

Sadwaviruses

T Iwanami, National Institute of Fruit Tree Science, Tsukuba, Japan

© 2008 Elsevier Ltd. All rights reserved.

Glossary

Natsudaidai A popular sour citrus grown in some parts of Japan.

Satsuma A major mandarin-type citrus grown in Japan and some Asian countries.

Introduction

The genus *Nepovirus* includes viruses which are transmitted by nematodes with polyhedral particles. Typical nepoviruses have a broad host range, a single coat protein, and a bipartite single-stranded RNA genome and are transmissible through seed. Sadwaviruses have been previously considered atypical and tentative members of the genus *Nepovirus*. Like typical nepoviruses, sadwaviruses have polyhedral virus particles which contain two species of genomic RNA, but can be distinguished on the basis of the genome organization, sequence homologies, and the number of coat proteins. Some sadwaviruses are transmitted by aphids.

The derivation of the name comes from the virus species, *Satsuma dwarf virus* (SDV), the type member of the genus *Sadwavirus*. The major disease caused by SDV is stunting, accompanied by the presence of boat-shaped leaves, in Satsuma mandarin (*Citrus unshiu* Marc.).

Taxonomy and Classification

SDV, *Strawberry latent ringspot virus* (SLRSV) and *Strawberry mottle virus* (SMoV) are the definite members of the genus *Sadwavirus*. Lucerne Australian symptomless virus (LASV), Rubus Chinese seed-borne virus (RCSV), and Black raspberry necrosis virus (BRNV) are tentative members (Table 1).

Virus species are demarcated on the basis of type of biological vector, if known, host range, absence of serological cross-reaction, absence of cross-protection, and difference in amino acid sequence (less than 75% in the large coat protein and the proteinase-polymerase region).

The genus *Sadwavirus* has not been assigned to any virus family.

Strains and Synonyms

Citrus mosaic virus (CiMV), Natsudaidai dwarf virus (NDV), and Navel orange infectious mottling virus (NIMV) are distantly related strains of *Satsuma dwarf virus*. Typical symptoms of CiMV-infected Satsuma mandarin are spotting and blotching of the fruit rind. NDV induces vein clearing and mottling on new leaves of Natsudaidai (*Citrus natsudaidai*). NIMV produces persistent chlorotic spots on leaves of sweet orange. The strains of *Satsuma dwarf virus* share around 80% sequence homology at the amino acid level.

Strawberry latent ringspot virus has a few synonyms, including rhubarb virus 5. Some isolates from olive, peach, raspberry, and grapevine were serologically distinguishable from the type strain, but sequence diversity among these isolates and strains has not been studied.

Geographic Distribution

SDV occurs mostly in Japan, but has also been found in China and Turkey. SLRSV is distributed throughout Europe and the USA, as well as Australia and New Zealand. SMoV is probably spread worldwide, as well as BRNV. Occurrence of LASV and RCSV is limited to Australasia and China, respectively.

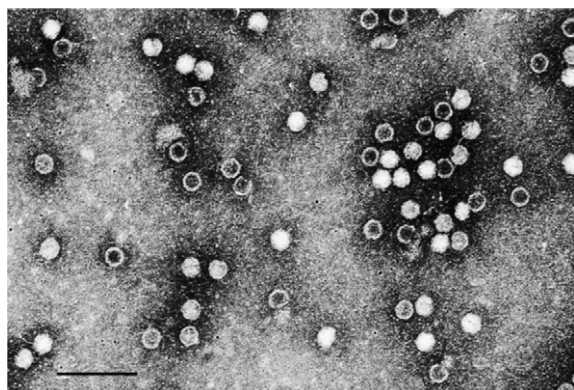
Virion Properties

Particles of sadwaviruses are icosahedral, about 26–30 nm in diameter (Figure 1). Some particles are penetrated by negative stain in the electron microscope. Typically, particles of sadwaviruses are of three types, named according to the relative rates of sedimentation of purified preparations. Top component (T) particles are empty shells. Middle component (M) and bottom component (B) particles contain genomic RNA. The buoyant densities in CsCl are about 1.43 and 1.46 g cm⁻³, respectively. SLRSV has only B particles with buoyant density about 1.46 g cm⁻³. Sadwavirus particles contain two sizes of RNA molecules. SDV has M and B particles that contain either of the different RNAs. In contrast, SLRSV has only B particles. Some particles contain one larger RNA, others contain two molecules of smaller RNA.

t0005 **Table 1** Species in the genus *Sadwavirus*^a

<i>Species and strains</i>	<i>Abbreviation</i>	<i>RNA-1 accession number</i>	<i>RNA-2 accession number</i>
<i>Satsuma dwarf virus</i>			
Citrus mosaic virus	CiMV		D64079 (partial)
Natsudaikai Dwarf virus	NDV		AB032750 (partial)
Navel orange infectious mottling virus	NIMV		AB000282 (partial)
Satsuma dwarf virus	SDV	AB009958	AB009959
<i>Strawberry latent ringspot virus</i>			
Strawberry latent ringspot virus	SLRSV	NC 006964	NC 006965
<i>Strawberry mottle virus</i>			
Strawberry mottle virus	SMoV	AJ311875	AJ311876
Tentative species in the genus			
Black raspberry necrosis virus	BRNV	NC 008182	NC 008183
Lucerne Australian symptomless virus	LASV		
Rubus Chinese seed-borne virus ^a	RCSV		

^aSpecies names are given in italic script; strain names and tentative species names are in roman script.



f0005 **Figure 1** Electron micrograph of negatively stained virus particles of Satsuma dwarf virus (the bar represents 100 nm).

s0030 **Genome Organization**

p0050 The genome of sadwaviruses consists of two molecules of positive-sense single-stranded RNAs called RNA-1 and RNA-2. The sizes of RNA-1 and RNA-2 are about 7 and 4–5.5 kb, respectively. The 3' termini of both RNAs are polyadenylated. In the case of SLRSV, both RNAs are linked at the 5' termini to a small protein (VPg). VPg's of other sadwaviruses are unknown.

p0055 Both RNA-1 and RNA-2 have a single large open reading frame (**Figure 2**). The general genome organization is similar to that of como- and nepoviruses. The polyprotein encoded by RNA-1 contains domains for helicase, protease, and RNA-dependent RNA polymerase, whereas the polyprotein encoded by RNA-2 has movement protein and coat proteins. The amino acid sequences of the N-termini of polyproteins encoded by RNA-1 and RNA-2 of SDV are highly conserved. The feature is observed in the polyproteins of tomato ringspot virus in the genus *Nepovirus*. The function of these regions is unknown.

s0035 **Sequence Comparisons**

p0060 Comparison among the sequences of sadwaviruses of different species at nucleotide and amino acid levels shows few marked similarities. Some regions show about 20–40% sequence identities, and other parts are less similar.

s0040 **Phylogeny**

p0065 Complete genomic nucleotide sequences of SDV, BRNV, SLRSV, and SMoV have been determined. Partial sequences of CiMV, NDV, and NIMV are available (**Table 1**). There is little information on the nucleotide sequences of other sadwaviruses. To reveal relationships, the RNA-dependent RNA polymerase region, which is the most conserved among sadwa-, como-, nepo-, and other plant picorna-like viruses, has been used for phylogenetic comparisons. Alignment of the most conserved regions of the RNA-dependent RNA polymerase region shows that all plant picorna-like viruses are separated to three distinct groups: the first and second groups include comoviruses and nepoviruses, respectively, whereas the third group consists of SDV (and closely related CiMV, NDV, NIMV), SMoV, apple latent spherical virus (ALSV) which is a member of a newly established genus *Cheravirus*, and viruses of the family *Sequiviridae*, which have monopartite RNA genome.

s0045 **Satellites**

p0070 SLRSV has strains that contain satellite RNAs. The SLRSV satellite encodes a polyprotein, which shows little homology with other known proteins. There is no evidence as to the function of the polyprotein. Other sadwaviruses do not contain a satellite RNA.

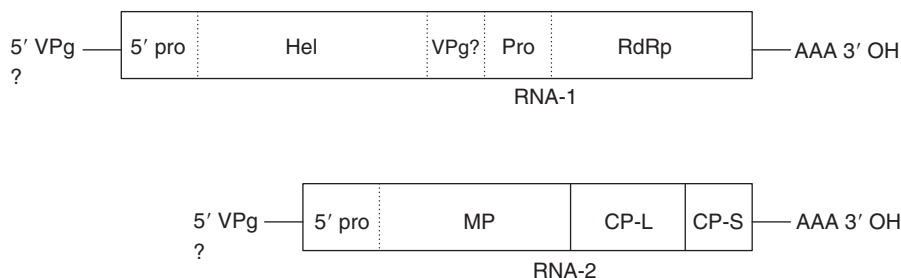


Figure 2 Genome organization of Satsuma dwarf virus. The boxes represent polyproteins. The vertical solid lines within the box show sites where cleavages occur in the polyprotein and the dashed lines indicate sites where cleavages are presumed to occur. Abbreviations: VPg, genome-linked viral protein; 5' pro, 5' protein; Hel, helicase; Pro, protease; RdRp, RNA-dependent RNA polymerase; MP, movement protein; CP-L and CP-S, large and small components of coat protein; AAA, poly (A).

Host Range and Virus Propagation

Natural host of SDV, CiMV, NDV, and NIMV is limited to woody plants, whereas SMoV, LASV, and RCSV are confined to herbaceous plants. BRNV infects *Rubus* spp. SLRSV has wide natural host range that includes both woody and herbaceous plants. All sadwaviruses are readily transmitted by mechanical inoculation to herbaceous plants of several families, including *Chenopodiaceae*, *Leguminosae–Papilionoideae*, and *Solanaceae*. Common experimental hosts used for the propagation of sadwaviruses are *Chenopodium quinoa*, *Cucumis sativus*, and *Physalis floridana*. SMoV propagates very poorly in any of the experimental herbaceous hosts, and purification of virus particles is difficult.

Epidemiology

SLRSV is transmitted by the soil nematode, *Xiphinema diversicaudatum*, and the transmission from plants to plants is slow, reflecting the restricted mobility of the nematode. SDV, CiMV, NDV, and NIMV are disseminated in a similar manner, and soil transmission is suspected, although vectors have not yet been identified. SMoV and BRNV are transmitted by aphids. All sadwaviruses but SMoV are seed-borne, and dissemination in seeds is important for long-distance movement of some sadwaviruses. Indeed, RCSV was first found in the UK from imported seeds from China.

Hosts of SDV, CiMV, NDV, and NIMV (citrus), BRNV (Raspberry), SMoV (strawberry), SLRSV (strawberry and fruit trees) are vegetatively propagated, and movement of contaminated budwoods and tubers plays an important role in the long-distance dissemination. For example, occurrence of SDV in China and Turkey is obviously related to unchecked budwoods from Japan.

Cytopathology

Tubules which contain virus particles arranged in a single file are formed in the cytoplasm of infected cells. A file of

virus particles is sometimes observed in a plasmodesma between two cells. Virus particles have also been detected in the vacuoles of infected cells in crystalline forms. These structures are also commonly observed in cell infected with como-, and nepoviruses.

Prevention and Control

Control measures consist of establishment of healthy stocks, chemical controls of vectors (nematode for SLRSV, aphids for BRNV and SMoV), and introduction of tolerant cultivars when available. Distributions of virus-free materials are important for vegetatively propagated crops (citrus for SDV, strawberry for SMoV and SLRSV, fruit trees for SLRSV). Several diagnostic tools including enzyme-linked immunosorbent assay (ELISA) and reverse transcriptase PCR (RT-PCR) are available for most of the sadwaviruses. Chemical fumigation of citrus field to prevent soil transmission of SDV is partially effective at best. Many strawberry cultivars are symptomless hosts for either SMoV or SLRSV. Mixed infection with other strawberry viruses induces apparent foliar symptoms and decline of tubers.

See also: Cheravirus (00724); Comoviridae (00744); Nepovirus (Comoviridae) (00449); Sequiviridae (00462).

Further Reading

- Halgren A, Tzanetakis IE, and Martin RR (2007) Identification, characterization, and detection of Black raspberry necrosis virus. *Phytopathology* 97: 44–50.
- Iwanami T, Kondo Y, and Karasev AV (1999) Nucleotide sequences and taxonomy of satsuma dwarf virus. *Journal of General Virology* 80: 793–797.
- Le Gall O, Iwanami T, Karasev A, et al. (2005) Genus *Sadwavirus*. In: Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (eds.) *Virus Taxonomy Eighth Report of the International Committee on Taxonomy of Viruses*, p. 799. San Diego: Academic Press.
- Mayo MA and Robinson DJ (1996) Nepoviruses: Molecular biology and replication. In: Harrison BD and Murrant AF (eds.) *The Plant Viruses*, vol. 5, p. 139. New York: Plenum.

Murant AF, Jones AT, Martelli GP, and Stace-Smith R (1996)
Nepoviruses: General properties, diseases, and virus identification.
In: Harrison BD and Murant AF (eds.) *The Plant Viruses*, vol. 5, p. 99.
New York: Plenum Press.

Thompson JR, Leone G, Lindner JL, Jelkmann W, and Schoen CD
(2002) Characterization and complete nucleotide sequence of
strawberry mottle virus: A tentative member of a new family of
bipartite plant picorna-like viruses. *Journal of General Virology* 83:
229–239.

ELSEVIER FIRST PROOF