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Plant Satellite Viruses (Albetovirus, Aumaivirus, Papanivirus, Virtovirus)

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1 **Plant satellite viruses (*Albetovirus, Aumaivirus, Papanivirus, Virtovirus*)**

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9
10 **Abstract**

11 Satellite viruses are a polyphyletic group of viruses encoding structural components of their virions,
12 but incapable of completing the infection cycle without the assistance of a helper virus. Satellite
13 viruses have been described in animals, protists and plants. Satellite viruses replicating in plants
14 have small icosahedral virions and encapsidate positive-sense RNA genomes carrying a single gene
15 for the capsid protein. Thus, for genome replication these viruses necessarily depend on helper
16 viruses which can belong to different families. Plant satellite viruses are classified into genera
17 *Albetovirus, Aumaivirus, Papanivirus*, and *Virtovirus*. This chapter describes the diversity and
18 properties of these viruses.

19
20
21 **Keywords:** satellite virus, helper virus, capsid protein, plant viruses, *Albetovirus, Aumaivirus,*
22 *Papanivirus, Virtovirus*, virus taxonomy

25 **Introduction**

26 Viruses span an entire range of morphological, genomic, and functional complexity. Some viruses are
27 exceedingly complex, surpassing many unicellular organisms in terms of physical dimensions and
28 genome sizes. For instance, members of the family *Mimiviridae* carry megabase-sized genomes
29 encoding over 1000 proteins, including many of the molecular machineries required for their
30 multiplication. On the other side of the complexity spectrum are viruses carrying just one or two
31 genes. However, no matter how big or how small they are, replication of all viruses depends on
32 certain functions provided by the host cell. Notably, some viruses depend not only on the host cells
33 but also on other viruses for reproduction.

34

35 The phenomenon whereby one virus depends for its propagation on another virus has been first
36 described in a plant virus system in the early 1960s. Certain preparations of tobacco necrosis viruses
37 (TNV; genera *Alphanecrovirus* and *Betanecrosisvirus*, family *Tombusviridae*) contained two types of
38 spherical particles that differed in size and antigenic properties; whereas the larger, TNV, particles
39 could propagate autonomously, the smaller ones were unable to replicate in the absence of the
40 larger ones. The smaller particles became known as particles of satellite tobacco necrosis virus
41 (STNV), whereas TNV is referred to as STNV's helper virus. Subsequently, several other plant viruses
42 having features similar to those of STNV have been discovered. Furthermore, viruses which depend
43 on another virus for reproduction have been described in protists and animals. Overall, satellite
44 viruses vary considerably in terms of complexity and evolutionary origins. Also, the functions
45 supplemented by the helper viruses vary from one virus system to another. For instance, satellite
46 viruses of plants rely on helper viruses for genome replication, whereas members of the
47 *Lavidaviridae* depend on giant mimiviruses for transcription.

48

49 The tripartite relationship between satellite viruses, helper viruses and host cells is an example of
50 hyperparasitism, which is not uncommon in complex natural ecosystems. Notably, there are other
51 genetic elements which parasitize viruses, including satellite nucleic acids. The key difference
52 between satellite nucleic acids and satellite viruses is that the latter necessarily encode components
53 of their virions, whereas the former do not. Instead, satellite nucleic acids commonly encode
54 proteins responsible for the replication of the cognate nucleic acid, whereas the components of the
55 virion for horizontal transfer are being provided by the helper viruses.

56

57 Due to their dependency on other, quasi-autonomous viruses for reproduction, most satellite
58 viruses, with a notable exception of members of the genera *Dependoparvovirus* and *Deltavirus*, have
59 been for a long time considered as sub-viral agents and not officially classified by the International
60 Committee on Taxonomy of Viruses (ICTV). However, in 2016, the arbitrary distinction between
61 satellite viruses and other viruses has been abandoned and satellite viruses were incorporated into
62 the ICTV classification scheme, resulting in establishment of several genera and families. Plant
63 satellite viruses have been classified into genera *Albetovirus*, *Aumavirus*, *Papanivirus*, and *Virtovirus*;
64 family *Sarthroviridae* has been created for classification of positive-sense (+)RNA satellite viruses
65 that infect arthropods, and *Lavidaviridae* includes double-stranded DNA viruses replicating in protist
66 cells and parasitizing giant viruses of the family *Mimiviridae*.

67

68 This chapter describes the diversity and properties of plant satellite viruses belonging to the genera
69 *Albetovirus*, *Aumavirus*, *Papanivirus* and *Virtovirus*.

70

71 **Albetoviruses: Viruses related to satellite tobacco necrosis virus**

72

73 STNV is one of the most extensively studied satellite viruses. Over the years, many properties of this
74 virus, including its genome sequence, virion structure and assembly, as well as interaction with the
75 helper virus, have been elucidated. The linear STNV genome consists of 1,239 nucleotides and

76 encodes a single capsid protein (CP) of 195 amino acids, which is necessary and sufficient for virion
77 formation. Assembly of icosahedral virions proceeds cooperatively via interactions between the
78 packaging signals, degenerated stem-loop structures distributed throughout the genome, and
79 multiple CP copies.

80

81 In the natural habitat, STNV is transmitted through the soil the same way as its helper virus, i.e., by
82 zoospores of a plant-pathogenic fungus *Oplidium brassicae*, suggesting that both viruses share
83 certain determinants. For both TNV and STNV, the 5' ends of the genomes are phosphorylated and
84 lack a 7-methylguanylate cap or a genome-linked protein, whereas the 3' termini lack a
85 polyadenylation sequence. Several *cis*-acting elements located within the 5' and 3' untranslated
86 regions (UTRs) are responsible for efficient translation and replication of the STNV genome. The 3'
87 and 5' UTRs of STNV and TNV can be exchanged without abolishing RNA accumulation, although the
88 translation elements at the 3'-terminal regions appear to be unrelated in the two viruses.

89

90 Three serotypes of STNV have been described, including STNV-1 (or STNV), STNV-2, and STNV-C.
91 Different STNV strains are activated by different viruses. The replication of STNV-1 and STNV-2 is
92 supported by isolates of tobacco necrosis virus A (TNV-A is the sole member of the type species of
93 the genus *Alphanecrovirus*, *Tobacco necrosis virus A*), whereas TNV-D, the sole member of the type
94 species of the genus *Betanecrovirus*, *Tobacco necrosis virus D*, supports the replication of STNV-C.
95 Genome sequences for the three STNV strains have been determined (Table 1). The organization of
96 the genomes of the three viruses is overall similar. CPs are ≈50-63% identical in sequence (Figure
97 1B). Whereas the 5' UTRs of STNV-1 and STNV-2 are 30 nt in length and are nearly identical, the 5'
98 UTR of STNV-C is significantly longer (101 nt). Similarly, the 3' UTR of STNV-C RNA is significantly
99 different compared to those of STNV-1 and STNV-2 (40 and 38% similarity, respectively), which are
100 approximately 64% similar to each other.

101

102 STNV-like viruses STNV-1, STNV-2, and STNV-C are classified into three species, *Tobacco albetovirus*
103 *1*, *2*, and *3*, respectively, within a genus *Albetovirus* (sigil: *Al-* for alphanecrovirus [helper virus], *be-*
104 for betanecrovirus [helper virus], *to-* for tobacco).

105

106 **Aumaivirus: Satellite maize white line mosaic virus**

107

108 The fourth, more divergent member of the STNV-like virus group is satellite maize white line mosaic
109 virus (SMWLMV). SMWLMV depends on maize white line mosaic virus (MWLMV; species *Maize*
110 *white line mosaic virus*, genus *Aureusvirus*, family *Tombusviridae*) for multiplication. MWLMV can
111 infect maize in the absence of SMWLMV, whereas the SMWLMV particle can infect maize only when
112 co-inoculated with MWLMV. The ssRNA genome of SMWLMV is 1,168 nucleotides in length and
113 encodes one capsid protein. Similar to STNV-like viruses, the SMWLMV virion is 17 nm in diameter.
114 SMWLMV CP displays 32% identity ($E=1e-14$) to the corresponding protein of STNV-1, indicating that
115 SMWLMV and the STNV-like viruses have diverged from a common ancestor. However, due to
116 limited sequence similarity between the CPs of STNV-like viruses and SMWLMV, the latter virus has
117 been classified into a species, *Maize aumaivirus 1*, within a separate genus *Aumaivirus* (sigil: *Au-* for
118 aureusvirus [helper virus], *mai-* for maize).

119

120 **Papaniviruses: Viruses related to satellite panicum mosaic virus**

121

122 Satellite panicum mosaic virus (SPMV) is completely dependent on panicum mosaic virus (PMV), a
123 member of the species *Panicum mosaic virus*, genus *Panicovirus*, family *Tombusviridae*, for
124 replication as well as systemic spread in plants. Like in the case of STNV, the 5'-terminus of the SPMV
125 genome is phosphorylated and lacks a 7-methylguanylate cap. Several secondary structure elements
126 implicated in the replication of the SPMV genome were predicted in the 5' and 3' UTRs. The 826 nt-

127 long ssRNA genome of SPMV contains two open reading frames. However, only one of them
128 (encoding CP) was found to be expressed in *in vitro* translation assays. The sequence of SPMV CP is
129 not appreciably similar to those of STNV-like viruses (below 15% identity; Figure 1B). However, X-ray
130 structure analysis of the SPMV particle revealed that the protein has a similar jelly-roll fold as the
131 corresponding protein of STNV (Figure 1A). Beside its structural role, SPMV CP has several other
132 biological functions, most notably systemic accumulation, maintenance, and movement of the
133 cognate SPMV RNA. Interestingly, the latter activities of SPMV CP apparently extend to the helper
134 virus RNA, assisting in its maintenance or stabilization. It is noteworthy that PMV and SPMV are
135 involved in a peculiar tripartite association with a 350 nt-long satellite RNA (satRNA), whereby PMV
136 provides necessary factors for satRNA replication and SPMV provides CPs for satRNA encapsidation.

137

138 Two other viruses encoding SPMV-like CPs have been reported. The first one, satellite St. Augustine
139 decline virus (SSADV), is associated with the St. Augustine decline strain of PMV. SSADV is 95%
140 identical to SPMV over the entire genome length (36 nt changes, 5 aa changes) and can be
141 considered as a different strain of SPMV. The second putative satellite virus, satellite grapevine virus
142 (SGVV), has been discovered by deep sequencing of total genomic RNA from grapevine. However,
143 neither the viral particles nor the associated helper virus have been characterized. SGVV CP shares
144 ≈24% sequence identity with SPMV CP (Figure 1B).

145

146 SPMV and SSADV have been assigned into a genus *Papanivirus* (sigil: *Pa-* for *panicovirus* [helper
147 virus], *pani-* for *panicum*), within a species *Panicum papanivirus 1*. By contrast, SGVV remains
148 unclassified due to lack of information on its ability to form virions as well as on the identity of its
149 helper virus.

150

151 Homologs of SPMV CP are encoded by certain satRNAs. Particularly, bamboo mosaic virus satellite
152 RNA (satBaMV; 836 nt) encodes a protein, P20, which is 44% identical to the CP of SPMV (Figure 1B).
153 P20 plays a role in the accumulation and movement of the satBaMV but does not participate in
154 satRNA encapsidation. Instead, satBaMV is packaged into rod-shaped particles by the CP of the
155 helper bamboo mosaic virus, a member of the family *Alphaflexiviridae*. In addition, a sequence of
156 olive viral satellite RNA (OVsatRNA) has been deposited to GenBank (Table 1) that encodes a protein
157 35% identical to P20 of satBaMV (Figure 1B). Considering the conservation of the SPMV-like CPs, it
158 appears likely that satBaMV and OVsatRNA have evolved from genuine satellite viruses, once again
159 emphasizing the apparent ease with which transitions between different types of mobile elements
160 (i.e., parasitic nucleic acids and viruses) occur.

161

162 **Virtovirus: Satellite tobacco mosaic virus**

163

164 Satellite tobacco mosaic virus (STMV) has been isolated from tree tobacco (*Nicotiana glauca*) and is
165 naturally associated with and dependent on tobacco mild green mosaic virus (TMGMV), a member
166 of the species *Tobacco mild green mosaic virus*, genus *Tobamovirus*, family *Virgaviridae*. However,
167 under experimental settings, STMV can adapt and replicate in many plant hosts (e.g., tobacco,
168 pepper, tomato) in association with other tobamoviruses, including tobacco mosaic virus (TMV).
169 Thus far, STMV is the only known satellite virus that uses rod-shaped viruses as helpers.

170

171 The STMV genome is a linear ssRNA molecule of 1,059 nt that contains two open reading frames
172 (ORF), both of which are functional in the *in vitro* translation assay. The first ORF encodes a protein
173 of 58 aa which lacks similarity to proteins in the public databases and appears to be dispensable for
174 STMV multiplication. Indeed, certain naturally occurring isolates of STMV contain a deletion within
175 ORF1 and do not produce the corresponding product. The second ORF encodes STMV CP, which also
176 has no identifiable homologs in sequence databases. However, structural analysis shows that the

177 STMV CP has a jelly-roll fold similar to those of STNV and SPMV (Figure 1A), suggesting that the three
178 satellite viruses might be evolutionarily related.

179

180 As in the case of STNV and SPMV, but different from the helper TMV virus, the genome of STMV
181 lacks a 7-methylguanylate cap and the first 6 nucleotides of the STMV RNA are identical to those of
182 the STNV genome. However, in contrast to STNV and SPMV, the 5' end of STMV genome is not
183 phosphorylated. The 3' UTR is predicted to contain a series of pseudoknots followed by a tRNA-like
184 structure which can be amino acylated with histidine. The latter features are strikingly similar to
185 those of the genome of helper TMV and other tobamoviruses, with 40–50 nt-long regions of near
186 identity among the STMV and TMV 3' UTRs. These secondary structure elements play critical roles in
187 STMV genome replication, translation, and initiation of virion assembly.

188

189 STMV is currently a sole representative of the species *Tobacco virtovirus 1* within the genus
190 *Virtovirus* (sigil: *Vir-* for *virgavirus* [helper virus], *to-* for *tobacco*).

191

192 **Effect of mixed infections on the host and the helper viruses**

193

194 The parasitic lifestyle of satellite viruses is usually associated with negative effects on the fitness of
195 the helper virus, whereas the effect on the host cell during a co-infection might differ drastically
196 between viruses. The negative effect of STNV on the propagation of its helper virus manifests as a
197 decrease in (i) the number of necrotic lesions formed in co-inoculated plant leaves, (ii) diameter of
198 the lesions, and (iii) the amount of TNV produced in inoculated leaves. However, several factors
199 influence the extent to which TNV multiplication is affected, particularly the relative concentrations
200 of the satellite and helper viruses in the inoculum, the physiological state of the host plants before
201 and during the infection, and the type of plant used for the assay. An excess of STNV present during
202 co-infection reduces the yield of TNV to non-detectable levels. This reduction is associated with a
203 selective decrease in the synthesis of TNV capsid protein, suggesting that STNV affects TNV virion
204 production. By contrast, co-infection of PMV with SPMV exacerbates PMV disease phenotype in
205 millet plants resulting in a severe chlorosis and stunting. Expression of the SPMV CP from a Potato
206 virus X-based vector was shown to induce the formation of chlorotic spots on the host as well as
207 non-host plants, confirming that SPMV CP is a pathogenicity determinant.

208

209 The effects of STMV on the multiplication of its helper virus, as well as on the helper virus-induced
210 symptoms, are dependent on the host. In tobacco plants, STMV does not change the mild mosaic
211 symptom caused by TMGMV, whereas in jalapeno pepper severe leaf blistering induced by TMGMV
212 is attenuated by STMV infection. Furthermore, tobamovirus titers are greatly decreased by STMV in
213 pepper compared to other hosts.

214

215

216 **Common ancestry of plant satellite viruses?**

217

218 Plant satellite viruses from the four groups described above all propagate in flowering plants
219 (angiosperms) and share several genomic and structural characteristics that distinguish them from
220 other known viruses. Namely, representatives of all four satellite virus groups form capsids with $T=1$
221 icosahedral symmetry and composed of 60 CP subunits (Figure 1A). Although common among ssDNA
222 viruses (e.g., nanoviruses and circoviruses), $T=1$ capsids are not used by other known ssRNA viruses,
223 which typically have larger $T=3$ or $T=4$ capsids. Furthermore, the CPs of all described plant satellite
224 viruses have the same jelly-roll fold (Figure 1A), despite negligible sequence similarity. The
225 similarities also extend to the genomic characteristics. In particular, in all plant satellite viruses, the
226 linear ssRNA genomes lack the 5' 7-methylguanylate caps and polyadenylation sequences in their 3'
227 UTRs. Furthermore, 5' ends of the STNV and SPMV genomes are phosphorylated, whereas the first

228 six nucleotides at the 5' terminus of the STMV genome are identical to those in STNV. Considering
229 these similarities, it is conceivable that all plant satellite viruses have evolved from a common
230 ancestor. Notably, in structural comparison of the satellite virus CPs with the jelly-roll CPs of other
231 viruses, satellite viruses formed a monophyletic clade, indicating that they indeed might share a
232 common ancestor, despite high sequence divergence.

233

234 **Concluding remarks**

235

236 Due to their simplicity, satellite viruses have been (and continue to be) used as models for
237 elucidating fundamental biological processes, including mechanisms of cap-independent protein
238 translation as well as virion assembly and viral genome encapsidation. For instance, it has been
239 recently demonstrated that assembly of the icosahedral STNV virion proceeds through

240

241

242

243 **Further reading list**

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- 277
- 278

279 **Figure legends**

280

281 **Figure 1.** Relationships between plant satellite viruses. A. Structural similarity between the virions
282 (top) and jelly-roll capsid proteins (bottom) of satellite tobacco necrosis virus (STNV; PDB ID: 2BUK),
283 satellite panicum mosaic virus (SPMV; PDB ID: 1STM) and satellite tobacco mosaic virus (STMV; PDB
284 ID: 4OQ8). All three virions have $T=1$ icosahedral symmetry. Images of the depicted virions were
285 downloaded from the VIPER database (viperd.b.scripps.edu/). B. Pairwise identities between capsid
286 proteins of plant satellite viruses were calculated using SIAS
287 (<http://imed.med.ucm.es/Tools/sias.html>). Identity values are highlighted in cyan, orange, green and
288 red, respectively. SPMV-like capsid protein homologs encoded by satellite RNAs (OVsatRNA and
289 satBaMV) and SGVV are shaded in light green. The boxes containing identity values among the
290 capsid proteins of STNV-like viruses, SMWLMV, SPMV-like viruses, and STMV are coloured according
291 to the proposed classification of the plant satellite viruses: *Albetovirus*, cyan; *Aumaivirus*, orange;
292 *Papanivirus*, green; *Virtovirus*, red. Abbreviations: SMWLMV, satellite maize white line mosaic virus;
293 SSADV, satellite St. Augustine decline virus; SGVV, satellite grapevine virus; OVsatRNA, olive viral
294 satellite RNA; satBaMV, bamboo mosaic virus satellite RNA. Note that OVsatRNA and satBaMV are
295 not satellite viruses but satellite nucleic acids because they are packed into the virions of helper
296 viruses.

297 **Table 1.** General properties of plant satellite viruses.

Satellite virus	Species	Helper virus	Accession #	Genome, nt	Capsid \varnothing , nm	Comments
Albetovirus						
satellite tobacco necrosis virus (STNV-1)	<i>Tobacco albetovirus 1</i>	tobacco necrosis virus A (<i>Tombusviridae</i>)	V01468	1,239	17	STNV suppresses the replication of its helper virus and ameliorates the TNV-induced symptoms in different hosts.
satellite tobacco necrosis virus 2 (STNV-2)	<i>Tobacco albetovirus 2</i>	tobacco necrosis virus A (<i>Tombusviridae</i>)	M64479	1,245	17	STNV and STNV-2 coat protein genes share 55% nucleotide sequence identity, whereas the UTRs are more similar.
satellite tobacco necrosis virus C (STNV-C)	<i>Tobacco albetovirus 3</i>	tobacco necrosis virus D (<i>Tombusviridae</i>)	AJ000898	1,221	17	STNV and STNV-C coat proteins share 62% sequence identity, whereas the 3'UTRs are 40% identical.
Aumaivirus						
satellite maize white line mosaic virus (SMWLMV)	<i>Maize aumaivirus 1</i>	maize white line mosaic virus (<i>Tombusviridae</i>)	M55012	1,168	17	CP is 32% identical to that of STNV-1.
Papanivirus						
satellite panicum mosaic virus (SPMV)	<i>Panicum papanivirus 1</i>	panicum mosaic virus (<i>Tombusviridae</i>)	M17182	826	16	Besides virion formation, CP of SPMV has several other biological functions, including systemic accumulation, maintenance and movement of the SPMV RNA.
satellite St. Augustine decline virus (SSADV)	<i>Panicum papanivirus 1</i>	St. Augustine decline virus strain of PMV (<i>Tombusviridae</i>)	L10083	824	ND	SSADV is a strain of SPMV (36 nt substitutions; 5 aa changes).
satellite grapevine virus (SGVV)	unclassified	grapevine virus F (<i>Betaflexiviridae</i>) ?	KC149510	1,060	ND	SGVV and GVF share stem-loop structures at the 5' ends of the genomes.
Virtovirus						
satellite tobacco mosaic virus (STMV)	<i>Tobacco virtovirus 1</i>	tobacco mosaic virus (<i>Virgaviridae</i>)	M25782	1,059	17	The 3'UTR is similar to that of tobamoviruses, with a clear sequence similarity between STMV and TMV.