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REVIEW

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Advances in the studies of Rice stripe virus

Abstract Rice stripe virus (RSV), the type member of the genus *Tenuivirus*, is one of the most economically important pathogens of rice and is repeatedly epidemic in China, Japan and Korea. The latest achievements of the studies on the biological functions of virus-encoded proteins, pathogenicity differentiation and genetic diversity of virus, virus-plant host interactions and management of virus were reviewed. The current problems encountered during studies and some approaches for further research were discussed.

Keywords Rice stripe virus, achievements, biological functions of virus-encoded proteins

1 Introduction

The rice stripe disease was first described in Japan in 1897 (Kisimoto, 1965). Its causative agent, designated as Rice stripe virus (RSV), is a typical member of the genus *Tenuivirus* (Haenni et al., 2005), which is not assigned to any virus family yet. RSV is one of the most economically important pathogens of rice and is repeatedly epidemic in China, Japan and Korea (Lin et al., 1990). Symptoms caused by RSV in rice vary with the plant cultivars and developmental stage, and include two types, i.e. folded-leaf and unfolded-leaf with common features of chlorotic mottling (Ishii and Ono, 1966; Lin et al., 1991). RSV is transmitted by a small brown planthopper, *Laodelphax striatellus* Fallen (Hemiptera, Delphacidae), in circulative–propagative and transovarial manners (Falk and Tsai, 1998).

The rice stripe disease was first reported to occur in Jiangsu–Zhejiang–Shanghai (JZS) district in 1963 and was later discovered in 16 provinces of China (Lin et al., 1990). Since 2000, the disease has circulated widely in Jiangsu Province and has become more severe. For instance, in the years 2004 and 2005, the RSV-affected areas in Jiangsu Province reached 1.7 million hm^2, while serious incidence areas were 1 million hm^2 (Zhang et al., 2007a). Due to climatic changes as well as cultivation of susceptible cultivars, the rice stripe disease is not only becoming increasingly serious in rice annually (Zhang et al., 2007c), but also extending to wheat crops and caused great losses in wheat production in recent years (Cheng et al., 2007). Many efforts have been made in investigating the biology and molecular biology of RSV, as reviewed previously (Xie et al., 2001; Sun and Jiang, 2006; Zhang et al., 2007a). Herein, we highlight the advances in the studies of molecular biology and virus-host interaction of RSV.

2 Physical properties

RSV is a multicomponent RNA virus comprising four single-stranded RNA segments, designated as RNA1-4 in the decreasing size (Toriyama and Watanabe, 1989). The 8.9-kb RNA1 is completely negative sense and contains a single open reading frame (ORF) in the viral-complementary (vc) sense encoding the 336.8-kDa protein, the putative RNA-dependent RNA polymerase (RdRP) (Toriyama et al., 1994). The ambisense 3.5-kb RNA2 encodes a 22.8-kDa nonstructural protein (NS2) in the viral (v) sense and the 94-kDa NSvc2 protein in the viral complementary sense (Takahashi et al., 1993). In an expression strategy similar to the RNA2, the 2.7-kb RNA3 encodes a 23.9-kDa nonstructural protein (NS3) in the v sense and a 35.1-kDa coat protein (CP) in the vc sense (Kakutani et al., 1991), while the 2.1-kb RNA4 encodes two nonstructural proteins, including a 20.5-kDa disease-specific protein (SP) in the v sense and a 32.4-kDa NSvc4 in the vc sense (Kakutani et al., 1990; Zhu et al., 1992).

Each genomic RNA is encapsidated by multiple copies of the viral CP to form virion (Gingery, 1988), a filamentous particle, 500–2000 nm, but with a diameter of only about 3–8 nm (Koganezawa, 1977). The infection

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of RSV in plant cells induces the formation of four types of inclusion bodies, including electron-dense amorphous semi-electron-opaque inclusion bodies (dASO), ring-like structure, fibrillar amorphous semi-electron-opaque inclusion bodies (fASO) and filamentous electron-opaque inclusion bodies (FEO), which contain distinct sets of viral protein(s) (Liang et al., 2005b).

The genomic RNAs share highly conserved and complementary terminal sequences in 5' ends (5'-ACACAAAGUCC-3') and 3' ends (5'-GACUUUGUGU-3'), with the exception of the varied sequence (5'-GACUAUGUGU-3') in 3' end of RNA1. Furthermore, 20 complementary pairing bases exist in 5' and 3' terminuses of each segment and form the characteristic panhandle structure typical of negative-strand viral RNAs, which may be the recognition site of RdRP, while the mismatch at the sixth base from the 3' end is probably involved in the replication, transcription and/or the assembly of ssRNA1 into the filamentous particles (Takahashi et al., 1990; Barbier et al., 1992). The A/U rich sequences locate in the intergenic regions of RNA2, RNA3 and RNA4 and potentially form inverted repeats, which are supposed to be involved in the regulation of transcription termination in negative-sense RNA viruses (Zhang et al., 2007b). The transcription of RSV mRNAs was presumed to be achieved by cap–snatching mechanism, as evidenced by the fact that the 5' terminus of mRNA, encoded by both vRNAs and vcRNAs, contains 10 to 23 host-derived bases, which may function as the capped RNA primers that initiate viral mRNA synthesis (Shimizu et al., 1996).

3 Biological functions of RSV-encoded protein

Basic knowledge on virus-encoded proteins is essential to understand this pathogen. The RdRP is presumed to be encoded by RNA1, as evidenced by the fact that a high level of RdRP activity associated with RSV filamentous particles *in vitro* is attributed to a minor polypeptide (Toriyama, 1986) with molecular weight (MW) of about 230 kDa, indicating that only the largest genome segment, RNA1, is enough to express such a protein. Sequence analysis reaffirmed that the vc sequence of RNA1 does contain an ORF encoding a putative protein that shares high similarity with the RdRP of phleboviruses L protein (Toriyama et al., 1994). Interestingly, the ORF within the RNA1 encodes a protein of 2919 amino acids with an estimated MW of 337 kDa, which differs in the MW (230 kDa) of the polypeptide described above, suggesting that vcRNA1 encoded protein probably undergoes post-translational cleavage. An ovarian tumour (OTU)-like domain was recently found within the N-terminal region (aa 1–500) of deduced RdRP and is absolutely conserved among all known RSV isolates (Zhang et al., 2007b). This finding indicates that the RSV polymerase should possess an endonuclease activity, allowing it to cleave host mRNAs 10–23 nt from their 5′-capped ends and, subsequently, use the resulting capped leader to prime transcription of the viral genome (Shimizu et al., 1996).

The RdRP is responsible for viral RNA transcription and replication in initial infected cells, whereas movement protein (MP) is required to assist viral spread from cell to cell. Rice grassy stunt virus (RGSV) is one of the known members in the genus *Tenuvirus*. A small amount of RGSV NS2 was detected in cell-wall, organelle-enriched and crude membrane fractions (Chomchan et al., 2002) typical of the subcellular localization of virus MP, suggesting that RGSV NS2 as well as its counterpart RSV NS2 functions as the putative MP of tenuviruses. Furthermore, previous reports showed that RSV NS2 was associated with cell wall in virus-infected rice plants (Takahashi et al., 2002), and the transient expression of NS2-GFP led to formation of punctate structures in association with cell membrane in *Nicotiana benthamiana* leaves (Wei et al., unpublished data). These data together suggest the possible function of RSV NS2 as the candidate of RSV MP. Recently, NSvc4 was shown to have the ability to move between cells and complement the cell-to-cell movement of a movement-defective mutant of Potato virus X in *N. benthamiana* leaves, indicating that RSV NSvc4 is a putative MP of RSV (Xiong et al., 2008), though the direct evidence to show that this protein assists RSV for cell-to-cell movement in infected rice cells is unavailable. The transient expression of RSV NSvc4-GFP led to formation of punctate structures targeting to plasmodesmata (PD). Furthermore, the early secretory pathway and actomyosin motility system are required for the proper targeting of NSvc4 to PD *in planta*. (Wei et al., unpublished dada). The ribonucleoprotein particles (RNPs) represent the minimal infectious unit for RSV, which contains at least the RdRPs, CPs, and genome length viral RNAs (Ramírez and Haenni, 1994; Falk and Tsai, 1998). RSV NSvc4 interacts with the CP by using *in vitro* binding experiments (Zhang et al., 2008a) and binds nucleic acid (Liang et al., 2005a), suggesting that NSvc4 associates with the viral ribonucleocapsid for transport from cell to cell. These data suggest that the NS2 and NSvc4 of RSV may coordinate the formation of PD-associated structures that facilitate the intercellular movement of RSV in infected plants.

Tenuivirus has phylogenetic similarity to the members of *Bunyaviridae* (Xie et al., 2001). RSV NSvc2 is analogous to the glycoproteins of bunyaviruses and topoviruses, the members of *Bunyaviridae*, which are involved in the receptor-mediated uptake of their particles (Liang et al., 2005b). Transient expression of seven proteins encoded by RSV fused with fluorescent proteins in *N. benthamiana* leaves revealed that only NSvc2 is associated with membranous structures, corresponding to two distinct transmembrane domains within the amino acid sequences of NSvc4 predicted by computer tools. The FEO-like inclusion bodies contain NSvc2 in gut lumen of epithelial

cells of insect vector (Liang et al., 2005b), suggesting that NSvc2 may have a role in mediating the entry of RSV RNPs into insect vector cells in the form of FEO inclusion bodies.

Characterization of the gene silencing suppressor is one of recent progress in RSV research. The RSV NS3 was demonstrated to be able to strongly suppress local GFP silencing and prevent long-distance spread of silencing signals (Xiong et al., 2009). This result is consistent with the previous finding that the NS3 protein of the Rice hoja blanca virus (RHBV), a tenuivirus, functions as a gene-silencing suppressor (Bucher et al., 2003). However, it seems that the RSV NS3 is not a pathogenicity determinant because no any visible symptom or deformation appears in transgenic rice and tobacco plants expressing this protein (Xiong et al., 2009). Like Cucumber mosaic virus (CMV) *2b* (Brigneti et al., 1998), a well-known gene-silencing suppressor, the RSV NS3 accumulates predominantly in nuclei leading by a nuclear localization signal (NLS), which is essential for silencing suppression (Xiong et al., 2009). The functional mechanism of the RSV NS3 is unknown yet. However, a counterpart of the RSV NS3, the NSs of Rift valley fever virus (RVFV, genus *Phlebovirus*), has been demonstrated to block interferon production by inhibiting host gene transcription (Billecocq et al., 2004). The RSV NS3 and RVFV NSs have the same sublocalization in nucleus (Billecocq et al., 2004; Xiong et al., 2009). It will be interesting to further investigate if these two proteins share similar functional manner.

The SP is the major non-structural protein often accumulating to a very high level in a form of cytoplasmic inclusion body in RSV-infected rice and *L. striatellus* cells (Liang et al., 2005b). This protein could be detected in chloroplast, cytoplasm and nuclear of infected rice (Liu et al., 2000) and in ovum, surface of chorion, the mid-gut lumen and the columnar cells of the viruliferous females *L. striatellus* (Wu et al., 2001). Interestingly, the total amount of SP in chloroplasts correlated very well with the severity of chlorotic symptom in rice (Lin et al., 1998; Liu et al., 2000), suggesting the potential role of this protein in pathogenesis. In addition, SP was presumed to have function in vector transmission during the early period of RSV-planthopper recognition (Gray and Banerjee, 1999) but lacking of direct evidence.

As described above, the infection of RSV induces various inclusion bodies containing different virus-encoded proteins in diseased plant or viruliferous insect vector. Because these inclusion bodies may be generated by the aggregation of virus-encoded proteins and host proteins, some of them may represent the viral replication sites at the later stage of viral infection or the aggresomes of dissociated proteins. The time course of observation of these inclusion bodies formation would help us to characterize their biogenesis in the process of viral infection. The application of protoplast or the cultures of small brown planthopper vector cells in monolayers would help us to understand the earlier biogenesis of these inclusion bodies in near future.

4 Pathogenicity differentiation and genetic diversity of RSV

Pathogenicity is usually varied among RSV isolates from different regions. According to the difference in molecular weight of SP, RSV was classified as three different strains, Hongchao, P and N (Hayashi et al., 1989). Based on the average infection rates to different varieties, RSV isolates from China were divided into 5 pathotypes, including High virulence (HV), Slight high (SH), Moderate virulence (MV), Slight low (SL) and Low virulence (LV) (Cheng et al., 2008).

The genetic diversity and population structure of RSV in China were estimated based on the nucleotide sequences of isolates collected from different geographical regions during 1997–2004. RSV isolates could be divided into two or three subtypes. The population from eastern China is composed only of subtype I/IB isolates. In contrast, the population from Yunnan province (southwest China) is composed mainly of subtype II isolates, but also contains a small proportion of subtype I/IB isolates and subtype IA isolates (Wei et al., 2009). However, the frequent gene flow of RSV occurs within the subpopulations from different districts in eastern China or Yunnan province. The most recent outbreak of RSV in eastern China was not due to the invasion of new RSV subtype(s) (Wei et al., 2009). Extensive reassortment events were found, but significant recombination event was rarely detected in RSV natural population.

5 RSV-plant host interaction

Virus-host interaction is always one of the hot topics in the field of virology. The interaction between RSV and both plant species and insect vector is largely unknown but has some recent progress specific in RSV-plant interaction. Investigation of the transcriptional profiles of RSV-infected rice variety WuYun3 revealed that host genes involved in pathways of phosphate, flavonoid and brassinoliele synthesis are remarkably induced, but genes involved in gibberellin synthesis pathway are repressed, indicating that these biological pathways are regulated under the RSV infection (Zhang et al., 2008b). Analysis of transcriptional profiles of RSV-infected rice variety Nipponbare in Japan indicated that RSV modifies the rice cellular conditions for the enhancement of activity of virus propagation, accumulation of substrates for production of progenies, and suppression of host defense systems (Satoh et al., 2010). The host endogenous hormone may play critical role(s) during the RSV-host interaction, as showing that the synthesis of endogenous IAA is

obviously enhanced in the early stage of RSV infection but is repressed after appearance of typical symptoms (Yang et al., 2008), and exogenous application of abscisic acid (ABA) is able to improve the host resistance to RSV (Ding et al., 2008). As a parasite, virus encoded a limited number of proteins; thereby, some unknown yet host factors are recruited and utilized to establish successful infection. Similar to TMV, two host factors, a J protein and a member of the hsp20 family, have been demonstrated to interact with the RSV NSvc4, the putative MP of virus (Lu et al., 2009). However, the biological function of the interaction is unknown.

6 Management of RSV

Based on the properties of rice virus diseases, it is important to skillfully use the criteria of resisting, averting, eradicating and curing according to the results of forecasting and admonishing (Xie et al., 1994). Transplanting or seeding date seriously affects the incidence of rice stripe disease, so it is essential to delay the date of cultivation to avoid the peak of migration of the vector planthopper, which is earlier multiplied in wheat fields (Bae and Kim, 1994). Since the large number of viruliferous planthoppers is one of the main factors causing disease epidemic, spraying pesticide is also an effective way to control this disease.

Comparably, screening the resistant genes as well as constructing virus-resistant varieties is a more economic and environment friendly method, and many positive steps have been taken towards this aim. By using techniques of plant genetic engineering, the transgenic japonica variety of rice harboring RSV *cp* gene was generated, conferring high level of resistance to RSV (Hayakawa et al., 1992); while two ribozymes were designed to cleave RSV genome RNA4 specifically *in vitro* (Liu et al., 1996), showing an alternative strategy against this virus. As the much valuable role of Quantitative trait locus (QTL) in assisting selective breeding, QTL analysis has been used widely to investigate host genes related to RSV resistance. The *Stv-a*, *Stv-b* and *Stv-b*^{i} are three rice genes well known for their essential role in RSV resistance. Both *Stv-a* and *Stv-b* exist in Japanese upland varieties, and *Stv-a* locates on chromosome 6 (Washio et al., 1968). The *Stv-b*^{i}, an allele of *Stv-b*, locates on chromosome 11 of indica-type varieties, and the resistance mechanism is different from other resistance genes producing HR (Hayano-Saito et al., 1998; Hayano-Saito et al., 2000). In addition, numbers of QTLs on chromosomes 1, 2, 3, 5, 7 and 8 (Ding et al., 2004; Maeda et al., 2006; Sun and Jiang, 2006; Wu et al., 2009) have been reported to be related to RSV resistance. Interestingly, the QTL on chromosome 11 is also associated with the resistance to brown planthopper (BPH) and small brown planthopper (SBPH) resistance (Ding et al., 2004; Sun and Jiang, 2006; Duan et al., 2007). A novel strategy, Vector-Insect-Symbiont Technology (VIST), was proposed recently (Wen et al., 2003), aiming to use one of the endosymbiont *Wolbachia* in *L. striatellus* to control RSV. This method needs further investigation, but is promising in application. Some countermeasures such as the introduction of RSV-resistant varieties, including Yangjing 93, Zhengdao 99, Yandao 8, Xudao 3, Yangliangyou 6 and Fengyouxiangzhan, and the abandonment of rice varieties, including Wuyujing 3 and Wujing, which are highly susceptible to RSV, have been adopted. As a result, in Shanghai and Jiangsu, the virus carrier rates of *L. striatellus* in 2005 to 2009 which were 1.3%, 23.2%, 23.1%, 17.2% and 11.2% respectively, were decreasing. This means that the epidemic potential of rice stripe disease has been significantly reduced.

7 Perspectives

Numerous approaches have been taken towards a better understanding of RSV molecular biology from the virus and host perspectives, leading to fundamental knowledge on aspects of RSV genomes, movement, and virus-host interactions as outlined above. However, due to the lack of a reverse genetic system, the investigation of RSV is greatly impeded, and the knowledge in areas of RNA synthesis, assembly, systemic movement, and transmission is still largely unknown. To greatly improve the ability to manage RSV and protect the rice production, we are looking forward to more significant progress in all of these areas of RSV in the near future, e.g., the cultures of small brown planthopper vector cells in monolayers would allow us to investigate the earlier RSV replication cycle, including entry, replication, assembly, intracellular trafficking and release; the serial passage of RSV in rice plants without insect vector transmission would select the transmission-defective virus isolate, which allows us to identify the transmission-related virus-encoded proteins; the application of artificial MicroRNAs and RNA inhibition constructs derived from viral or host replication-related genes would confer efficient RSV resistance in plants; the screening of rice mutant lines would select effective inherent RSV-resistant genes. As the typical member of the genus *Tenuivirus*, RSV has several unique characteristics such as genome containing four negative-sense RNA segments, exploiting ambisense gene expression strategy, multiplication in plant and insect vector cells, as well as using various mutation mechanisms, including deletion, insertion, recombination and reassortment. Thus, the studies of RSV would help us to extend our understanding of plant virology.

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