

Plant pararetroviruses: replication and expression

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True retroviruses are not known in plants; however, plant pararetroviruses (caulimoviridae) share many retroviral properties, replicating by transcription in the nucleus followed by reverse transcription in the cytoplasm. Pararetroviruses have circular DNA genomes that do not integrate into the host genome, and display several unique expression strategies. Typical of plant pararetroviral pregenomic RNA is a highly structured leader of about 600nt long that is bypassed by scanning ribosomes. Caulimoviruses and Soymoviruses have a further interesting translation mechanism: at least six of the seven open reading frames are translated via polycistronic translation mediated by a specific transactivator (TAV), which modifies the translation complex. TAV also forms large intracellular inclusion bodies, which are the site of translation and virus assembly.

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General properties, genera and expression strategies

Plant pararetroviruses, or Caulimoviridae, replicate via transcription/reverse transcription much like mammalian retroviruses but differ from the latter in that they do not integrate into the host genome [1^{*}]. Instead, they accumulate as thousands of episomal copies (minichromosomes) in the host cell nucleus [2^{*}]. Accordingly, while plant pararetroviruses, like mammalian retroviruses, harbor a POL gene comprising protease-, reverse transcriptase and RNase H-coding functions [3], they lack an integrase gene. Plant pararetrovirus capsids can be either icosahedral or bacilliform and are packed with double-stranded open-circular DNA. Typical features of these packed viral DNAs are discontinuities, that is, small overhangs. These are remnants of the reverse transcription process, which overshoots by a few nucleotides. Apparently, these discontinuities are repaired by repair polymerases and ligase after transfer into the nucleus.

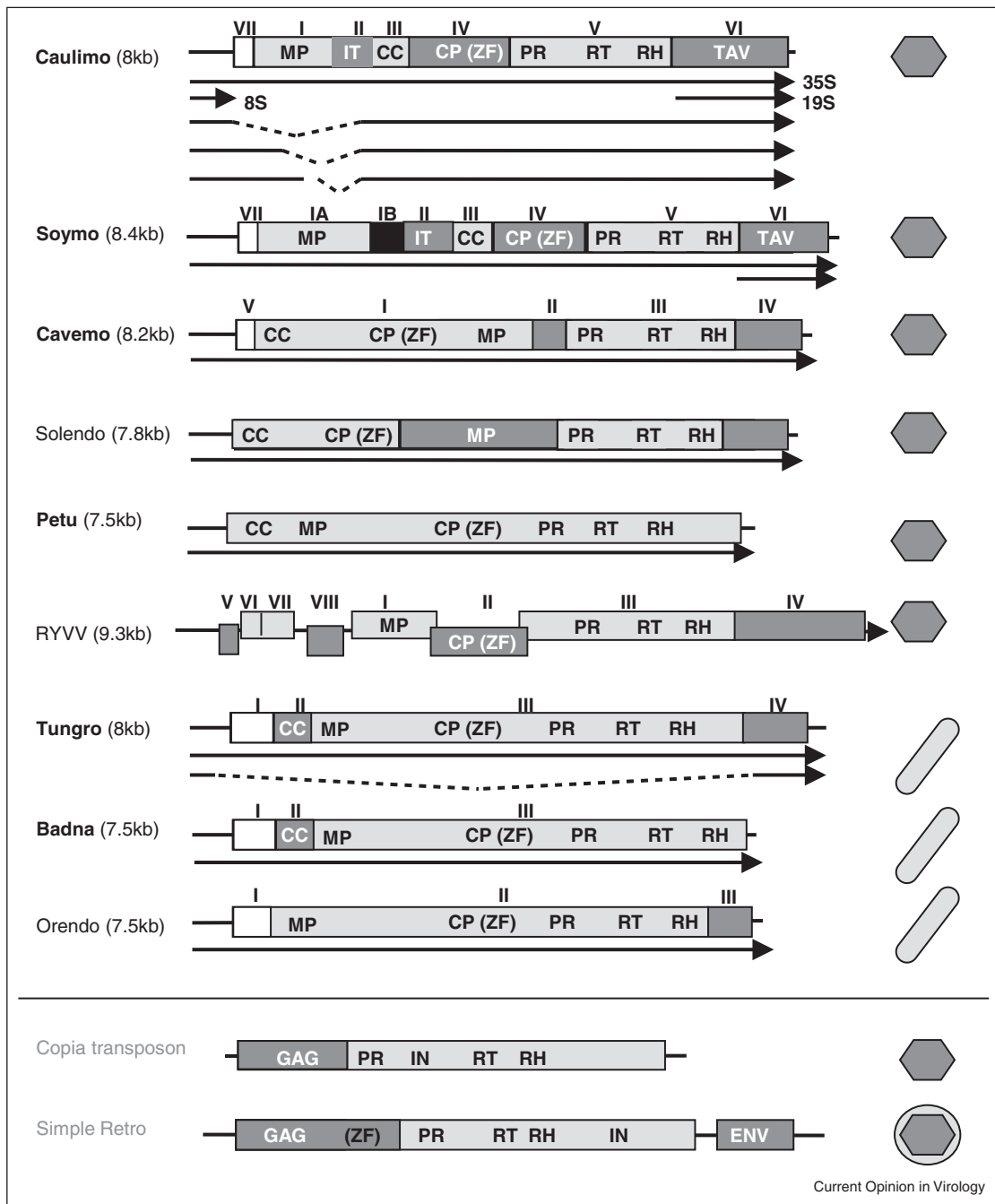
Interestingly the packed DNA also includes ‘knotted’ forms [2^{*}]. This observation gave the first indication that CaMV is reverse transcribed from a linear, and therefore once in a while knotted, precursor, that is, one form of pregenomic RNA.

Six ‘classical’ genera of plant pararetroviruses have been identified, with genome sizes between 7.5 and 9.3 kilobase pairs (Figure 1); the icosahedral Caulimo-viruses, Soymo-viruses, Cavemo-viruses and Petuviruses and the bacilliform Badna-viruses and Tungroviruses. Recently, the bacilliform Orendoviruses and the icosahedral Solendoviruses were suggested as two additional genera [4]. Furthermore, a newly discovered virus, *Rose yellow vein virus* (RYVV) has been described [5], for which a ninth genus might have to be created. Members of at least 5 of the genera exist also as defective integrates (endogenous plant pararetroviruses, EPRV) in the respective plant genomes. At least two of them (PVCV and BSV) can escape by transcription and recombination (see contribution by Chabbanes *et al.*, this volume).

In general, eukaryotic mRNAs each encode a single function, but pregenomic pararetro-virus transcripts encode several. Consequently, these viruses have evolved means of increasing the number of functions produced from a single translation product, the number of mRNAs and/or the number of translation initiation sites per mRNA. Solutions include producing polyproteins that are cleaved by a virus-encoded protease; by using sub-genomic promoters; by employing various forms of polycistronic translation; and by alternative splicing.

The different pararetrovirus genera have adopted a range of such strategies, and vary in the type and number of subgenomic RNAs produced, the number and arrangement of their open reading frames (ORFs), the degree of ORF-fusion and in their translation strategies. For instance, at least six of the seven Caulimovirus ORFs are produced from the polycistronic viral 35S RNA by a viral transactivator-viroplasm (TAV)-mediated reinitiation mechanism [6,7^{*}] (see below). TAV itself is translated from a monocistronic subgenomic 19S RNA. Taking another approach, ORF1 of *Rice tungro bacilliform virus* (RTBV) is translated only weakly from a non-AUG start codon, which allows leaky scanning. The AUG start codon of the second ORF is also in a ‘weak context’, allowing further leaky scanning of ribosomes, which can then reach and translate the third ORF [8]. The fourth RTBV ORF is translated from a spliced RNA [9]. All pararetroviruses identified so far have a ‘POL’-fusion

Figure 1



ORF arrangements of plant pararetroviruses. Top panel: Arrangement of ORFs on the pregenomic RNAs. Arrows beneath each viral sequence indicate transcripts (dotted lines indicate introns). MP: movement protein, IT: insect transmission, CC: coiled coil, CP: coat protein, ZF: zinc finger, PR: protease, RT: reverse transcriptase, RH: RNase H, and TAV: transactivator/viroplasmin. Lower panel: Comparison with a canonical retrotransposon and a simple mammalian retrovirus.

protein much like that of mammalian retroviruses — consisting of protease (PR), reverse transcriptase (RT) and RNase H (RH) (but lacking integrase) domains — that is cleaved into its constituent parts by the viral (aspartic) protease [10]. The ORFs of the other caulimoviridae are all fused to some degree, with Petuviruses

being the most extreme case, encoding all viral functions in a single ORF [11].

The capsid (equivalent to retroviral GAG) protein of Caulimoviruses is produced as a pre-protein, which is truncated at both ends at some stage during or after

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