Review article

Molecular biology of tenuiviruses, a remarkable group of plant viruses

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Introduction

The tenuiviruses are a most unusual type of virus about which little was known until recently. They were officially recognized as a plant virus group in 1983 (reviewed in Gingery, 1988). They are described in the Fifth Report of the International Committee on Taxonomy of Viruses as non-enveloped plant viruses, with possibly a negative ssRNA genome (Francki et al., 1991). Five viruses belong to this group, the type member rice stripe virus (RSV) first discovered in Japan in the 1890s, followed by maize stripe virus (MStV) in Mauritius in 1929, rice hoja blanca virus (RHBV) in Colombia in 1935, European wheat striate mosaic virus (EWSMV) in England in 1956, and rice grassy stunt virus (RGSV) in the Philippines in 1963 (reviewed in Gingery, 1988). Epidemics of RSV and of RHBV cause important yield losses in rice-growing areas of Asia and the former U.S.S.R. (Toriyama, 1983), and of tropical America (Morales & Niessen, 1985) respectively. Tenuiviruses exhibit unique properties that make them different from other plant viruses. Some properties of tenuiviruses are the following. (i) The peculiar flexuous ‘viral particles’ have an unexpected thread-like morphology and can adopt circular forms; they are referred to here as ribonucleoproteins (RNPs). (ii) Tenuiviruses infect plants of the Graminae family. They are distributed in all the leaf tissues and in the roots of infected plants. (iii) The viruses are persistently transmitted by delphacid planthoppers in which they are transovarially passed through successive generations. Multiplication of the viruses in their insect vectors may have deleterious effects on the latter. (iv) Purified RNP preparations are composed of a single nucleocapsid (NC) protein, and four (in RSV, RHBV and RGSV) or five (in MStV) ssRNA segments. Three to five species of dsRNA are also detected in some preparations, and are believed to result from annealing of separately encapsidated complementary ssRNA. (v) A non-structural protein of 16K to 21K accumulates in large amounts in infected plants, forming large amorphous inclusions or needle-like structures of different shapes, such as rings, rods and eight-like figures. (vi) The cDNA sequences of the genome segments so far determined suggest that the genome of tenuiviruses is mainly of an ambisense nature. (vii) An RNA-dependent RNA polymerase is associated with the RNP.

Not all of the properties described above have been verified for each of the five known tenuiviruses.

This paper reviews our present knowledge of the molecular biology of tenuiviruses, and the features that tenuiviruses share with negative-strand RNA viruses from the genera Phlebovirus and Tospovirus of the Bunyaviridae family (this family is divided into five genera, Bunyavirus, Hantavirus, Nairovirus, Phlebovirus and Tospovirus). Tospovirus is the only genus of this family whose members are plant pathogens; its type member is tomato spotted wilt virus (TSWV; Francki et al., 1991).

Morphology and structural components

The RNPs of tenuiviruses isolated from infected plants are most unusual in that they appear as fine filamentous strands in the electron microscope. In RSV they have been described as 3 nm-wide filaments adopting branched configurations (Koganezawa et al., 1975), as 8 nm-wide filaments (Toriyama, 1983), and as circular filaments of different lengths that can be separated into four groups with modal lengths of 510, 610, 840 and 2110 nm by repeated sucrose density gradient centrifugation; each group is associated with an ssRNA and a dsRNA species (Ishikawa et al., 1989; Ramirez et al., 1992). For RHBV, Morales & Niessen (1985) reported both 3 nm- and 8 nm-wide filaments that may adopt helical or loose configurations. Mostly circular RHBV RNPs, 8 nm wide and of variable lengths were also observed (Espinoza et al., 1992, 1993). For MStV, 3 nm-wide filaments (Gingery et al., 1981), but also circular and 8 nm-wide rod-shaped forms have been described (reviewed in Gingery, 1988). For RGSV, 4 nm-wide filaments and 6 to 8 nm-wide linear and circular
forms have been observed (Hibino et al., 1985). The filamentous particles of tenuiviruses might be defective forms of putative enveloped virions, as in the defective form of TSWV (Le, 1982; Resende et al., 1991; Kitajima et al., 1992). If this is the case, the defective nature would be a characteristic feature of tenuiviruses, since so far no enveloped virions have been observed for any of the members of this virus group.

Physical properties

All the tenuiviruses examined so far show a heterodisperse pattern after rate-zonal sedimentation. The distribution of material among the various peaks observed varies between preparations (reviewed in Gingery, 1988). The material contained in the various peaks of a particular tenuivirus bands at the same buoyant density by isopycnic sedimentation in CsCl, 1.290 g/ml for RSV (Gingery et al., 1983), 1.281 g/ml for MStV (Gingery et al., 1983) and 1.288 g/ml for RHBV (Morales & Niessen, 1985), indicating that for a given tenuivirus the protein to RNA ratio is the same for the various peaks observed by rate-zonal sedimentation.

Structural components

The tenuivirus RNPs are composed of RNA (Table 1) and a single NC protein (Table 2). An RNA polymerase has been found associated with purified preparations of RSV (Toriyama, 1986b; Barbier et al., 1992) and of RGSV (Toriyama, 1987), and RNA polymerase activity was also observed in RHBV RNP preparations (Ramirez, 1993). As seen in Table 1 the genomes of RSV, RHBV and RGSV are composed of four ssRNAs and that of MStV of five ssRNAs.

A feature of the individual genome segments of

### Table 1. Size of the tenuivirus ssRNA segments*

<table>
<thead>
<tr>
<th>Virus</th>
<th>RNA1</th>
<th>RNA2</th>
<th>RNA3</th>
<th>RNA4</th>
<th>RNA5</th>
</tr>
</thead>
<tbody>
<tr>
<td>RSV</td>
<td>9090</td>
<td>3514</td>
<td>2475</td>
<td>2137</td>
<td>5</td>
</tr>
<tr>
<td>MStV</td>
<td>9121</td>
<td>3575</td>
<td>2157</td>
<td>1317</td>
<td>8</td>
</tr>
<tr>
<td>RHBV</td>
<td>9600</td>
<td>3500</td>
<td>2300</td>
<td>1991</td>
<td>8</td>
</tr>
<tr>
<td>RGSV</td>
<td>4594</td>
<td>3940</td>
<td>3636</td>
<td>3485</td>
<td>15</td>
</tr>
</tbody>
</table>

* Sizes are in nucleotides. Underlined values represent size estimations from agarose gels; these are based on 330 daltons/nucleotide for RNA1, RNA2 and RNA3, and on RNA markers of known size for RNA4 and RNA5. For RNA1 and RNA2, the values were reported in daltons and are converted here to nucleotides. Other values are from cloning and sequencing data. Toriyama & Watanabe (1989); Takahashi et al. (1993); Kakutani et al. (1991); Zhu et al. (1991); Kakutani et al. (1990); Zhui et al. (1992); Ishikawa et al. (1989); the only report of a fifth RSV RNA of 1671 nucleotides in one isolate; Falk & Tsai (1983); Huiet et al. (1991); Huiet et al. (1992); Ramirez et al. (1992); Ramirez et al. (1993); Toriyama (1985).

### Table 2. Size of the structural and non-structural proteins of tenuiviruses*

<table>
<thead>
<tr>
<th>Structural</th>
<th>Non-structural</th>
</tr>
</thead>
<tbody>
<tr>
<td>Virus</td>
<td>RNA</td>
</tr>
<tr>
<td>RSV</td>
<td>230K</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>MStV</td>
<td>32K</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>RHBV</td>
<td>34K</td>
</tr>
<tr>
<td>RGSV</td>
<td>230K</td>
</tr>
</tbody>
</table>

* Underlined values are sizes estimated from analysis in SDS–polyacrylamide gels of purified proteins. Values in italics are size estimates of proteins synthesized by in vitro translation of transcripts containing the complete ORF and obtained from cDNA clones. Underlined values in italics are sizes estimated from in vitro translation of the RNA isolated from RNP. Other values are sizes predicted from nucleotide sequence data. +, Two or more proteins have been detected. /, Two values reported for the size of the protein. ND, Not detected by in vitro translation of RNP RNA. Toriyama (1986b); Toriyama (1986a); Kakutani et al. (1991), Zhu et al. (1991); Takahashi et al. (1993); Kakutani et al. (1990), Zhu et al. (1992); Hamamatsu et al. (1993); Gingery et al. (1981); Falk & Tsai (1983); Huiet et al. (1991); Huiet et al. (1992); Huiet et al. (1993); Huiet et al. (1990); Falk et al. (1987); Morales & Niessen (1983); Ramirez et al. (1992); Ramirez et al. (1993); Toriyama (1987); Hibino et al. (1985); Toriyama (1985), the 31-5K may be a degradation product of the 34-5K.
sequences are written 5' to 3'. X, tenuiviruses RNA segments. Colons indicate potential base-pairing in circular forms observed by electron microscopy. Circular tenuiviruses is the complementarity between the 5' and 3' termini (Takahashi 1990). Such base-paired structures may play a role in recognition by the RNA polymerase and in encapsidation. It was reported that when the RNA polymerase associated with RSV is dissociated from the RNA, it transcribes an RNA template containing the 3'-terminal conserved sequences of the four RNA segments (Barbier et al., 1992), suggesting that the 3'-terminal conserved sequences might constitute the promoter for the RSV RNA polymerase. (ii) RNA2, RNA3 and RNA4 are ambisense. Each contains two ORFs, one in the 5' half of the viral (v) RNA, and the other in the 3' half of the viral complementary (vc) RNA (Fig. 2a). The ambisense coding strategy (Fig. 2b) has been found previously in the small (S) RNA segment of phleboviruses and TSWV (reviewed in Elliott et al., 1991) and in the medium (M) RNA segment of the tospoviruses, Impatiens necrotic spot virus (INSV) and TSWV (de Haan et al., 1990; Kormelink et al., 1992a; Law et al., 1992); it is also observed in the two RNA segments of Arenaviridae (Auperin et al., 1984; reviewed in Bishop & Auperin, 1987). (iii) RNA2 encodes two proteins, NS2 on vRNA, and NSvc2 on vcRNA. (iv) RNA3 encodes two proteins, NS3 on vRNA, and the NC protein on vcRNA. (v) RNA4 encodes on vRNA the major non-structural protein (NS4) that accumulates in infected plants, and NSvc4 on vcRNA. ~u:A 

RNA1 segments

A nucleotide sequence has not been reported for the RNA1 segments of any of the tenuiviruses. Direct RNA sequencing of the termini of RSV RNA1 (Takahashi et al., 1990) revealed that the 5' and 3' ends are complementary to each other (Fig. 1a), and contain the conserved sequences (Fig. 1b) characteristic of tenuiviruses. Based on the size of the putative RNA polymerase associated with tenuiviruses (Table 2), on the information available about the ORFs of the other RNA segments, and by analogy with the large (L) RNA (Fig. 2b) of TSWV (de Haan et al., 1991), and of the

<table>
<thead>
<tr>
<th>Virus</th>
<th>5' terminus</th>
<th>3' terminus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tenuivirus</td>
<td>ACACAAAGUCGAGGTYA</td>
<td>UXCCOAACCUUGGUGU</td>
</tr>
<tr>
<td>Phlebovirus</td>
<td>ACACAAAG</td>
<td>CUGCGCU</td>
</tr>
<tr>
<td>Tospovirus</td>
<td>AGACAGAU</td>
<td>AUUGGGCU</td>
</tr>
</tbody>
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phleboviruses Rift Valley fever (RVF) virus (Muller et al., 1990) and Uukuniemi (UUK) virus (Elliott et al., 1992), RNA1 most probably encodes the RNA polymerase. However, it is still impossible to search for 'polymerase' domains within this RNA segment. This segment could be of negative polarity or ambisense.

**RNA2 segment**

The nucleotide sequence of RSV RNA2 has been determined (Takahashi et al., 1993). It contains two ORFs located in the 5' regions of the vRNA and vcRNA respectively (Fig. 2a and Table 2). Purified RHBV
vRNA2 directs the synthesis in vitro of a 23K protein (Ramirez et al., 1992) that probably corresponds to the 22-8K protein encoded by the ORF in RSV vRNA2. The ORF of the 94K protein encoded by RSV vcRNA2 shows stretches of weak amino acid similarity (Takahashi et al., 1993) with parts of the glycoproteins (G1 and G2) of the phleboviruses Punta Toro (PT) virus (Ihara et al., 1985) and UUK virus (Rönholm & Petterson, 1987), supporting the possible evolutionary relationship that exists between these virus groups.

RNA3 segment

The sequence of the RNA3 segment of RSV has been reported by two different groups (Kakutani et al., 1991; Zhu et al., 1991). This segment is ambisense (Fig. 2a). It encodes the NS3 and the NC (designated by the authors as coat protein) proteins (Table 2).

The sequence of MSTV RNA3 has also been determined (Huiet et al., 1991). This ambisense RNA (Fig. 2a) encodes the NS3 and the NC proteins (designated N protein by the authors; Table 2). The NC proteins of RSV (Kakutani et al., 1991) and of MSTV (Huiet et al., 1991) show 44% overall sequence similarity with that of PT virus (Ihara et al., 1985). Two subgenomic (sg) RNA3 species of opposite polarity were detected in MSTV-infected Zea mays (Huiet et al., 1991). These sgRNAs hybridize to clones with the regions containing ORFs of the NS3 and NC proteins (Fig. 2a). This situation is similar to that encountered in the S RNA segment (Fig. 2b) of PT, RVF and UUK viruses (Ihara et al., 1984; Simons et al., 1990; Giorgi et al., 1991), of the S and M RNA segments (Fig. 2b) of TSWV, of the M RNA segment of INSV (de Haan et al., 1990; Kormelink et al., 1992a; Law et al., 1992), and of the two RNA segments of the Arenavirusidae (reviewed in Bishop & Auperin, 1987). In RSV, the non-coding intergenic region (IR) located between the ORFs contains several U and A tracts; RNA folding analyses of sequences from this IR revealed inverted complementary sequences capable of forming a stem–loop structure (Kakutani et al., 1991; Zhu et al., 1991). A similar possible secondary structure was found in the S RNA segment of PT and UUK viruses and TSWV. The possible functional significance of this secondary structure could be related to transcription termination (Emery & Bishop, 1987).

RNA3 of RHBV of which the partial sequence has been established (L. A. Calvert, I. Lozano, A.-L. Haenni & B.-C. Ramirez, unpublished) demonstrates that in line with RSV and MSTV, it is also ambisense.

The 5′- and 3′-terminal panhandle structure (Fig. 1a) is similar to that found in the M RNA of PT virus (Ihara et al., 1985) and RVF virus (Collett et al., 1985), and in the S RNA of UUK virus (Simons et al., 1990), PT virus (Ihara et al., 1984), and sandfly Sicilian fever virus, another phlebovirus (Marriott et al., 1989).

RNA4 segment

The nucleotide sequence of the RNA4 segments of RSV (Kakutani et al., 1990; Zhu et al., 1992), MSTV (Huiet et al., 1992) and of RHBV (Ramirez et al., 1993) has been determined. This segment uses the ambisense coding strategy (Fig. 2a). The ORF in vRNA4 encodes the major non-structural protein that accumulates in infected plants. For RSV, MSTV and RHBV, this protein has been designated disease-specific (S) protein, major non-capsid protein (NCP), and non-structural RNA4 protein (NS4) respectively; in MSTV and RHBV, it is the major component of the amorphous inclusions and needle-like structures (Espinoza et al., 1993). The ORF located in the vcRNA4 encodes a protein designated here as NSvc4 (Table 2). NS4 of RHBV possesses 59% amino acid identity with the corresponding proteins of RSV and MSTV (Ramirez et al., 1993). Between RSV and MSTV this protein presents 74% identity. The RHBV NSvc4 and the corresponding proteins of RSV and MSTV follow the same trend. The similar organization of RNA4, and the similarity of its deduced proteins between RSV, MSTV and RHBV reflect the evolutionary relatedness that exists between these viruses. The amino acid similarity between the proteins corresponding to the NS4 and NSvc4 of RSV and MSTV is greater than with the NS4 and NSvc4 proteins of RHBV. It thus appears that RSV and MSTV are more closely related to each other evolutionarily than to RHBV. In addition, NS4 of RHBV has limited amino acid sequence identity with the helper component of tobacco vein mottling potyvirus; this similarity suggests that NS4 of tenuiviruses may be involved in virus transmission by the plant hopper (Ramirez et al., 1993).

Two sgRNA4s of complementary polarity (Fig. 2a) were detected in MSTV-infected Z. mays (Huiet et al., 1992). One sgRNA corresponds to the 5′ part of vRNA4 and should contain the NS4 (or NCP) coding region. The other sgRNA corresponds to the 5′ part of vcRNA4 and should contain the NSvc4 coding region (referred to by the authors as NS4). RNA4 of the two polarities as well as a sg-vRNA4 and a sg-vcRNA4 were detected in RHBV RNP (Ramirez et al., 1992; Ramirez, 1993).

Although, it has not been proven that the sgRNAs are indeed the mRNAs for the corresponding ORFs, their sequence relationships, sizes and polarities suggest them to be mRNA. The presence of sgRNAs of opposite polarity reported for tenuiviruses is similar to the situation observed for the ambisense RNA segments (Fig. 2b) of phleboviruses, tospoviruses (de Haan et al., 1990; Kormelink et al., 1992a; Law et al., 1992; reviewed...
in Elliott et al., 1991) and Arenaviridae (reviewed in Bishop & Auperin, 1987). Indeed for some of the animal viruses, the sgRNAs have been shown by in vitro translation to direct the synthesis of the corresponding protein (Ulmanen et al., 1981).

RNA5 segment

The nucleotide sequence of the RNA5 segment of MSTv (Huiet et al., 1993) has been determined. An RNA5 species was also observed in one isolate of RSV (Ishikawa et al., 1989). Sequence data showed that this segment in MSTv is negative-sense rather than ambisense, and encodes the NS5 protein (Fig. 2a and Table 2). The 5’ and 3’ ends are complementary to each other and possess the conserved terminal nucleotide sequences (Fig. 1) characteristic of tenuiviruses, except that the 3’-terminal sequence has an A instead of a U residue at position 6, as does RSV RNA1. Database comparisons did not reveal significant similarity between NS5 and any other protein.

Genome replication and transcription

Very little is known about the replication and transcription strategies of tenuiviruses. Analyses by primer extension of the RHBV RNA4 mRNA have shown that the 5’ ends contain 10 to 17 non-viral nucleotides and are capped (B.-C. Ramirez, D. Garcin, L. A. Calvert, D. Kolakofsky & A.-L. Haenni, unpublished). When RHBV RNA4 was directly examined by primer extension, a single 5’ end was detected (designated position +1). This suggested that the extra sequences on the mRNA might be due to the presence of primers derived from host cell mRNA and used by the viral RNA polymerase to initiate mRNA synthesis, by analogy with the cap-snatching mechanism used for influenza virus mRNA synthesis (Bouloy et al., 1978; Braam et al., 1983; reviewed in Krug, 1981). This cap-snatching mechanism has been observed in Bunyaviridae, Bunyavirus, Phlebovirus and Tospovirus mRNA synthesis (Bishop et al., 1983; Patterson et al., 1984; Bouloy et al., 1990; Kormelink et al., 1992b; Vialat & Bouloy, 1992; reviewed in Bouloy, 1991 and in Kolakofsky & Hacker, 1991) and in the Arenaviridae mRNA synthesis (Garcin & Kolakofsky, 1990; Raju et al., 1990). By analogy with the cap-snatching mechanism of Bunyaviridae one would expect mRNA synthesis to be primer-dependent. On the other hand genomic vRNA and vcRNA syntheses would be primer-independent and would initiate at position +1; these RNAs are not capped. The regulation and control of transcription and replication of tenuiviruses have not been studied.

Virus–plant and virus–insect interactions

Tenuiviruses show other similarities to viruses of the Bunyaviridae family, such as transmission by insect vectors and ability to replicate in two different types of cells, vertebrate and invertebrate cells for the phleboviruses (reviewed in Elliott, 1990) and plant and invertebrate cells for the tenuiviruses (reviewed in Gingery, 1988) and tospoviruses (Ulmanen et al., 1993).

The symptoms induced by Bunyaviridae in vertebrates and invertebrates are often very different. Usually in vertebrates infection is acute and leads to cell death, whereas in insects infection can be asymptomatic and become persistent (reviewed in Elliott, 1990).

The outcome of infection by tenuiviruses is also different between plants and insects. In plants the symptoms appear as chlorotic bands or stripes that may ultimately lead to completely chlorotic leaves; such chlorotic leaves may die prematurely as in the case of infection by RSV. Plants are generally stunted and yields are often drastically reduced. Tenuiviruses are transovarially transmitted by delphacid planthoppers in a persistent manner and virus multiplication has been shown to occur in the insects (Toriyama, 1986a). Contradictory reports have been published on the effects of tenuivirus infection on the insect vectors (reviewed in Gingery, 1988); in RSV infection, a decrease in longevity and in the number of eggs laid was observed on the one hand, but also no effect on egg mortality and insect longevity on the other; similar contradictory reports have appeared on the effects of MSTv and EWSMV on their vectors. In the case of RHBV infection, reduction in fertility, in female longevity and in nymph viability have been described (Jennings & Pineda, 1971; Zeigler et al., 1988; Zeigler & Morales, 1990).

Interestingly, RHBV RNA4 was detected in RHBV-infected planthoppers but not the NS4 protein, indicating that the protein was present in amounts too low to be detected, that it was unstable, that it was present transiently during virus multiplication in the insect and did not accumulate as it does in the plants, or that it was not synthesized (Ramirez et al., 1993). Likewise, neither the MSTv sgRNA4 (Huiet et al., 1992) nor the corresponding protein (Falk et al., 1987) were detected in MSTv-infected planthoppers. On the other hand the corresponding protein was detected in RSV-infected planthoppers (Toriyama, 1986a).

Conclusions

Studies of tenuiviruses based on molecular biology techniques, such as gene cloning and nucleotide sequencing, have considerably increased our knowledge of the genome structure and expression strategies of these remarkable viruses. However, important pieces of in-
formation are still lacking, such as the sequence of RNA1 which would define the genomic organization and expression strategy of this segment. In addition, cloning of the complete cDNA sequence of tenuivirus RNA would be the first step on the way to establishing a system for applying reverse genetics in the study of these viruses. Such an approach has been of great value in the study of negative-strand RNA viruses (Luytjes et al., 1989; Palese, 1993).

The purification and characterization of the RNA polymerase would make it possible to establish an in vitro transcription system indispensable for studying several aspects of RNA synthesis, such as the switch from transcription to replication. What, for instance, are the mechanisms involved in transcription termination? Establishing rice and insect cell culture systems in which the virus would multiply, would shed light on the host factors that presumably participate in viral RNA synthesis, in addition to facilitating production and purification of the virus particles.

Very little is known about the role of the viral proteins in replication and in interaction with the host plant and/or the insect vector, or in insect cell recognition. For instance, does NS4 function as a helper component for insect transmission?

Another intriguing aspect concerns the morphology of the virus particles that multiply in the insect vector. The weak similarity between the ORFs of the 94K protein of RSV and the glycoproteins of PT and UUK viruses suggests that enveloped RSV particles could exist, although to date such particles have not been detected. The proteins of such an envelope could be involved in insect cell recognition.

The information obtained from studies on the molecular biology of tenuiviruses is of paramount importance in designing strategies to engineer plants resistant to virus infection. A first step in this direction was recently reported by Hayakawa et al. (1992): a certain level of protection against RSV infection was achieved with transgenic rice plants expressing the NC gene.

From the comparison of the RNA segments of tenuiviruses on one hand, and of the phleboviruses and tospoviruses on the other, one can begin to draw a parallel between these virus groups and genera. RNA1 of tenuiviruses and the L RNAs of the phleboviruses and the tospoviruses can be considered as comparable, based on their size and the putative role of the corresponding protein as an RNA polymerase. As for RNA2, it can be considered comparable to M RNA based on the weak sequence similarities that exist between some of their ORFs. Finally, RNA3 and RNA4 appear to possess features that are combined in S RNA, since the S RNA of the phleboviruses and the tospoviruses encodes the N and NSs proteins the equivalents of which might be the NC and the NS4 proteins encoded by RNA3 and RNA4 of tenuiviruses respectively. Indeed, N and NC are both nucleocapsid components which in the case of PT virus and RSV show sequence similarity, and NS4 of tenuiviruses accumulates in the cytoplasm of infected cells as does NSs of TSWV. The presence of RNA3 and RNA4 in tenuiviruses in place of the S RNA in phleboviruses and tospoviruses results in two additional ORFs in the tenuiviruses. Could it be that one or both of these proteins participates in cell-to-cell movement of the virus in the plant or in recognition of the insect cell?

Taken together these observations show that phleboviruses, tospoviruses and tenuiviruses share common genome organization and expression strategies and common features in the potential secondary structures of their genome, and that in addition the phleboviruses and tenuiviruses share sequence similarity in some of their gene products. This, together with the similarity that exists between them with respect to their transcription strategy and persistent infection in the insect vectors, raises the question of the evolutionary relationships that exist between these virus groups. Among the different characteristics commonly used to classify viruses, some are highly conserved during evolution whereas others have evolved. If one accepts that the nature, structure and organization of the viral genome and the strategies of expression and transcription/replication of this genome are properties conserved during evolution, then the tenuiviruses are indeed close to the phleboviruses and should probably be classified in the Bunyaviridae family.

Note added in proof: It has been recently reported that the 5′ ends of the MSV mRNA4 population contain 10 to 15 additional nucleotides and that they are heterogeneous in sequence [Huiet et al. (1993) Virology 197, 808–812].

We wish to express our gratitude to F. Morales and F. Chapeville for their interest and encouragement in this work, and to L. Calvert and D. Kolakofsky for constructive suggestions and fruitful discussions. B.-C. Ramirez is holder of a fellowship from the Ministère des Affaires Etrangères et de la Coopération. This study was supported in part by the Rockefeller Foundation, the Appel d’Offre: ‘Virologie Fondamentale’ of the Ministère de l’Éducation Nationale de la Jeunesse et des Sports, the Ministère de l’Enseignement Supérieur and the Ministère de l’Agriculture et de la Pêche. The Institut Jacques Monod is an ‘Institut Mixte, CNRS – Université Paris VII’.

References


