

Molecular and biological factors regulating the genome packaging in single-strand positive-sense tripartite RNA plant viruses

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Plant pathogenic single strand positive-sense RNA viruses with the tripartite genome are classified into two families: *Bromoviridae* and *Virgaviridae*. Family *Bromoviridae* contains four genera *Bromo*, *Cucumo*, *Alfamo*, and *Ilarviruses* characterized by icosahedral particles. By contrast family *Virgaviridae* contains only one genus, *Hordeivirus*, with tripartite genome and characterized by helical particles. Unlike in monopartite plant viruses, packaging in tripartite RNA viruses requires a well-orchestrated process to ensure that viral progeny is selectively encapsidated and distributed optimally into three or four different viral capsids. Among the tripartite RNA viruses mentioned above, brome mosaic virus (BMV), the type member of the genus *bromovirus*, has been extensively used as a model system to unravel the mechanism of genome packaging. Using the available research data on BMV, this review is focused in updating the readers on how various macromolecular interactions (e.g. packaging signals) and biological factors (i.e. type of host plant) modulate genome packaging. The review also offers new directions of research to further our knowledge on the genome packaging in tripartite viruses.

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Introduction

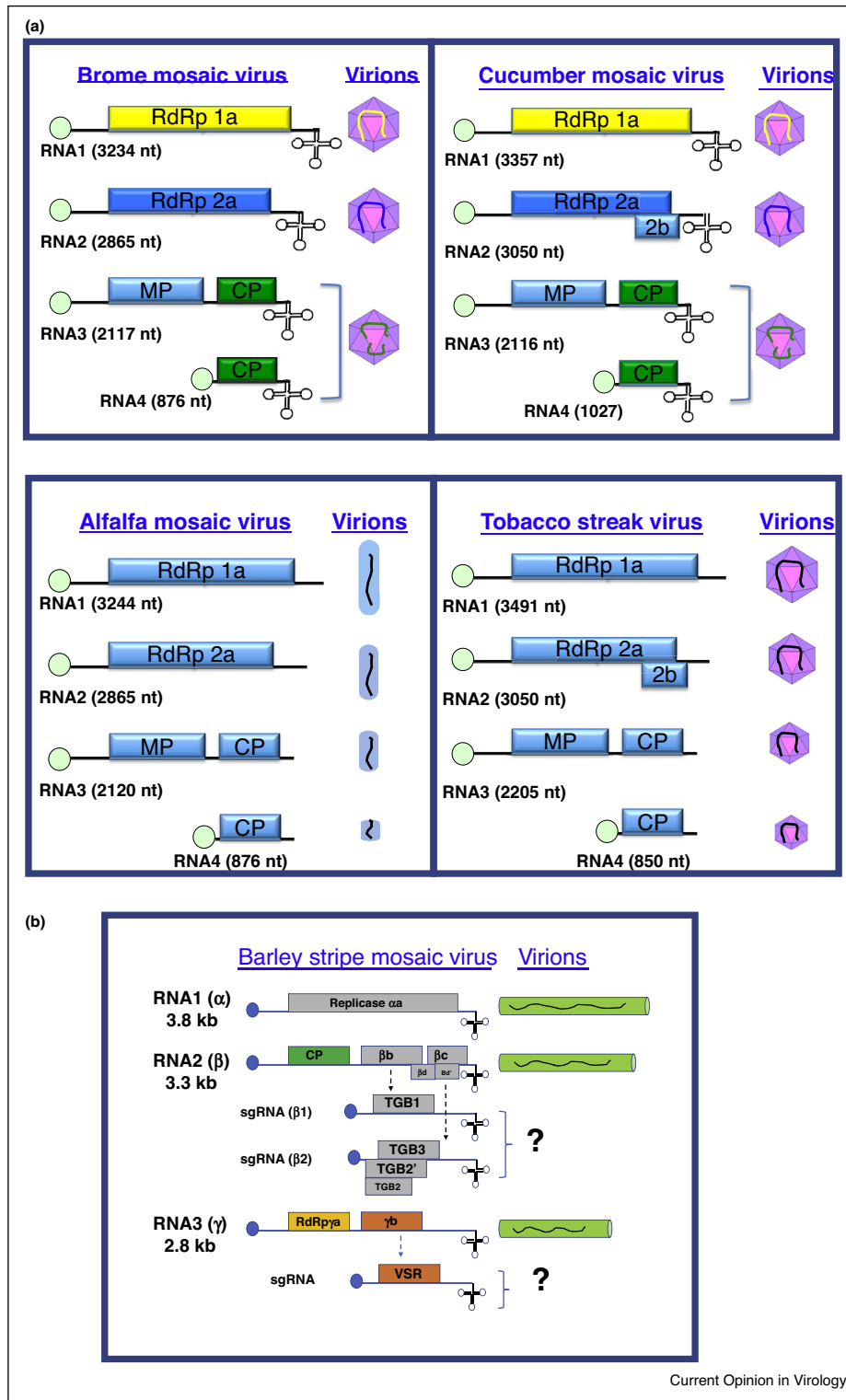
A wide range of sequential events regulates the life-cycle of a given virus with single-strand (ss), (+)-sense RNA genome. Among these events, packaging of infectious progeny into stable virions is an essential step in the establishment of a successful infection in

eukaryotic cells [1[•],2,3]. In almost all viruses, genome packaging is considered to be a highly specific process since that the majority of the virions contain exclusively viral progeny genomes [1[•],2,3]. Consequently, during packaging, viral nucleic acids must be distinguished from other cellular RNAs such as tRNAs, rRNAs, mRNAs [4]. Available molecular and genetic evidence suggested that the structural component, that is, the capsid protein (CP), selectively recognizes and directs the packaging of progeny RNA into virions [2].

A group of non-enveloped, ss, (+)-sense plant viruses belonging to families *Bromoviridae* and *Virgaviridae* are characterized by having tripartite genomes (Figure 1) [5[•]]. Virions of the genera *Bromo*, *Cucumo*, *Alfamo* and *ilarviruses* of the family *Bromoviridae* exhibit icosahedral symmetry [6]. The genome organization and the packaging scheme of these viruses are schematically shown in Figure 1a. In all tripartite viruses the largest three genomic RNAs are obligatory to initiate infection in whole plants [6]. A hallmark feature of the species *alfalfa mosaic virus* (AMV) of the genus *Alfamo* and members of the genus *Ilarviruses* are distinguished from the member viruses of *Bromo*, *Cucumo* and *Hordeivirus* in that, in addition to the three largest RNAs, either a few molecules of the capsid protein or its mRNA are required to initiate infection (called ‘genome activation’) [7]. Another feature that distinguishes *Bromo*, *Cucumo*, *Alfamo* and *Ilarviruses* is the distribution pattern of the genomic and subgenomic RNAs into virions. In *Bromo* and *Cucumoviruses* the three genomic and a single subgenomic RNA are packaged into three physically and morphologically identical virions [1[•],8] (Figure 1a). By contrast, in AMV and *Ilarviruses* four RNAs are packaged into four differentially sized virions [9]. Virions of AMV are distinguished from other viruses by having bacilli-form shaped particles (Figure 1a).

In contrast to virions with icosahedral symmetry, member species of the genus *Hordeivirus* of the family *Virgaviridae* are of rigid-rod shaped with helical symmetry [10] (Figure 1b). Barley stripe mosaic virus (BSMV), the type member of the genus *Hordeivirus* is characterized by having three genomic and three subgenomic RNAs [10] (Figure 1b). Each of the three genomic RNAs is separately encapsidated in rod-shaped virions of different size. Encapsidation of the subgenomic RNAs in BSMV is not clearly understood [10].

Figure 1



Schematic representation of the genome organization of a representative member of selected genera of tripartite plant viruses. (a) *Bromo mosaic virus* (genus *Bromovirus*); *Cucumber mosaic virus* (genus *Cucumovirus*); *Alfalfa mosaic virus* (genus unassigned); *Tobacco streak virus* (genus *Ilarvirus*) and (b) *Barley stripe Virus* (genus *Hordeivirus*). Non-coding sequences are represented as single lines and coding sequences are shown as open boxes. The morphology of virions produced in each virus is shown to the right.

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