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New insights on the transmission mechanism of tenuiviruses by their vector insects

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Tenuiviruses, which cause serious diseases in rice, wheat, maize and other gramineae crops, recently have been assigned to the family *Phenuiviridae* in the order *Bunyavirales*. Transmission of tenuiviruses to host plants depends on the specific vector planthoppers. The interaction between the virus and insect offers critical points for developing an efficient management strategy. This review focuses on recent advancements in our understanding of the interactions between the virus and insect components. Vector components such as various proteins play major roles in virus replication, stability and transovarial transmission. The virus can either directly interact with these proteins or regulate expression of genes that encode them to alter the metabolism or defense mechanisms of the insect vectors. However, the vector components that are involved in virus infection and movement in midgut and salivary glands are not as well explored and are targets for further study.

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Basic characteristics of tenuiviruses

Tenuivirus is the only plant-infecting genus of family *Phenuiviridae* in the order *Bunyavirales*. The combination of characteristics of tenuiviruses are more similar to vertebrate-infecting phenuiviruses, that is, highly conserved octanucleotide at 5′ (5′-ACACAAAG) and 3′ (CUUUGUGU-3′) termini, homologous RNA-dependent RNA polymerases (RdRp) and glycoprotein, and similar infection cycle [1,2]. Rice stripe tenuivirus (RSV) is the type member of this genus, which includes six other members: maize stripe tenuivirus (MSpV), rice grassy stunt tenuivirus (RGSV), rice hoja blanca tenuivirus (RHBV), echinochloa hoja blanca tenuivirus (EHBV), Iranian wheat stripe tenuivirus (IWSV) and urochloa hoja blanca tenuivirus (UHBV) [1]. The virion particle of tenuiviruses is a non-enveloped nucleocapsid with helical symmetry, forming branched or thin, filamentous spirals 3–10 nm in diameter and 500–2100 nm long [3,4]. They cause typical symptoms such as chlorotic stripes on affected leaves of their host plants rice, maize, sorghum and other gramineous crops [5].

The genomes of tenuiviruses are segmented into four to six strands of negative-sense, single stranded RNAs, which adopt the negative-sense and ambisense coding strategies to encode proteins [6–8]. Total estimated genome size of tenuiviruses is between 19.2 and 24.9 kb (RNA 1: 8.8–9.7 kb, RNA 2: 3.4–4.0 kb, RNA 3: 2.3–3.1 kb, RNA 4: 1.8–2.9 kb, RNA 5: 1.3–2.7 kb and RNA 6: 2.6 kb) (Table 1) [7–13]. RSV, IWSV and RHBV consist of four segments RNA 1–4; MSpV, EBHV and UHBV have an additional segment, RNA5; and RGSV has six RNA segments (Table 1). In general, RNA 1, the largest genomic segment in tenuiviruses, has one large open reading frame (ORF) on the viral complementary sequence coding for putative RNA-dependent RNA polymerase [9]. The other segments RNA 2, RNA 3 and RNA 4 have ambisense coding strategies to encode six proteins; RNA 3 encodes a nucleocapsid protein (pc3) in the negative-sense [14]. RNA 5 has only one ORF in the viral complementary sequence that encodes a highly basic protein [10,11]. Interestingly, RNA 5 and RNA 6 in RGSV are equivalent to RNA 3 and RNA 4 of other tenuiviruses, whereas RGSV RNA 3 and RNA 4 are unique to the genus *Tenuivirus* [15]. Among the above viral proteins, the nucleocapsid proteins are thought to be involved in interaction with the insect vector [16]. There was also a report that nonstructural protein NS4 encoded by RSV RNA 4 might play a critical role in viral spread in the vector insect [17].

Biological transmission

Horizontal transmission of tenuiviruses to the plant host depends on specific vector planthoppers, in which the viruses can persistently propagate. After ingestion by the insect, these viruses first arrive at the gut lumen, then must move from the gut to the hemolymph, then to ovary or other tissues and finally into the salivary glands, along with the saliva to be transmitted to a new plant host [16]. In general, tenuiviruses can be acquired by an insect

Table 1

Size of genomic RNAs in tenuiviruses

Segment	RSV (kb)	MSpV (kb)	RGSV (kb)	EHBV (kb)	IWSV (kb)	UHBV (kb)	RHBV (kb)
RNA-1	8.9	8.8	9.7	–	–	–	9.0
RNA-2	3.5	3.4	4.0	–	3.5	–	3.6
RNA-3	2.5	2.3	3.1	2.3	2.3	2.3	2.3
RNA-4	2.1	2.2	2.9	1.9	1.8	1.9	2.0
RNA-5	ND	1.3	2.7	1.3	ND	1.7	ND
RNA-6	ND	ND	2.6	ND	ND	ND	ND
Reference	Toriyama *et al.* [9]	Huiet *et al.* [10]	Toriyama *et al.* [7]	De Miranda *et al.* [11]	Heydarnejad *et al.* [12]	De Miranda *et al.* [13]	Ramirez *et al.* [2,8]

ND, not detected; –, not characterized.

within 25 min to 4 hours, and incubation (latent) period in the vector ranges from 4 days to 31 days [6]. The threshold period for viral inoculation to the host is similar to the acquisition period; however, some virus can be transmitted in as short as 30 s [18]. Although tenuiviruses usually persist within the insect throughout the life of the insect, nymphs are more efficient than the adults at virus transmission, perhaps due to ultrastructural variations in the gut or salivary gland tissues between nymphs and adults [12,19]. Moreover, longer acquisition periods, that is, feeding periods on infected plants enhance viral transmission efficiency. Certainly, transmission efficiency is also influenced by a number of biotic and abiotic factors [20]. In addition, RSV can be acquired from frozen infected rice leaves and subsequently transmitted, which may provide a progressive step to rapid screening of genetic sources for potential resistance against the virus [21].

With the exception of RGSV, vertical transmission of a virus from a viruliferous insect appears to be more prevalent for tenuiviruses than other viruses [22]. Most tenuiviruses can be transmitted transovarially by viruliferous females to the next generation at a rate from about 60% to 100% for RSV [18], 21% to 58% for MiSpV [23], 88% to 100% for ISWV [24] and 60% to 100% for RHBV [5]. In general, these viruses are thought to be transmitted via insect eggs for many generations (as many as 40 in the case of RSV) [6]. RHBV is the only tenuivirus known so far to be transmitted by male insects to progeny. However, the efficiency of maternal transmission is higher than that of paternal transmission [25].

Molecular mechanism transmission by their vector insects

Viral components involved in transmission

Tenuiviruses can infect various tissues of vector insects including the alimentary canal, fat bodies, hemolymph, reproductive tracts and salivary glands. As early as 1992, RSV has been detected by immunogold microscopy in the midgut, the principal salivary gland, ovarioles and fat body of viruliferous insect vector [26]. Liang *et al.* then used immunofluorescence and immunogold microscopy to show filamentous electron-opaque inclusion bodies (FEO) in the lumen and epithelial cells of mid-gut in small brown planthoppers (SBPHs) [27].

For tenuiviruses, at least four negative-stranded RNAs encode seven proteins. Among these proteins, nucleocapsid protein (pc3) plays a very important role in transmission [16]. Nonstructural protein NS4, encoded by RNA4 of RSV, is involved in the formation of cytoplasmic inclusions in various insect tissues [17]. The ribonucleoprotein particle of RSV becomes attached to NS4-specific inclusions in the insect through a direct interaction between pc3 and NS4. An RNA interference study showed that NS4 of RSV is essential for movement of the virus in vector tissues, but viral replication is not affected [17]. NS3 encoded by RNA3 of RHBV suppresses RNA silencing in both the insect vector and the plant host and is thought to interfere with miRNA-regulated gene expression because of its high affinity for miRNA duplexes [28]. In the case of RGSV, NS5, encoded by RNA5, is equivalent to RNA 3 of other tenuiviruses and predicted to play an essential role in the infection cycle in its vector, the brown planthopper [29].

Insect components involved in transmission

After virus particle entry into the vector body, the virus first infects the epithelial layer of the midgut, then the visceral muscle tissues. Thereafter, it accumulates within the entire alimentary canal. But for successful delivery to the host plant, the virus has to colonize the salivary glands of the vector [22,17]. RSV can also infect the ovary, which becomes a source of inoculum for progeny, but RGSV lacks this mechanism for transovarial transmission. Thus, for successful transmission by their vector insects, tenuiviruses have to overcome barriers to midgut infection and dissemination, salivary gland infection and escape, transovarial transmission and immune response (Figure 1). Therefore, vector components and substances are highly important for viral acquisition and subsequent transmission, and specific interactions between viral and vector components are essential [16] to support various viral function such as infection, replication and movement [30].