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Biology of viral satellites and their role in pathogenesis

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Extraviral components that can influence the accumulation and pathogenesis of their associated helper viruses are known as 'satellites'. The maintenance of satellites requires their ability to associate with their helper viruses. Satellites can be categorized as either satellite viruses or satellite nucleic acids based on their ability to encode capsid proteins. Understanding the biology of satellites is important since they are pathogenic to a wide range of plant, animal, and yeast organisms. Most satellites influence the pathogenesis of their helper viruses by altering the interaction between the host and helper virus. However, the molecular mechanism that governs the trilateral interaction between host, satellites, and helper virus remains largely unexplored. This review comprehensively describes details of the association and interaction of helper viruses with satellite viruses, satellite RNAs, and satellite DNAs, and their implications for pathogenesis.

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Introduction

Certain subviral agents known as satellites cannot perform crucial functions of their infection cycles, such as replication, movement, transmission, and/or encapsidation, without being associated with various helper viruses [1,2]. With very few exceptions, the genomes of most satellites lack genes that encode proteins required for multiplication, and a substantial portion of the satellite genome is distinct from that of the helper virus genome. Satellites and their dependence on helper viruses for their replication and/or encapsidation were initially identified in the early 1960s [1,2]. Most satellites may be classified as satellite viruses and satellite nucleic acids (with the latter including both satellite DNA and satellite RNA). Satellite viruses encode structural proteins essential for the encapsidation of their own genome. Thus, satellite viruses are nucleoprotein complexes distinct from helper viruses. In contrast, satellite nucleic acids do not encode any structural proteins and are encapsidated instead by helper virus-encoded capsid proteins (CPs) [3,4].

The molecular mechanism that governs the trilateral interaction between host, satellites, and helper virus and the basis of either synergistic or antagonistic association of satellite with cognate helper virus remain largely unexplored. Due to the above-described association and dependence of satellites on helper viruses, satellite viruses generally accumulate to higher levels in infected host cells than do the cognate helper viruses [1,3,4].

Several salient features of satellites have been identified: first, most satellites are dependent on cognate helper viruses for the replication machinery, as they do not encode RNA/DNA polymerases; second, despite this dependence, satellites do not share any substantial sequence similarity with their associated helper viruses; third, barring few exceptions, satellites usually exacerbate or attenuate the induction of cognate helper virus-mediated symptoms in the infected host; and fourth, satellites can alter, and usually impede, the accumulation of cognate helper virus nucleic acid in the infected host cell.

Classification of satellites

Based on the ninth report of the International Committee of Taxonomy of Viruses (ICTV) and the classification criteria of satellites recently proposed by Krupovic [5•], satellites may be categorized and subcategorized as

1 Satellite viruses
   a Satellites that resemble Tobacco necrosis satellite virus (includes Tobacco necrosis satellite virus, Maize white line mosaic satellite virus, Tobacco mosaic satellite virus, Panicum mosaic satellite virus).
   b Chronic bee-paralysis virus-associated satellite virus.
   c Nodavirus-associated satellite virus.
   d Adenovirus-associated satellite virus (Dependovirus).
   e Mimivirus-associated satellite virus (Sputnik).
2 Satellite nucleic acids
   a Single-stranded satellite DNAs.
   b Double-stranded satellite RNAs.
   c Single-stranded satellite RNAs.

The biological impacts of satellite viruses, satellite DNAs, and satellite RNAs on their respective associated

helper viruses and the implications of these impacts on viral pathogenesis and disease development are summarized in Table 1 and discussed in the following sections.

Satellite viruses

Satellites that resemble Tobacco necrosis satellite virus

Tobacco necrosis satellite virus

The term 'satellite virus' was coined to denote the smaller, serologically unrelated isometric particle with dimensions of 18 nm associated with Tobacco necrosis virus (TNV) having dimensions of 22 nm. Tobacco necrosis satellite virus (STNV), being the first recognized and most extensively studied satellite virus, contains a small single-stranded RNA genome of about 1240 nucleotides (nt) [1]. STNV encodes for a single capsid protein (CP) of 195 amino acid residues (aa), which is essential and sufficient for the assembly of the satellite virus. The packaging of the virus particle occurs through cooperative interactions between the stem-loop structure widely distributed in the RNA genome and 60 copies of its self-encoded CP [6••]. The STNV genome is encapsidated by its self-encoded CP. The degenerate RNA structural motifs present in the genomic RNA act as packaging signals and bind specifically with the CP protein, thereby facilitating the encapsidation [6••]. The sequence-specific interaction of STNV RNA with its coat protein contributes to the assembly of the satellite virus particle, as this interaction helps overcome the electrostatic hindrance to the coat protein assembly [7]. Three major strains of STNV, denoted as STNV-1, STNV-2, and STNV-C, have been identified based on their different serological features, amino acid compositions, and replication-facilitating TNV isolates [8,9]. Tobacco necrosis virus strain A (TNV-A) supports the replication of STNV-1 and STNV-2, while Tobacco necrosis virus strain D (TNV-D) maintains STNV-C in the root of the tobacco plant but not in its leaves [10].

Maize white line mosaic satellite virus

The Maize white line mosaic satellite virus (SMWLMV) particle has dimensions of 17 nm, contains a positive-sense single-stranded RNA genome of about 1168 nt, and is associated with the Maize white line mosaic virus (MWLMV) particle [11]. In the infected maize plant (*Zea mays* L.), SMWLMV depends on the helper virus MWLMV for its replication. Encapsidation of SMWLMV genomic RNA is carried out by the capsid protein encoded by its single open reading frame (ORF).

Tobacco mosaic satellite virus

The Tobacco mosaic satellite virus (STMV) is a small icosahedral particle with dimensions of 17 nm, and contains a single-stranded RNA genome of 1059 nt [12,13]. STMV is the only satellite virus shown to be associated with a rod-shaped helper virus, specifically tobamovirus, for its replication. The polycistronic messenger RNA of STMV possesses two ORFs that encode for a 6.8 kDa protein with unknown function and a 17.5 kDa capsid protein [14].

Panicum mosaic satellite virus

Panicum mosaic satellite virus (SPMV) is positive-sense single-stranded RNA virus of about 824 nt that depends on Panicum mosaic virus (PMV) for its replication as well as its spread [15–17]. SPMV exaggerates the mild symptoms of PMV to produce severe symptoms, and specifically leads to chlorotic mottle and stunted growth of the millet [15]. Use of a Potato virus X (PVX)-based vector to express SPMV-CP was shown to induce the formation of chlorotic spots on the host plant as well as non-host plants, and confirmed the role of CP as a pathogenicity determinant [18].

Chronic bee-paralysis virus-associated satellite virus

Chronic bee paralysis satellite virus (CBPSV), the single member of this category, produces small virus particles with dimensions of 17 nm that is associated with cloudy wing disease in the honey bee (*Apis mellifera*). In 1980, Bailey and associates observed an association between CBPSV and Chronic-bee paralysis virus (CBPV)-infected honey bees. The distinguishing feature of CBPSV is that it is the only satellite shown to have a segmented genome. The genome of CBPSV consists of three single-stranded RNA molecules, denoted as RNA-A, RNA-B, and RNA-C, each of which consisting of about 1100 nt [19]. CBPSV is encapsidated with its self-encoded CP, and hence differs serologically from the CBPV particle. However, the nature of the encapsidation of the CBPSV particle (i.e. whether the three segments are encapsidated together or separately) is not known. Later studies demonstrated CBPSV to be dispensable for the replication of CBPV. Although the replication of CBPSV depends on the presence of CBPV, CBPSV interferes with the replication of CBPV. The amount of CBPV virus particle as well as the amounts of CBPV-RNA1 and RNA2, are greatly reduced in infected queen pupae with increased levels of multiplication of CBPSV. CBPSV multiplication interferes with replication of the helper virus CBPV, probably because of their competition for proteins required for replication.

Nodavirus-associated satellite virus

Nodavirus-associated satellite virus contains a linear single-stranded RNA genome of about 0.8–0.9 kb in size [20]. White tail disease (WTD) of the large freshwater prawn *Macrobrachium rosenbergii* was first reported in 1995 for prawn from the islands of Guadeloupe [21], and subsequently in 1999 for prawn from Taiwan and the Republic of China [20,22], and later from India. The small non-enveloped Macrobrachium rosenbergii nodavirus (MrNV) particle, with a diameter of 25 nm, and the associated non-autonomous satellite-like virus (XSV) particle, with a diameter of 15 nm, were found to constitute

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