnaviruses appears to be structured at least into three major clades (Fig. 1) as proposed by Harper et al. (2005) and Gayral and Iskra-Caruana (2009). Interestingly, another clade only grouping two viruses, *Bougainvillae spectabilis chlorotic vein-banding virus* (BCVBV) and *Taro bacilliform virus* (TABV), is also observed and considered as outgroup according to the low bootstap values (55) attesting of the increasing complexity of this genus as discussed by Borah et al. (2013). The badnaviruses described so far in banana exhibit extensive genetic diversity as do badnaviruses of yam (Bousalem et al., 2009; Kenyon et al., 2008) and of sugarcane (Muller et al., 2011); however banana and sugarcane badnaviruses are the only ones polyphyletic. They spread over Clades 1, 2 and 3 and Clades 1 and 3 respectively proposing banana as well as sugarcane as one of the host plants for the badnavirus ancestor (Gayral and Iskra-Caruana, 2009) (Muller et al., 2011). Interestingly, three BSV species of Clade 1 clustered separetely with three SCBV species unlike species of Clade 3 as described by Muller et al. (2011) suggesting that each couple of viruses share the same ancestor virus (Iskra-Caruana et al., accepted for publication). Indeed *Sugarcane bacilliform Guadeloupe C virus* (SCBGCV) and *Banana streak Cavendish virus* (BSCAV), *Sugarcane bacilliform Guadeloupe D virus* (SCBGDV) and *Banana streak Mysore virus* (BSMYV) as well as *Sugarcane bacilliform Guadeloupe A virus* (SCBGAV) and *Banana streak Peru virus* (BSPEV) showed each a high level of nucleotide identity and belong to a commun ancestor virus present either in banana or sugarcane. However, both SCBGDV/BSCAV and SCBGAV/BSPEV host colonization appeared more recent than those of SCBGDV/BSMYV. Experimental data showed that SCBV infected banana, rice and sorghum causing similar symptoms to those of BSV in banana (Bouhida et al., 1993) while BSV infected sugarcane without any symptoms (Lockhart and Autrey, 1988). Then, host shifts between banana and sugarcane could be one explanation of these phylogenetic observations.

3. *Badnavirus* genetic diversity in banana

3.1. Clade 1 – *Banana streak virus (BSV) and its endogenous counterpart (eBSV)*

Clade 1 encompasses badnaviruses inducing/causing banana streak disease in banana worldwide. They are named banana streak viruses (BSVs) and are composed of several distinct species rather than strains of the same virus species based on ICTV classification (King et al., 2012). Hence, the disease is triggered by various BSV species, all showing common symptoms (among a range of other reported symptoms) of yellow streaks progressing to necrosis and pseudostem cracking. Today, eight distinct BSV species are fully described as infecting banana plants: *Banana streak OL virus*-BSOLV (Harper and Hull, 1998), *Banana streak GF virus*-BSGFV (Gayral et al., 2008), *Banana streak IM virus*-BSIMV (Geering et al., 2011), *Banana streak MY virus*-BSMYV (Geering et al., 2005b), *Banana streak VN virus*-BSVNV (Lheureux et al., 2007), *Banana streak CA virus*-BSCAV (James et al., 2011), *Banana streak PE virus*-BSPEV (Muller, unpublished) *Banana streak Uganda A virus*-BSUAV (James et al., 2011) (Fig. 1). They are all transmitted horizontally to banana in a semi-persistent manner by mealybugs, of which *Planoccocus citri* is the most prevalent, and vertically by either the mass micropropagation—the main way to propagate banana plants—of infected plants or suckers. Curiously, three BSV species show an alternative means of vertical transmission from endogenous viral sequences (named eBSVs) present only within the *Musa balbisiana* banana genome (Chabannes et al., 2013; Gayral et al., 2008). The three species BSOLV, BSGFV and BSImV are able to release active viral genomes and contribute to plant infection just as much as their episomal counterparts, and are all encountered in the context of epidemics worldwide.

Chabannes et al. (2013) performed an in-depth characterization of these viral integrants for each species in the genome of the *Musa balbisiana* seedy diploid Pisang Klutuk Wulung (PKW) by studying their molecular structure, genomic organisation, genomic landscape, as well as their cytogenetic localisation and infectious