caulimoviruses the precapsid protein is cleaved at both ends removing its very acidic termini. This process might be coupled to virus assembly and maturation. The capsid protein is both methylated and glycosylated. The Pol protein is cleaved to yield the aspartic proteinase and reverse transcriptase/RNase H. At least some of these cleavages occur by the action of the viral proteinase. In contrast, the ORF III product is cleaved by a host cysteine proteinase. The genome arrangement and the presence of protease domains suggest that protein processing also occurs in CVMV and PVCV. It can be assumed that this is even more extensive, since the primary translation products are fewer and larger.

See also: **Plant pararetroviruses: Badnaviruses; Plant pararetroviruses (*Caulimoviridae*): Cassava vein mosaic virus, Caulimoviruses: general features, Legume caulimoviruses; Plant pararetroviruses: Rice tungro bacilliform virus; Vectors: Plant viruses.**

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Cassava Vein Mosaic Virus

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History, Taxonomy and Classification

The symptoms induced on cassava plants by cassava vein mosaic virus (CsVMV) were recognized as early as 1940 but the virus itself was first described by Kitajima and Costa in 1966. Based on preliminary observations, which showed that it has isometric particles and that its genome consisted of double-stranded DNA (dsDNA), it was tentatively classified in the *Caulimovirus* genus. More recent work led to the characterization of its genomic organization and showed important features which differ from caulimoviruses as well as from badnaviruses, the two genera of plant dsDNA formerly recognized. In response to these results and additional observations made on other plant dsDNA viruses, executive committee of the International Committee on Taxonomy of Viruses (ICTV) created a new genus (not yet named) with CsVMV designated as the type species. It was also decided to create and name *Caulimoviridae,* the family which contains all the plant dsDNA viruses including the genera *Caulimovirus, Badnavirus,* and three newly created genera. One includes CsVMV, another the former caulimoviruses infecting legumes (Soybean chlorotic mottle virus, SbCMV, and peanut chlorotic streak virus, PCSV) and the third has rice tungro bacilliform virus (RTBV) as its type species.

Geographic Distribution, Host Range and Virus Propagation

CsVMV was described in Brazil, with detailed accounts of its presence in the states of São Paulo and Ceará, but this limited description is certainly a consequence of the very few studies carried out on this virus. It infects plants from the cultivated cassava species, *Manihot esculenta* Crantz, which originated from the Amazon basin. Its complete host spectrum is not known, in particular no surveys have been made on wild cassava relatives. The impact on cassava production seems to be limited. Caulimoviruses are aphid-transmitted but in the case of CsVMV the natural vector is unknown. As cassava is mainly reproduced vegetatively, the virus is propagated very easily through cuttings. Experimentally it is possible to infect cassava plants by introducing an infectious clone using microbombardment. It has also been

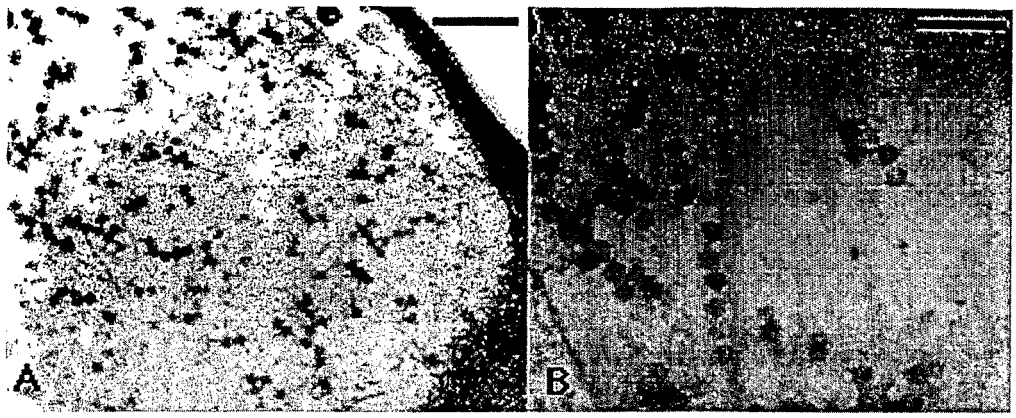

Figure 1 Electron microscopy views of CsVMV particles: (**A**) in inclusion bodies, ×40 000, bar = 250 nm; (**B**) as a cluster in the cytoplasm, ×80 000, bar = 125 nm.

shown that several dsDNA viruses are mechanically transmissible, namely cauliflower mosaic virus (CaMV) and cacao swollen shoot virus (CSSV).

The symptoms developed by the plants while in tissue culture, include discoloration of the veins, mottling, reduced leaf lamina and necrosis, starting from the tip and extending to the whole leaf. When the plants are grown under growth chamber conditions, the appearance of symptoms is very slow; only old leaves, over one month old, present symptoms similar to those observed in tissue culture except that the necrosis does not extend to the entire leaf.

Virus Structure and Genome Organization

Particles of CsVMV were observed by electron microscopy (Fig. 1). They appear to be isometric and about 50 nm in diameter. The particles accumulate in inclusion bodies in the cytoplasm of infected cells. The shape and the size of the virions of CsVMV are similar to those of CaMV which contain 420 subunits of a single coat protein (CP) arranged with $T = 7$ icosahedral symmetry. No studies have been made on CsVMV ultrastructure. CsVMV encodes its CP as a portion of a polyprotein which undergoes a post-translational processing. The exact size of the CP has not yet been determined.

The genome of CsVMV is a single circular molecule of a dsDNA 8159 nucleotides long. Figure 2 depicts the organization of the genome which contains four open reading frames (ORFs), with a possible fifth one, and a large intergenic region in which is located a promoter suspected to govern the transcription of a genome length, terminally redundant RNA. No biological studies were made on CsVMV, all the following information results from predictions deduced from sequence comparison and similarities with the genomes of plant dsDNA viruses. The large ORF 1 of CsVMV contains domains that are equivalent to the CP and the movement protein (MP) of caulimoviruses. ORF 3 shares a high degree of similarity with ORF 5 of the caulimoviruses, and the second half of ORF 3 of the badnaviruses and RTBV, which encode an aspartic proteinase (PR) and a reverse transcriptase (RT) including a RNase H domain. The aspartic PR is responsible for the post-translational processing of the polyproteins resulting from the translation of ORF 4 and ORF 5 of caulimoviruses and ORF 3 of badnaviruses.

Several unique features were identified in the genome organization of CsVMV that led to the creation of a new genus with CsVMV as the type species. The low proportion of GC, 25% vs. 34–39% for caulimoviruses, the presence of a large ORF 1, and the relative order of encoded functions. All the retroelements, including plant and animal pararetroviruses, retroviruses and retrotransposons, have in their genome a continuum between the so-called *gag* (CP) and *pol* (PR+RT) genes. The genome of CsVMV in contrast, displays first the CP (*gag*) followed by the MP and an additional ORF (ORF 2) instead of having the PR-RT (*pol*) immediately downstream of the CP (Fig. 3). ORF 4 of CsVMV shares a low but significant level of similarity with ORF 6 of caulimoviruses. This ORF encodes a protein involved in various functions. It plays a major role in the regulation of the translation of the polycistronic RNA (it is called transactivator or TAV in that case) and it is the main component of the viral inclusion body matrix (in that case it is called inclusion body protein or IBP).

Replication

The genome of CsVMV contains all the necessary

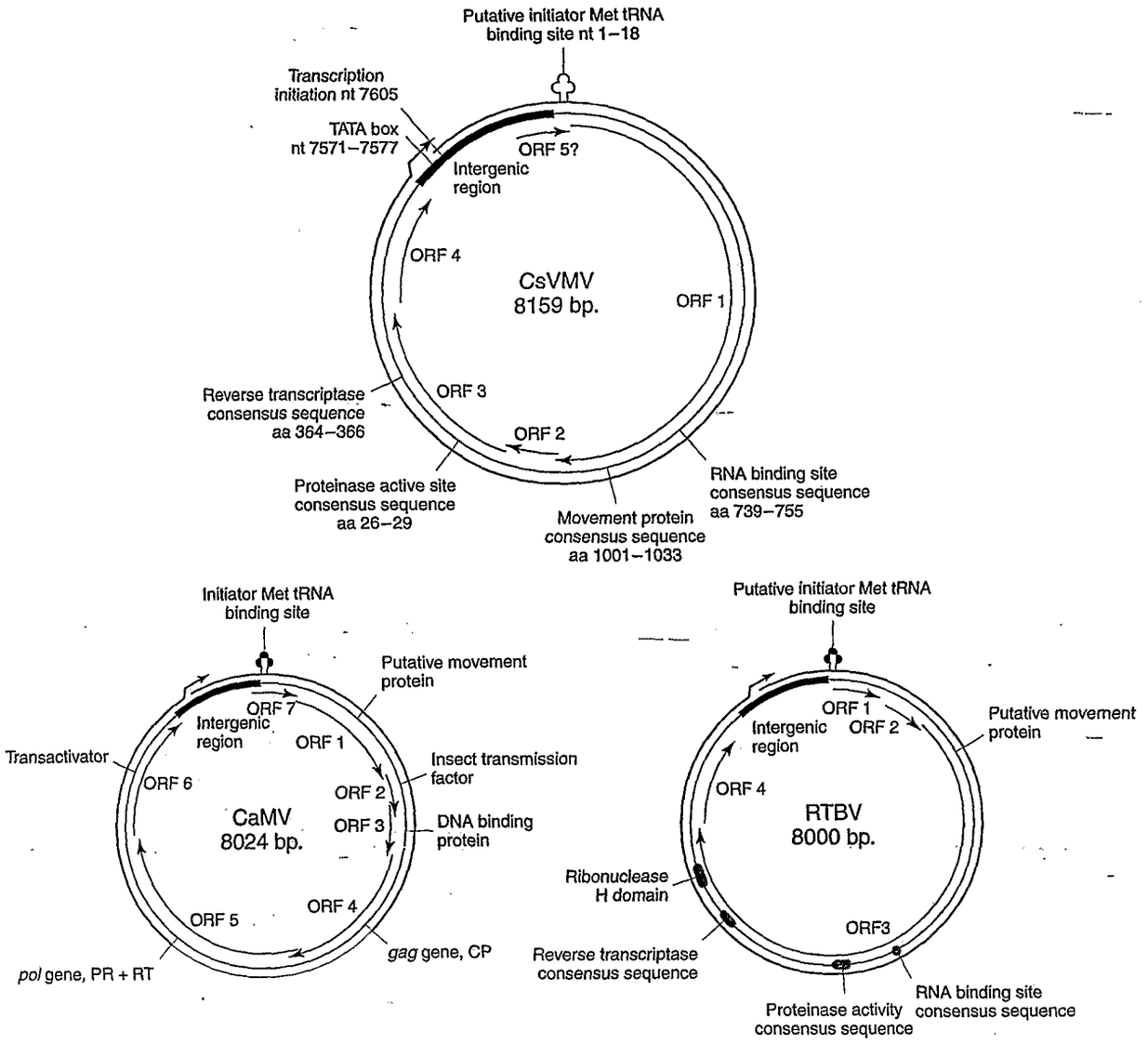

Figure 2 Genomic maps of CsVMV, CaMV and RTBV. Inner circles represent the genomic DNA on which the identified functions have been indicated. Outer circle represents the terminally redundant genome-length RNA transcript. The arrows inside the circle represent the ORFs. CsVMV has 4 ORFs (maybe 5) with a long polygenic ORF 1. CaMV, the type species of the *Caulimovirus* genus, has 7 ORFs, and RTBV, type species of a new genus of plant dsDNA viruses, has 4 ORFs; badnaviruses have three ORFs (see **Fig. 3**).

elements to make it compatible with the model of replication for the plant pararetroviruses. After infection of the host cell, the viral DNA migrates to the nucleus where the replication cycle begins with the synthesis of a terminally redundant genome-length RNA under the control of the genomic viral promoter. This synthesis is performed by a host RNA polymerase. The resulting transcript is used as a template by the viral-encoded RT when primed by a host methionine tRNA which recognizes a complementary sequence on the transcript. The RT synthesizes a minus-strand DNA and the RNase H degrades the RNA strand in the heteroduplex RNA–DNA leaving one or more specific short RNA fragments. The RT, acting now as a DNA-dependent DNA polymerase, uses these RNA fragments to prime the synthesis of the plus strand of viral DNA resulting in the circular double-stranded viral genome containing as many gaps as short RNA fragments were left. Except for the viral promoter which has been shown to be active, no experimental data have been obtained to demonstrate that CsVMV replication follows this cycle. Nevertheless, predictions deduced from sequence similarities indicate that this model should

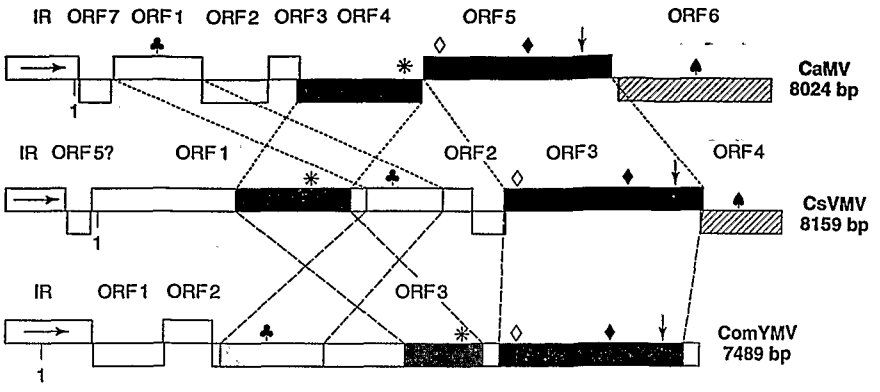

Figure 3 Comparison between genomic organization of CsVMV, CaMV, the type species of the genus *Caulimovirus*, and commelina yellow mottle virus (ComYMV) the type species of the genus *Badnavirus*. The three genomes start at the beginning of the large intergenic region for clarity purposes. ORFs or ORF segments encoding similar putative function are linked by vertical lines; the number 1 indicates the origin of DNA replication. ♣, MP active site; ✳, RNA binding site; ◇, PR active site; ◆, RT active site; ♠, TAV active center; ⸸, RNAse H consensus sequence.

be applicable to CsVMV. After assembly and accumulation in the infected cell, CaMV moves as a virion to adjacent cells through plasmodesmata where the viral MP contributes to the elaboration of tubular structures. As CsVMV encodes a predicted MP similar to the one of CaMV, it is probable that the cell to cell spread occurs by a mechanism comparable to that of CaMV.

Promoter Function and Organization

Verdaguer *et al* have shown that similarly to the 35S promoter of CaMV, the expression of CsVMV promoter is strong and constitutive. In unpublished results the same authors described that this expression requires a synergistic or combinatorial interaction between different *cis*-elements which individually confer tissue specificity and/or variation in the strength of expression. Figure 4 represents a functional map of the CsVMV promoter. This promoter is a valuable tool for genetic engineering and a good alternative to 35S. It can be used for expressing transgenes in dicotyledonous as well as monocotyledonous plants. Its organization permits the expression of the introduced gene(s) to be modulated by removing some of the *cis*-elements.

See also: **Plant pararetroviruses: Badnaviruses; Plant pararetroviruses (*Caulimoviridae*): Caulimoviruses: general features, Caulimoviruses: molecular biology, Legume caulimoviruses; Plant pararetroviruses: Rice tungro bacilliform virus.**

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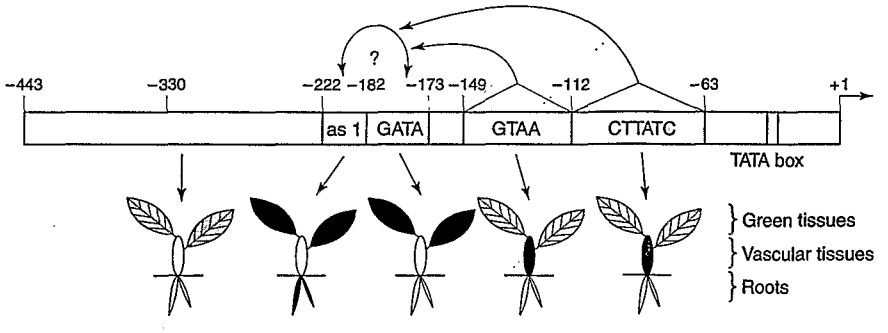

Figure 4 Functional design of the CsVMV promoter. Effect of the different regions of the promoter on gene expression in transgenic plant are represented. Three types of tissue are considered: green tissue, vascular tissue and roots. Dark area represents strong expression, gray area indicates lower expression and white area symbolizes undetectable expression. Arrows indicate the synergistic interactions between different domains of the promoter. Sequence motifs that might play an important role for CsVMV promoter expression are also mentioned. The numbers indicate the position relative to the transcription start site (+1). Adapted from Verdaguer *et al*, unpublished results.

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Legume Caulimoviruses

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History

The occurrence of a legume caulimovirus was first reported in 1980. The virus, subsequently identified as Peanut chlorotic streak virus (PC1SV), was found to occur naturally on peanut (groundnut, *Arachis hypogaea*) in the state of Andhra Pradesh in India. The first comprehensive report on a legume caulimovirus, Soybean chlorotic mottle (SoyCMV), was published in 1984. The virus was observed during surveys in Aichi Prefecture in 1981. To date PC1SV and SoyCMV appear to be the only caulimoviruses which were reported to occur under natural conditions on legumes.

Taxonomy and classification

DNA-containing plant viruses are included under the family *Caulimoviridae*. PC1SV and SoyCMV are in the genus Caulimovirus.

Virion Structure and Proteins

Virus particles are icosahedrical, c. 50 nm in diameter. Similar to other caulimoviruses they produce inclusions in cytoplasm which are circular or ovoid and consist of an amorphous, vacuolated, electron-dense matrix. The virus particles are embedded in the matrix.

Strains

No strains have so far been reported for SoyCMV. However a strain of PC1SV, designated as 'Chlorotic Vein-banding' strain (PC1SV-CVB) has been reported, which produces distinct symptoms on peanut. It differs from PC1SV in host range, symptoms and also in the physical map.

Geographic Distribution

SoyCMV occurs in Japan although its distribution in the various Prefectures in Japan is currently not known. PC1SV occurs in the states of Andhra Pradesh, Karnataka, Maharasthra and Tamil Nadu in India.

Symptoms and Host Range

Symptoms are here only given for the principal hosts. PC1SV in peanut causes reduced leaflets, chlorotic streaks and stunting. Symptoms produced by SoyCMV on soybean are mosaic or mottle on leaves and stunting of plants. Some soybean cultivars have been reported to produce different symptoms. A typical feature with both the viruses is the appearance of symptoms after three weeks of inoculation. The host range is given in **Table 1.**

Serological Relationships

PC1SV and SoyCMV do not react serologically with each or with a number of other caulimoviruses which include cauliflower mosaic (CaMV), figwort virus (FWV) or carnation etched ring virus (CERV). The serological tests employed were ELISA and agar gel double diffusion.

Transmission

PC1SV and SoyCMV are readily transmitted by mechanical sap inoculations. Although the majority of caulimoviruses are transmitted by aphids, attempts to transmit PC1SV or SoyCMV, both nonpersistently and persistently, by a range of aphids have so far been unsuccessful. PC1SV could not be transmitted by *Aphis craccivora* or *Myzus persicae* and SoyCMV by *Acyrthosiphon pisum, A. craccivora, Aulacorthum*

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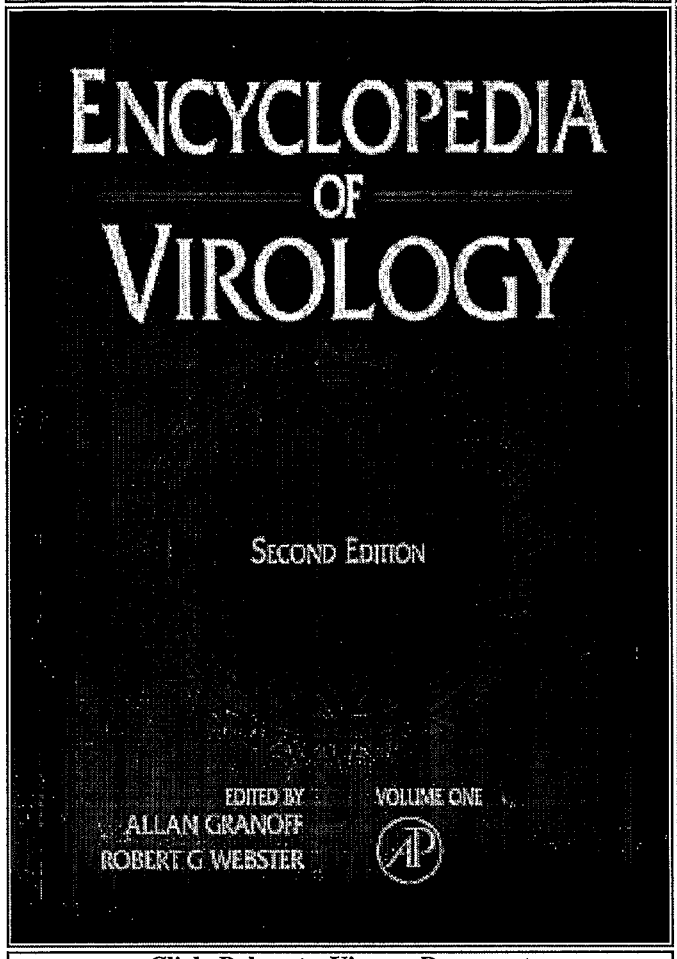

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