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Viruses of Pepper Crops in the Mediterranean Basin: A Remarkable Stasis.

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CONTENTS

Abstract

Compared to other vegetable crops, the major viral constraints affecting pepper crops in the Mediterranean basin have been remarkably stable for the last 20 years. Among these viruses, the most prevalent ones are the seed-transmitted tobamoviruses, the aphid-transmitted *Potato virus Y* and *Tobacco etch virus* of the genus *Potyvirus*, and *Cucumber mosaic virus* member of the genus *Cucumovirus*, and thrips-transmitted tospoviruses. The last major viral emergence concerns the tospovirus *Tomato spotted wilt virus* (TSWV), which has undergone major outbreaks since the end of the 1980s and the worldwide dispersal of the thrips vector *Frankliniella occidentalis* from the North-western part of the US. TSWV outbreaks in the Mediterranean area might have been the result of both viral introductions from Northern America and local re-emergence of indigenous TSWV isolates. In addition to introductions of new viruses, resistance breakdowns constitute the second case of viral emergences. Notably, the pepper resistance gene *Tsw* towards TSWV has broken down a few years after its deployment in several Mediterranean countries while there has been an expansion of L^3-resistance breaking pepper mild mottle tobamovirus isolates. Beyond the agronomical and economical concerns induced by the breakdowns of virus resistance genes in pepper, they also constitute original models to understand plant – virus interactions and (co) evolution.

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I. Introduction

Viral diseases constitute the major limiting factor in pepper cultivation throughout the world (Martelli and Quacquarelli, 1983, Yoon *et al*., 1989, Florini and Zitter, 1987, Green and Kim, 1991). Forty-nine virus species have been shown to infect pepper (Hanssen *et al*., 2010) among which about twenty, belonging to fifteen different taxonomic groups have been reported to cause damages in pepper crops. Mechanically transmitted viruses like tobamoviruses are predominant in protected crops whereas insect-transmitted viruses like potyviruses, cucumoviruses and tospoviruses are more frequent and severe in open fields.

Generally speaking, viral emergences, *i.e*. outbreaks of novel virus entities or increase of the prevalence of, or damages induced by known viruses are favoured by several factors frequently linked to the intensification of agricultural practices or of international trade (Gómez *et al*., in this volume). Given the wide geographical distribution of pepper crops, which exposes them to a large diversity of parasites, trade of infected plant material allows the introduction of viruses and their vectors in new countries or areas. Intensive and monovarietal pepper cultivations in Mediterranean regions favour virus adaptation, spread and persistence from one crop cycle to the following. Finally, climate changes affect the distribution of virus vectors and/or the susceptibility of plants to virus infections and consequently increase the exposure of pepper crops to new viral diseases. In spite of these threats, few viral emergences have been recorded in pepper crops in the Mediterranean basin during the last 20 years which contrasts with the situation of other vegetable crops such as tomato (Hanssen *et al*., 2010) or cucurbits (Desbiez and Lecoq in this volume).

In this review, we describe the biological properties of the most important viruses which affect pepper crops in the Mediterranean surrounds and the methods used to control them, with an emphasis on varietal resistances.

II. Aphid-transmitted viruses

A. Potyviruses

The genus *Potyvirus* constitutes one of the largest groups of plant viruses as a whole; potyviruses are responsible for particularly important diseases in a wide range of plant species all over the world. All of them involve aphid vectors for their transmission, while some of them are additionally seed transmitted. Potyviruses are single-stranded RNA viruses with flexuous particles 680 to 900 nm long and 11 to 13 nm wide possessing a helical symmetry with a pitch of about 3.4 nm. Virions contain a linear, positive-sense RNA of about 9.7 kb in size, with a poly-adenylated tract at the 3' end and a viral protein, the VPg, covalently-linked at the 5' end. The RNA encodes a single polyprotein which is subsequently cleaved into 10 proteins by three viral proteinases. A shift during translation allows the synthesis of an 11th protein (Chung *et al*., 2008). Diversification of potyviruses was estimated to be quite recent and contemporaneous to the development of agriculture, around 10,000 years ago (Gibbs *et al*., 2008).

Species that infect solanaceous plants belong to three separate clades within the genus *Potyvirus* (Fig. 1). The largest clade includes *Potato virus Y* (PVY), the type member of the genus, and a number of virus species infecting or not solanaceous plants (Fig. 1 and 2). The fact that potyvirus species infecting or not solanaceous plants are interspersed in this part of the phylogenetic tree is indicative of several host jumps during evolution of this group (Fig. 1 and 2), a feature that is observed in other virus genera (Fig. 4). The two other clades include a lower number of virus species all infecting solanaceous plants: the *Tobacco etch virus* (TEV) group which contains *Potato virus A* and *Tobacco vein mottling virus* and a group including *Pepper veinal mottle virus*, *Chilli veinal mottle virus*, *Wild tomato mosaic virus* and *Tobacco vein banding mosaic virus* (Fig. 1). Only two potyvirus species are prevalent in pepper crops in the Mediterranean basin: PVY, which is widespread in all this area and TEV which is prevalent only in Turkey. There are four major clades among PVY isolates named N, O, C and Chile (Moury 2010). Among them, only members of clades C and Chile can infect pepper crops efficiently and only clade C isolates are prevalent in the

Mediterranean basin. Members of the other PVY clades are mostly prevalent on potato or other solanaceous species and poorly infectious in pepper after inoculation in laboratory conditions (Gebre Selassie et *al.,* 1985; Moury, 2010). Recombinant isolates possessing genome regions that belong to different clades are also frequent in PVY (Revers *et al.,* 1996; Glais *et al.*, 2002; Moury *et al*., 2002; Schubert *et al*., 2007; Hu *et al*., 2009a, 2009b; Ogawa *et al.*, 2008). However, they are rather rare in pepper crops, except an Italian isolate that induces veinal necrosis in pepper leaves (Fanigliulo *et al.,* 2005). The largest part of the genome of that isolate belongs to clade C while the 5' untranslated region (UTR) and part of the P1-coding region cluster with clade O and the 3' UTR clusters with clade N (Schubert *et al*., 2007). This isolate is therefore the result of at least two independent recombination events involving three different PVY isolates.

PVY is common in open field or plastic tunnel pepper cultivation in warm climates. Its prevalence is quite high all around the Mediterranean basin, especially where traditional cultivars that are devoid of the most durable resistance genes (*pvr2*^{2} or *Pvr4*) are grown or where growers produce their own seeds which can therefore be the result of cross-pollination with susceptible cultivars (Buzkan *et al.,* 2006; Ben Khalifa *et al.,* 2009).

PVY host range includes mostly solanaceous plants but also plants in the families Amaranthaceae, Asteraceae, Chenopodiaceae and Fabaceae. The most common symptom induced by PVY in pepper is systemic vein clearing progressing into a mosaic or mottle and generally dark green vein banding in leaves (Pernezny *et al.,* 2003). Vein and petiole necroses often develop, depending on the pepper genotype and, possibly, on the PVY isolate (Dogimont *et al*., 1996). In some pepper genotypes, systemic necrosis upon PVY infection was shown to depend on the presence of one major dominant gene (Dogimont *et al.,* 1996). In some extreme cases, stem and apical bud necrosis can lead to plant death. Necrotic spots, mosaic patterns and distortions may develop on fruits of some cultivars. However, fruit symptoms do not always occur in PVY-infected plants. Yield losses greatly depend on the earliness of infection and can reach 100% (Avilla *et al.*, 1997a). *Myzus persicae* is one of the most efficient PVY vectors. In Spain, the most frequent alate aphids landing on open-field pepper crops were *Aphis* spp., *Aphis fabae*, *M. persicae* and *Diuraphis noxia* (Pérez *et al.,* 2003), all being potential PVY vectors (Pérez *et al*., 1995). Usually, *M. persicae* and *Aphis* spp. colonize pepper plants only in warm climate areas (Satar *et al*., 2008; Rahman *et al*., 2010) or in greenhouse or plastic tunnel crops.

TEV induces severe mosaic and mottle in leaves in addition to leaf distortion and general stunting of pepper plants. It can also provoke abortion of floral buds and distortion and mosaic on fruits, especially in plants infected at a young stage. On some cultivars (*Capsicum frutescens* cv. Tabasco), root necrosis and severe wilting symptoms can be followed by death of plants. These specific symptomatology traits have been shown to be determined by two regions in the TEV genome: the 3' one-third of the P3 coding region and a region spanning the 3' end of the CI coding region, the region coding the 6K2 protein and the 5' end of the VPg coding region (Chu *et al*., 1997). In the Mediterranean basin, TEV was reported only in Turkey. Its prevalence reaches 23% of plants in pepper crops in south-east Anatolia and the eastern Mediterranean region of Turkey (Buzkan *et al.,* 2006). Yield reduction caused by TEV infection can reach 70% (Pernezny *et al.*, 2003).

Two main control methods have been used against potyviruses in pepper: prophylactic methods aiming to reduce the inoculation of viruses to plants and genetic control where plants are resistant to inoculated potyviruses. Among prophylactic measures, insecticides or biological control of the aphid vectors have often failed to prevent the virus spread because potyviruses are non-persistently transmitted viruses that can be acquired and inoculated by aphids during superficial and brief probes in the plant epidermal cells (Raccah, 1986; Collar *et al.,* 1997). Application of mineral oil in pepper fields was shown to reduce the incidence of PVY and other nonpersistent viruses by about 40% (Marco, 1993) and is used in pepper integrated pest management programmes in eastern Spain (Martín-López *et al*., 2006). Mineral oil sprays cause high mortality (>80%) of colonizing aphids, probably by asphyxia, and are also efficient to control aphid transmission of nonpersistent viruses (Martín-López *et al*., 2006). However, the use of these methods at a regional scale could reduce the aphid population size and partially decrease secondary infections.

Weeds, especially in the family Solanaceae like black nightshade (*Solanum nigrum*), can also increase the PVY inoculum pressure in pepper fields and even be more efficient virus sources than infected pepper plants (Fereres *et al*., 1996). Consequently, weeding the pepper fields and their edges is of prime importance to reduce epidemics. Polypropylene floating rowcovers were also shown to reduce access of vectors to pepper plants and to control virus infections in the field and are economically profitable in areas with a high virus pressure (Avilla *et al.,* 1997b). Barrier crops (sunflower, maize, vetch or sorghum) used within pepper fields or around them were also shown to reduce PVY and *Cucumber mosaic virus* (CMV) (see below) spread in pepper (Simons, 1957; Avilla *et al.,* 1996; Fereres, 2000; Anandam and Doraiswamy, 2002). The effect of the barrier crop on viruses was to act as a sink for the virus, thereby reducing the virus secondary spread and inoculum pressure, to prevent the aphid colonization on pepper plants or to reduce the landing of alate aphids (Hooks and Fereres, 2006). Insecticide sprays on the barrier plants could further reduce the disease spread.

In addition to these approaches, two major resistance systems have been used to protect pepper against potyviruses. Recessive resistance genes at the *pvr2* locus, mapping on chromosome P4, have been used successfully for more than 50 years. The *pvr2* gene was the first cloned natural recessive gene conferring resistance to viruses in plants (Ruffel *et al.*, 2002). It was shown to encode a translation initiation factor (eIF4E; eukaryotic initiation factor 4E) essential to the translation of cellular mRNAs (Ruffel *et al.*, 2002). Plant eIF4Es interact directly with the cap of mRNAs as an initial step toward the building of a scaffold of cellular proteins allowing the recruitment of ribosomes. Together with other virus groups, potyviruses evolved to highjack this system to enhance their multiplication. The key step allowing PVY or TEV multiplication is the direct physical interaction between the virus VPg, which replaces the cap of mRNAs at the 5' end of the viral RNA, and plant eIF4E (Kang *et al*., 2005; Charron *et al.,* 2008). Nucleotide substitutions in the *pvr2* gene can create amino acid substitutions in the encoded eIF4E that can disrupt the interaction with the virus VPg and thus create a recessive resistance gene. At least 9 such *pvr2* alleles have been described in the pepper germplasm. They differ from one another and from the wild-type susceptibility $pvr2^{+}$ allele by a small number of nucleotide substitutions, almost all of them being nonsynonymous (Charron *et al.*, 2008). In turn, nonsynonymous substitutions in PVY or TEV VPg coding regions can restore the physical interaction between the mutated eIF4E and virus VPg (Charron *et al.,* 2008) and be the cause of resistance breakdowns. Two *pvr2* alleles have been used extensively to breed potyvirus resistant pepper cultivars for more than 50 years, $pvr2^{1}$ and $pvr2^{2}$. Both alleles confer efficient resistances towards PVY while only $pvr2^{2}$ is effective against TEV. The resistance of $pvr2^{2}$ proved extremely durable against PVY. After over 50 years of usage, only two $pvr2^{2}$-breaking PVY isolates have been described. The first one was selected in laboratory conditions from a $pvr2^{1}$–breaking isolate by serial passages in a $pvr2^{2}$-carrying pepper cultivar (Gebre Selassie *et al.,* 1985). The other one was found in Málaga, Spain, in 1988 (Luis-Arteaga *et al.*, 1993) but was not the cause of epidemics since. $pvr2^{1}$–breaking PVY isolates are much more frequent but usually less prevalent than avirulent isolates (Luis-Arteaga and Gil-Ortega, 1986). Consequently, cultivars carrying the $pvr2^{1}$ resistance continue to be used and are economically satisfactory in many growing regions. Other *pvr2* alleles are almost not used to breed elite pepper F_1 hybrids but can be found in traditional pepper populations. Though possessing extremely similar sequences, the different *pvr2* alleles show extremely contrasted durability. For example, plants carrying the $pvr2^{3}$ allele, which has not been used to breed cultivars, can be infected by PVY isolates presently prevalent in pepper crops (Ben Khalifa *et al*., in press). One reason of these durability differences seems to be the number of mutational pathways toward resistance breakdown and the number of mutations involved in these pathways. At least five to nine nucleotide substitutions in the VPg-coding region have been shown to confer independently $pvr2^{3}$–breaking properties (Ayme *et al*., 2006; Montarry *et al.,* in press; Fig. 3). In contrast, only one pathway involving a single nucleotide substitution allows breakdown of $pvr2^{1}$ and breakdown of $pvr2^{2}$ involves two or more consecutive substitutions, depending on the wild-type avirulent PVY isolate (Ayme *et al*., 2007; Fig. 3). In accordance, the fixation of two given nucleotide substitutions

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in a virus seems to be a threshold that determines plant resistance durability in general (Harrison, 2002; Lecoq *et al.*, 2004). When two or more substitutions are needed for resistance breakdown, the resistance is usually quite durable while it is not if a single substitution suffices. Breakdown of the *pvr2*^{2} resistance by TEV seems to be much more frequent than by PVY (Depestre *et al.*, 1993; Muhyi *et al.,* 1993). However, no Turkish isolate breaking down *pvr2*^{2} has been described yet (Palloix *et al.,* 1994).

The other resistance that is widely used in pepper cultivars is that based on the *Pvr4* dominant gene that maps on chromosome P10. *Pvr4* controls an extreme resistance phenotype to all natural PVY isolates but not to TEV. It has a very broad range of action since it also confers resistance to five additional potyvirus species that are prevalent in the Americas. The mechanism of the *Pvr4* resistance is related to hypersensivity but hypersensitive reactions (HR) appear only on inoculated cotyledons or under very high inoculum pressure such as through graft inoculation (Janzac *et al.*, 2009). Though being used in pepper crops for about 20 years, the *Pvr4* resistance is highly durable since no field PVY isolate can infect any *Pvr4* cultivars so far. Graft inoculations have consequently been undertaken to favour the selection of *Pvr4*-breaking PVY isolates (Janzac *et al*., 2009) and, further, to identify causal mutations (Janzac *et al.*, 2010). That mutation maps to the NIb coding region which encodes the RNA-dependent RNA polymerase (RdRp) (Fig. 3). The fact that only one nucleotide substitution suffices for the breakdown of the *Pvr4* resistance seems to contradict the high durability of this resistance. However, that mutation induces a very high competitiveness cost to PVY in *Pvr4*-devoid pepper cultivars and this cost cannot be easily compensated by the virus (Janzac *et al.*,2010).

In addition to these monogenic resistances, polygenic resistances to PVY have also been investigated. A number of resistance QTLs have been mapped in a cross involving the Indian line 'Perennial' as a resistant parent (Caranta *et al.,* 1997a). By themselves, these QTLs reduced PVY symptom intensity and progress but do not impair the invasion of the plant by the virus. However, these minor-effect QTLs were shown to improve greatly the durability of the major-effect gene *pvr2*^{3} which alone is rapidly broken down (Palloix *et al.,* 2009). This was one of the first demonstrations of the higher durability of a polygenic over a monogenic resistance. However, a two-step adaptation of PVY, first to *pvr2*^{3} and secondarily to the gene "pyramid" consisting of *pvr2*^{3} and QTLs was still possible. This showed that the components of a polygenic resistance should better be used together than separately in order not to jeopardize simultaneously all of these resistance factors.

B. Cucumoviruses

Cucumber mosaic virus (CMV), the type member and most widespread species of the genus *Cucumovirus*, is one of the most prevalent viruses worldwide, infecting 85 distinct plant families and more than 1000 species experimentally, including a large number of weeds or wild plant species that can act as reservoirs between successive growing periods.

The genome of CMV consists of three linear, positive-sense single-stranded RNAs with 5' terminal cap structures. The 3' ends are not polyadenylated but show aminoacylated tRNA-like structures. Virions are icosahedral, 29 nm in diameter, uniform in size and have electron dense centers. They encapsidate the three genomic RNAs separately and occasionally subgenomic or satellite RNAs. CMV is the only cucumovirus that affects significantly pepper crops. It is distributed all over the world and can induce severe economic losses by affecting the growth of the vegetative parts of the plants and also by inducing symptoms in fruits. Symptoms include punctiform mosaic and dull leaves, filiformism of young leaves associated to a curling of the nerves, necrotic "oak-leaf" symptoms in older leaves, misshaped fruits with annular discolorations and sterility when infection occurred at plantlet stage. In fruits, CMV can induce distortions, reduction of size and irregular maturation. Early infections can induce stem necrosis and death of plants. Yield losses greatly depend on the earliness of infection and can reach 80% (Avilla *et al.,* 1997b). Moreover, synergism between CMV and other viruses co-infecting the same plant can

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increase CMV accumulation or symptom intensity (Mascia *et al.*. 2010). Reassortment between two CMV isolates induced more severe symptoms on pepper plants as compared to single inoculations of the parental viruses (Hellwald *et al.*, 2000). Co-infection by CMV can also enhance infection by other viruses, as in *Pepper mottle virus* (PepMoV)-resistant pepper plants by stimulating systemic movement of PepMoV in the internal phloem (Guerini and Murphy, 1999).

CMV isolates are classified into two subgroups named I and II which are distantly related according to molecular analyses of the genome and can be distinguished serologically (Owen and Palukaitis, 1988). Members of these two subgroups share from 69% to 77% nucleotide identity, depending on the RNA and isolates compared (Palukaitis and Garcia-Arenal, 2003). Within subgroup I, clade IA containing closely related isolates was separated from the rest of subgroup I (themselves included in the polyphyletic subgroup IB), on the basis of phylogenetic evidence (Roossinck *et al.,* 1999). Isolates from subgroups IA and II are distributed worldwide while almost all isolates of subgroup IB are from East Asia. A few subgroup IB isolates have probably been introduced in Italy, Spain and California (Gallitelli, 2000; Lin *et al.,* 2003; Bonnet *et al.*, 2005). The prevalence of isolates from subgroups I and II varies also according to climatic conditions; with isolates from group I being mostly found under warm climate and isolates from group II under colder conditions (Marchoux *et al.*, 1976; Quiot *et al.,* 1979). Given that pepper crops are more widely distributed in geographic regions with a hot climate, they are therefore probably more frequently affected by subgroup I isolates.

Like potyviruses, CMV is transmitted by aphids in a non-persistent manner. At least 86 aphid species have been described as CMV vectors, two of the most efficient and prevalent being *Myzus persicae* and *Aphis gossypii*. In contrast with potyviruses, a single viral protein, the coat protein (CP), is directly involved in aphid transmissibility (Gera *et al.,* 1979; Chen and Francki, 1990). As a consequence, mutations in the CP of CMV were shown to affect the specificity of transmission by different aphid species (Perry *et al*., 1998) and, consistently, aphid species and populations seem to exert strong diversifying selection and population differentiation on CMV (Martínez-Torres *et al*., 1998; Moury 2004).

CMV is seed transmitted in a number of host species including possibly pepper. Using RT-PCR for detection, Ali and Kobayashi (2010) showed that both the coat (53 to 83%) and embryo (10 to 46%) of seeds were CMV positive after inoculation of pepper plants with isolate Fny, which belongs to subgroup IA. The observed transmission rate to the progeny was 10 to 14%. Since no sanitary problems linked to seed infection by CMV in pepper had been mentioned before, it will be important to estimate this risk on a larger scale.

Since they share many similarities at the epidemiological level, prophylactic methods used to control CMV are the same as those used against potyviruses. Both kinds of viruses are transmitted in a non-persistent manner by numerous aphid species and many of these species can transmit both CMV and potyviruses. Consequently, methods that reduce aphid population sizes, virus transmission, the ability of aphid vectors to move in fields and the inoculum sources as weed reservoirs can also be used to decrease the impact of CMV infections in pepper crops.

Genetic resistance has been largely exploited to control CMV infections in pepper. Only one major-effect resistance gene has been described in the pepper germplasm so far (Kang *et al*., 2010). This dominant resistance gene, named *Cmr1*, is located on the pepper chromosome P2 and was identified in a Korean cultivar. *Cmr1* was shown to restrict the systemic movement of CMV isolates belonging to subgroup IA but plants carrying *Cmr1* can be infected by an isolate (named P1) belonging to subgroup IB (Kang *et al.,* 2010). Similarly, following the deployment of pepper cultivars resistant to subgroup IA CMV isolates in South Korea during the 1990s, resistance breakdowns involving subgroup IB CMV isolates have been observed in the mid-2000 (Lee *et al.,* 2006). It remains to be determined if these CMV infections observed in resistant cultivars correspond to "true" resistance breakdowns or to a narrow spectrum of action of the resistance. Almost all other CMV resistance sources in pepper are partial and polygenic. They act by inhibiting virus establishment in inoculated tissues (Caranta *et al.,* 1997b), or virus movement (Caranta *et al.,* 2002) or by decreasing symptoms (Ben Chaim *et al*., 2001). Several of these resistances are

ontogenic, *i.e*. they depend on a particular developmental stage of plants (Dufour *et al.,* 1989; García-Ruiz and Murphy, 2001). Seven QTLs with additive or epistatic effects are involved in resistance to CMV systemic movement, and three in CMV establishment in inoculated tissues (Caranta *et al.*, 1997b, 2002). The QTLs controlling these two resistance traits are independent of each other. These resistances restrict only partially the virus translocation within plants, but proved to confer a good level of resistance in the field, particularly when different resistance sources were combined into a cultivar (Nono-Womdim *et al.*, 1993, Lapidot *et al.*, 1997, Palloix *et al.*, 1997). Though polygenic resistances are thought more durable than monogenic and qualitative ones, there has been no investigation of their durability concerning CMV. Since these resistances are largely based on mechanisms controlling the systemic movement of CMV within plants and since resistant cultivars carrying similar mechanisms of resistance have been infected by CMV isolates from subgroup IB in Korea, the recent introduction of subgroup IB isolates in the Mediterranean basin (Italy and Spain) possibly from Asia, questions their durability.

C. Other aphid-transmitted viruses

In addition to the previous and economically most important viruses, *Alfalfa mosaic virus* (AMV) and *Broad bean wilt virus* (BBWV) are two non-persistently transmitted viruses that are widely distributed in pepper crops in the Mediterranean basin although at a usually low prevalence. The persistently transmitted poleroviruses are confined to a few areas but could represent a future threat to pepper crops.

AMV is the type species of the genus *Alfamovirus* and belongs to the family *Bromoviridae.* Its natural host range includes over 250 plant species belonging to 48 families, mostly herbaceous plants. More than 20 aphid species are known to transmit AMV in a non-persistent manner. AMV occurs mainly in temperate climates, causing significant diseases in alfalfa and sweet clover and also occasionally in neighbouring crops like soybean, tobacco, tomato or pepper. AMV has been described in pepper plants since 1939 in Italy and 1965 in France (Marchoux *et al.,* 2003). Infected plants develop local chlorotic and necrotic rings on the leaves followed by a systemic foliar mosaic, often brilliant yellow or white. Some AMV isolates cause severe necrosis in pepper cultivars like 'Yolo Wonder', 'Yolo Y', 'Tabasco' or 'Sucette'. Bleaching can also occur on pepper fruits.

Broad bean wilt virus (BBWV), which is the type species of the genus *Fabavirus*, has been described for the first time in *Vicia faba* in Australia in 1947. BBWV comprises 2 distinct viral species recognizable by the divergence of their genome: BBWV-1 and BBWV-2 (van Regenmortel *et al.,* 2000). The natural host range of BBWV includes more than 200 plant species in 41 families and its dissemination is by aphids in a non-persistent manner. In Mediterranean countries, BBWV is frequently found in tomato and pepper plants, especially in France, Italy and Spain. Sequence analyses have demonstrated the presence of BBWV-1 isolates in Spain (Rubio *et al*., 2002). Infected pepper plants develop mosaic and concentric rings on leaves and fruits. BBWV can also cause partial to general bleaching of pepper fruits reducing their commercial value. However, in pepper crops BBWV shows a rather low prevalence and is thus not an economical concern.

Viruses belonging to the genus *Polerovirus* are restricted to the phloem and are transmitted by aphids in a persistent, circulative and non-propagative mode. The high specificity of aphid transmission is mediated by the minor capsid protein of poleroviruses which has specific intestinal tropism into the aphid (Brault et al., 2005). Among poleroviruses, one species, *Pepper yellow leaf curl virus* (PYLCV), caused devastating diseases in pepper crops in Israel since 1998 (Dombrovsky *et al.,* 2010). PYLCV symptoms in pepper include shortening of the internodes, interveinal yellowing, upward rolling of leaf margins, accompanied by fruit discoloration and size reduction. PYLCV is closely related to *Tobacco vein distorting virus* (TVDV) and is transmitted by *Myzus persicae* and *Aphis gossypii*. The virus was not mentioned yet in pepper crops in other countries.

However, it is genetically close and probably belongs to the same species as a Japanese isolate tentatively named pepper vein yellows virus (Murakami *et al.*, 2011) and as a Turkish isolate of pepper yellows virus collected in Antalya (Lotos *et al.*, unpublished data; GenBank accession number FN600344) since it shares more than 90% identity with these viruses at the nucleotide level (Murakami *et al*. 2011).

III. Thrips-transmitted tospoviruses

The genus *Tospovirus* in the family *Bunyaviridae*, includes important species of plant viruses with pleomorphic particles (80-120 nm) enveloped by a double-membrane layer and which contain tripartite single-stranded RNAs, designated L, M and S (De Haan *et al,*. 1990; 1991; German *et al.,* 1992; Law *et al*., 1992). The negative L RNA (8.9 kb) consists of a single open reading frame (ORF) in the viral complementary sense that encodes a 331 kDa protein containing RdRp motifs required for virus replication (Adkins *et al.*, 1995; De Haan *et al.,* 1991; Van Poelwijk *et al.*, 1997). The ambisense M RNA (4.8 kb) (Kormelink *et al.,* 1992; Law *et al.*, 1992) consists of two ORFs that encode a 36 kDa nonstructural protein, NSm, in the viral sense, and a 127.4 kDa precursor for G1 and G2 glycoproteins in the viral complementary sense. NSm protein may be involved in cell-to-cell movement (Storms *et al.,* 1995) whereas G1 and G2 structural glycoproteins are included in the outer membrane of the virion generating spikes (Adkins *et al.*, 1996; Law *et al.*, 1992) and are essential for thrips transmission (Sin *et al*., 2005) probably through their interaction with thrips receptor proteins. The ambisense S RNA (2.9 kb) (De Haan *et al*., 1990) encodes 2 proteins: the 52.4 kDa nonstructural NSs, and the 29 kDa structural nucleocapsid protein (NP) in the viral and the complementary senses, respectively. The NSs protein is associated to fibrous inclusions in infected plant cells (Kormelink *et al.,* 1991) and has been shown to be a suppressor of post-transcriptional gene silencing (Takeda *et al*., 2002).

Tospoviruses cause great losses in many economically-important crops, including pepper, worldwide. Two virus species belonging to this genus infect pepper in the Mediterranean surroundings: *Tomato spotted wilt virus* (TSWV) and *Impatiens necrotic spot virus* (INSV) (Fig. 4). In pepper, TSWV is more prevalent than INSV, which infects mainly ornamentals (Daughtrey *et al*., 1997). TSWV is also the most widespread, occurring in all countries of the Mediterranean region, even if it has not been confirmed in a few ones (Morocco and Tunisia) and has one of the largest host ranges among plant viruses (Parrella *et al.,* 2003). INSV seems to be restricted to France, Spain, Italy and Israel and has not been described in North Africa. Several studies have shown that high temperatures (>30°C) promote TSWV infections (Llamas-Llamas *et al*., 1998; Roggero *et al.,* 1999) and the resistance of some pepper cultivars can be impaired under continuous high temperatures, resulting in systemic infection of the plants (Black *et al.*, 1991; Moury *et al.,* 1998). By contrast, high temperatures decrease the systemic movement of INSV in *C. chinense* and *C. annuum* (Roggero *et al.,* 1999), which may explain the rarity of natural INSV infections in pepper crops in the Mediterranean area. Most of the time, symptoms caused by TSWV are similar to those due to INSV. Symptoms in *C. annuum* include stunting and yellowing of the whole plant, mosaic or necrotic spots and curling of the leaves. Infected fruits often show deformations, necrotic ring patterns and arabesque-like discolororations.

In nature, tospoviruses are transmitted from plant to plant almost exclusively by thrips (order Thysanoptera*;* family Thripidae) in a persistent and multiplicative manner. TSWV, like INSV, is transmitted mainly by the western flower thrips (*Frankliniella occidentalis*) (de Angelis, 1994), but other Thripidae, like *Thrips tabaci* and *F. intonsa*, can also participate to the spread of TSWV. Outbreaks of TSWV in Europe have been associated to the introduction of *F. occidentalis* from western USA in the early 1980s. An estimation of the speed of spread across Europe and northern Africa was 229±20 km/year (Kirk and Terry, 2003). The western flower thrips is established in glasshouses but also outdoors in areas with mild winters like the Mediterranean basin. Vectors can acquire tospoviruses only during larval stages while both larval (late stage) and adult thrips can transmit the virus. For TSWV, it has been shown that the ability to acquire and transmit

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tospoviruses was lost during the development to adults, probably because of the formation of a midgut barrier (Ullman *et al.,* 1992). No transovarial transmission has been reported for tospoviruses.

Various management procedures have been undertaken during the last decades to reduce the spread of tospoviruses. Control of vectors is complicated by the high fecundity of thrips and their capacity to develop insecticide resistances. The wide host range of tospoviruses, including weeds that constitute virus reservoirs, increases the difficulties to control the disease. The application of sanitation measures must be intensified in glasshouses, particularly the eradication of weeds inside and outside the cultivated area, the use of blue (more attractive) or yellow sticky cards to monitor the presence of winged adults thrips (Matteson and Terry, 1992; Roditakis *et al*., 2001), the regular examination of the crops and the eradication of infected plants. Biological control of thrips on pepper crops relies on the use of predatory mites like *Neoseiulus cucumeris* or predatory bugs (*Orius* spp.) (Hatala Zseller and Kiss, 1999; Maisonneuve and Marrec, 1999) and can decrease the virus inoculum pressure. Genetic resistance has been developed on several plants species, especially tomato and pepper, to control the dissemination of viral diseases associated with tospoviruses. Concerning pepper, several *C. chinense* lines possess monogenic resistances conferred by the *Tsw* gene (Boiteux, 1995; Moury *et al*., 1997) and have been used to breed *C. annuum* cultivars resistant to TSWV. *Tsw* controls HR against most TSWV isolates and prevents the virus movement from cell to cell (Soler *et al*., 1999). It is not efficient against other tospovirus species like INSV.

Appearance of TSWV isolates adapted to the *Tsw* resistance has been observed first in laboratory conditions (Black *et al.,* 1991; Moury *et al.,* 1997). In southern Europe, breakdowns of the resistance were observed very rapidly after the release of *Tsw*-carrying cultivars and have been described in 1999 in Italy and Spain (Garcia-Arenal and McDonald, 2003). The TSWV genetic factors involved in the breakdown of the *Tsw* resistance are still under investigation. Some authors designated the NSs non structural protein (Margaria *et al,* 2007; Tentchev *et al.,* 2011) whereas others demonstrated the role of the NP encoded by the N gene (Lovato *et al.,* 2008). A way to reconcile these findings would be that two separate TSWV genes interact with the *Tsw* resistance in pepper: a gene which induces the resistance process (potentially the NP gene which was shown to be a specific elicitor of hypersensitive response in *Tsw* pepper plants) and a second gene which is targeted by the defence reactions and where resistance-breaking mutations can occur (presumably the NSs gene).

Resistance to the thrips vectors is known in several pepper (*C. annuum*) accessions and affect the level of feeding damage, host preference and host suitability for reproduction. Some authors have shown that TSWV transmission was little affected by vector resistance under experimental conditions (Maris *et al*., 2003). Owing to the lower reproduction rate and the lower attraction of thrips for resistant pepper plants, these authors supposed that beneficial effects might be expected from resistant cultivars under field conditions. Relationships between TSWV and its vectors are complex since TSWV-infected pepper plants increase attraction for female thrips compared to non-infected plants, thus improving TSWV dissemination (Maris *et al*., 2004). Also, male thrips infected with TSWV fed more than uninfected males, with a three-fold increase of noningestion probes during which they salivate, thus increasing the probability of virus inoculation (Stafford *et al.,* 2011).

Finally, *Polygonum ringspot virus*, a new tospovirus species, was recently discovered in northern and central Italy in wild buckwheat (*Polygonum convolvulus*) and in *P. dumetorum* (Ciuffo *et al*., 2008). *Polygonum ringspot virus* is closely related to *Tomato yellow ring virus* (TYRV; Fig. 4), a tospovirus infecting ornamental and vegetable crops in Iran (Rasoulpour and Izadpanah 2007; Hassani-Mehraban *et al*., 2007). Although this virus was found only in wild plants and was not detected in neighboring crops, it was shown to infect a large number of solanaceous plants, including pepper, after mechanical inoculation in laboratory conditions and could be a future threat for Italian and Mediterranean horticulture.

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IV. Whitefly-transmitted viruses

Two groups of whitefly-transmitted viruses, belonging to the genera *Begomovirus* and *Crinivirus*, are found in pepper in the Mediterranean area but have presently low economical impacts on this crop.

Begomoviruses are single-stranded DNA viruses transmitted by the whitefly *Bemisia tabaci* in a persistent and circulative manner that infect important crops, including *Cucurbitaceae* (watermelon, melon and squash), *Euphorbiaceae* (cassava), *Fabaceae* (common bean), *Malvaceae* (cotton) and *Solanaceae* (tomato, tobacco and pepper) and are the cause of devastating plant diseases, particularly in many tropical and sub-tropical regions of the world. Among them, *Tomato yellow leaf curl virus* (TYLCV) is one of the most destructive viruses affecting tomato crops throughout the Mediterranean region since its first description in the 1930s in Israel. In 1999, TYLCV has been reported for the first time on *C. annuum* plants in south-eastern Spain (Reina *et al.,* 1999) and later in Tunisia (Gorsane *et al.,* 2004; Gharsallah Chouchane *et al.,* 2007). TYLCV affecting pepper plants is also strongly suspected in Egypt and Morocco. The prevalence was estimated from 2 to 6% in southern Spain, much lower than that estimated in Florida. Morilla *et al*. (2005) detected also the related species *Tomato yellow leaf curl Sardinia virus* (TYLCSV) in some pepper plants in Spain. TYLCV-infected pepper plants are frequently symptomless (Morilla *et al.*, 2005; Polston *et al*., 2006). Although many pepper cultivars appear susceptible to TYLCV, large differences in infection rates have been observed, both in field conditions and after inoculation under controlled conditions. In transmission experiments with the Q biotype of *B. tabaci* and infected pepper plants as virus sources, Morilla *et al*. (2005) did not succeed to transmit TYLCV-Mld to tomato or pepper plants, which could be related to the low virus titer in the source plants compared to that in infected tomato plants. An uneven distribution of TYLCV in infected pepper plants was also observed (Morilla *et al*., 2005; Polston *et al*., 2006). Consequently, Morilla *et al*. (2005) suggested that pepper could be a dead-end host for TYLCV. However, using the B biotype of *B. tabaci* and a larger set of pepper cultivars, Polston *et al*. (2006) observed high rates of TYLCV transmission from infected pepper plants to tomato plants. However, they did not observe any TYLCV transmission when acquisition was from infected pepper fruits. Pepper and tomato crops are often close to each other and *B. tabaci* populations are able to feed and reproduce on peppers as well as on tomato plants. These data suggest a potential role of pepper plants in the epidemiology of TYLCV, as pepper plants could act as reservoirs for TYLCV dissemination, but the economical incidence of TYLCV on pepper production is probably very low.

Tomato infectious virus (ToCV) is a phloem-restricted bipartite *Closteroviridae* and belongs to the genus *Crinivirus*. It is transmitted by a number of whiteflies including *B. tabaci* and *Trialeurodes vaporariorum*. ToCV was first described on tomato plants in Florida in 1989 (Wisler *et al.,* 1998). In the Mediterranean region, ToCV has been reported in Spain, Italy, Greece, France, Turkey, Israel, Lebanon and Morocco. Although tomato is the main crop affected by ToCV, the virus has been reported on sweet pepper plants in greenhouses of southern Spain in 1999 (Lozano *et al.,* 2004). Infected pepper plants developed interveinal yellowing, leaf curling and stunting. The HSP70h gene of the pepper isolate of ToCV was 100% identical to ToCV isolates collected from tomato plants in the same region of Spain.

V. Tobamoviruses

Among pepper viruses that are not transmitted by biological vectors, tobamoviruses are, by far, the most important ones even though the potexvirus *Potato virus X* (PVX) can locally reach high prevalence (up to 70% of plants in some areas in Turkey; Buzkan *et al.*, 2006). There are very few epidemiological data on this latter virus in other countries.

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Tobamovirus is a genus of single-stranded RNA viruses whose particles are particularly stable. Tobamovirus particles are elongated rigid cylinders approximately 18 nm in diameter and 300 nm long, with a central cavity and a helical symmetry (2.3 nm pitch), containing the genomic RNA. Shorter virions constituting a minor component of the virus population encapsidate the subgenomic RNAs. The genome of tobamoviruses consists of one linear positive-sense single-stranded RNA, 6.3 to 6.6 kb in size. A cap structure and a tRNA-like structure are found at the 5' and 3' ends, respectively, of the genomic RNA. The CP is the only structural protein. Two non-structural proteins are produced from the genomic RNA: an ORF allows the production of a 124 to 132 kDa protein and a 181 to 189 kDa protein is produced by occasional readthrough of the stop codon of this ORF. These two non-structural proteins are required for virus replication and contain methyltransferase or guanylyl transferase, helicase and RdRp motifs. The CP and a third non-structural movement protein (MP) of 28 to 31 kDa required for cell-to-cell and systemic movements of the virus are expressed from subgenomic RNAs. Molecular clock analyses of tobamovirus genomes sampled over the last century have indicated that the genus is probably not older than 100,000 years (Pagán *et al.*, 2010).

Species infecting solanaceous crops build a distinct clade among tobamoviruses and several of these have been isolated from pepper all over the world and induce important economic losses in pepper crops (Nagai *et al.,* 1981; Wetter et al., 1984; Pares, 1985; Avgelis, 1986; Rast, 1988; Alonso *et al.,* 1989; Beczner *et al.,* 1997) (Fig. 5). The presently most prevalent pepper tobamoviruses in the Mediterranean basin are *Tobacco mild green mosaic virus* (TMGMV) (Font *et al.,* 2009; Fraile *et al.,* 2011), *Pepper mild mottle virus* (PMMoV) (Buzkan *et al.*, 2006; Güldür and Çağlar 2006; Fraile et al., 2011), *Tobacco mosaic virus* (TMV) and *Tomato mosaic virus* (ToMV) (Arli-Sokmen *et al.,* 2005) (Fig. 5). Both the yield and quality of pepper production can be severely reduced upon tobamovirus epidemics. Tobamoviruses induce leaf chlorotic mosaic or mottling, leaf distortion and surface reduction, irregular shapes and colours associated with a reduction of size of fruits which, consequently, cannot be commercialized. Necroses can also be observed on leaves and fruits.

Due to their high stability, tobamoviruses remain infectious in contaminated plant debris, compost, soil and irrigation water. Tobamoviruses cannot infect the seed embryo or albumen but are found in maternal tissues such as seed coat or residual perisperm, or as contaminant on the seed surface allowing infection of seedlings during germination. PMMoV is more efficiently seed transmitted than TMV or ToMV, probably due to a more internal contamination of seeds. Seed transmission has facilitated the introduction of tobamoviruses into different parts of the world through the international trade of pepper or tomato seeds. Given the absence of a biological vector of tobamoviruses, the primary measure of control involves prophylaxis, including disinfection and/or control of seed lots, eradication of infected plants and care during handling of plants since the viruses can be transmitted by the physical contact between plants. Several seed disinfection methods can reduce significantly tobamovirus transmission by seeds, such as a 2-hour treatment of seeds in 10% (w/v) trisodium phosphate (Na_3PO_4) solution (Rast and Stijger, 1987) or a 15-minute treatment in trisodium phosphate followed by a 30-minute treatment in a 0.525% (w/v) sodium hypochlorite (NaOCl) solution (Gooding, 1975). A heat treatment (3 days at 76°C) can also avoid seed transmission of tobamoviruses but adversely affects germination (Rast and Stijger, 1987).

TMV or PMMoV variants with attenuated virulence have also been used to develop cross protection control methods in pepper (Goto et al 1984; Hagiwara et al 2002; Yoon et al 2006; Ichiki et al 2009) but have not yet been used in commercial conditions in the Mediterranean region. Mutations responsible for attenuated symptoms have been mapped in the 126 kDa protein or in the 3' UTR (Hagiwara *et al.*, 2002; Yoon *et al.*, 2006; Ichiki *et al.*, 2009).

Another important control method against tobamoviruses in pepper is growing resistant cultivars. Different dominant alleles at the *L* locus, located on chromosome P11, have been identified in different *Capsicum* species (Table I) and shown recently to encode a coiled-coil, nucleotide-binding, leucine-rich repeat type of resistance protein (Tomita *et al.*, 2011). These alleles differ by their specificity towards tobamovirus species and isolates (Table I) and by their efficiency

under temperature stresses. Several of these alleles at the *L* locus lack efficiency above 30°C (Boukema, 1982) and show a higher efficiency at the homozygous state (Boukema, 1980, 1984). Other alleles show an enhanced efficiency at high temperature (Sawada *et al.*, 2005). The CP gene of tobamoviruses was shown to be responsible for the specificity and breakdown of the resistances conferred by the *L* gene (Berzal-Herranz *et al.*, 1995; Cruz *et al.*, 1997; Gilardi *et al.*, 1998, 2004). The *Hk* dominant gene was also shown to confer a temperature-dependent resistance to *Paprika mild mottle virus* (PaMMV) (Sawada *et al.*, 2005) but, in contrast, is not efficient at lower temperatures (24°C). It is also incompletely dominant. The methyltransferase domain of the replicase of PaMMV was shown to be involved in breakdown of *Hk* (Matsumoto *et al.*, 2009).

Infections of peppers carrying the L^1 or L^2 resistance genes seem to be the result of the emergence of new tobamovirus species rather than by "classical" resistance breakdowns (i.e. breakdown resulting from accumulation of a small number of mutations in the genome of non-adapted, avirulent, virus isolates). Indeed, no TMV, ToMV or TMGMV isolate breaking down the L^1 or L^2 resistances and no PaMMV or ObPV isolate breaking down the L^2 resistance have been described so far (Table I). Consequently, the wide use of L^1- or L^2-carrying pepper cultivars together with the efficiency and durability of these genes against ToMV, TMV and TMGMV could have created free "host niches" for other tobamoviruses, and might have contributed to the emergence of PMMoV.

In contrast, breakdown of the L^3 and L^4 resistances by PMMoV variants has been observed and mutations involved in these events identified (Tsuda *et al.*, 1998; Hamada *et al.*, 2002, 2007; Genda *et al.*, 2007; Antignus *et al.*, 2008). PMMoV is composed of three major clades (Fig. 6) and evolution of resistance breakdown capacities occurred independently in all of them. One PMMoV clade (clade 3; Fig. 6) is composed essentially of Mediterranean isolates of pathotype $P_{1,2,3}$ that all carry the $M_{139}N$ substitution in their CP, sufficient for breaking down the L^3 resistance (Berzal-Herranz *et al.*, 1995). Until now, only resistance-breaking isolates from this group have spread in different countries.

One Israeli isolate from this group was also shown to break down the L^4 resistance. A few Asiatic PMMoV isolates belonging to other clades were also shown to break the L^3 or L^4 resistances (Genda *et al.*, 2007) but have not been observed in Mediterranean countries. These resistance breakdown events show several remarkable common points: (i) they were frequently observed first in pepper varieties heterozygous at the *L* locus, (ii) they result from independent events (except clade 3) involving different mutations and (iii) they were the results of particular mutational pathways usually involving several nucleotide and amino acid substitutions. The latter two points suggest that these events are rather rare and could explain why the L^4 resistance was rather durable. Breakdown of the L^4 resistance was caused apparently by a (former) pathotype $P_{1,2}$ isolate in Japan and by a (former) pathotype $P_{1,2,3}$ isolate in Israel (Fig. 6).

The capacity to infect pepper cultivars with the L^1, L^2 or L^3 resistance genes seems to confer a high fitness cost to tobamoviruses. In susceptible L^+/L^+ pepper plants, TMGMV is more competitive and accumulates to higher rates than PMMoV. Similarly, pathotype $P_{1,2}$ PMMoV isolates are more competitive and accumulate to higher rates than pathotype $P_{1,2,3}$ PMMoV isolates (Fraile *et al.*, 2011). As a consequence, the relative acreage grown in peppers with different alleles at the *L* locus during the last 15 years has had a strong influence on the composition in, and prevalence of the different tobamovirus species and pathotypes (Fraile *et al.*, 2011). This suggests that management of tobamovirus epidemics at a regional scale by growing pepper cultivars carrying different alleles at the *L* locus, including the susceptible L^+/L^+ genotypes, should be feasible.

VI. Other viruses

In 2004, *Parietaria mottle virus* (PMoV), a member of the genus *Ilarvirus*, has been identified in bell pepper plants grown in greenhouses in south-east Spain (Janssen *et al.*, 2005). Infected pepper plants develop stem necrosis as well as brown patches and corky rings on the fruit surface. More recently, similar symptoms have been observed in pepper plants collected in South-eastern France

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and were associated with PMoV using serological and molecular diagnostic tools (Verdin, *unpublished results*). Initially, PMoV was described on the wild plant species *Parietaria officinalis* (pellitory-of-the-wall) showing yellow mosaic and mottling in Italy (Caciagli *et al.*, 1989) and further in tomato crops in Italy, Southern France, Greece and the Mediterranean coast of Spain (Lisa *et al.*, 1998; Marchoux *et al.*, 1999; Roggero *et al.*, 2000; Aramburu, 2001) as well as in *Mirabilis jalapa* plants in Italy (Parrella, 2001). PMoV, as the other ilarviruses, is a single-stranded RNA virus with a tripartite genome. Tomato and pepper PMoV isolates have distinct genome sequences (92 % nucleotide identity in the P1 gene) and do not share the same biological host range (Caciagli *et al.*, 1989; Janssen *et al.*, 2005). Several studies described the transmission of ilarviruses by seed or pollen from infected plants (Mink, 1993), but no specific natural vectors are known even if transmission by thrips, mites or nematodes have been reported for some ilarviruses (Fulton, 1981). Mechanical transmission of PMoV using pollen collected on PMoV-infected tomato plants has also been described (Verdin *et al.*, 2005). Transmission of PMoV by several insects (including the thrips species *F. occidentalis*) has been reported to pepper and tomato plants using PMoV-infected *P. officinalis* plants at the flowering stage as sources for virus acquisition (Aramburu *et al.*, 2010). These results suggest that the high incidence of PMoV observed in some Mediterranean countries, especially Italy and Spain, could be reduced by removing *P. officinalis* plants around pepper and tomato crops.

VII. Conclusion

Compared to other vegetable crops, very few viral emergences or novel threats have been mentioned in pepper crops in the Mediterranean basin during the last 20 years (Hanssen *et al.*, 2010). Two major explanations can be invoked.

Pepper, as many other crop species from the family Solanaceae, originates from the Americas and was introduced to Europe and other areas of the Old World approximately 500 years ago. As a consequence, viral diseases that affect pepper in the Mediterranean basin are only a small subset of those that are prevalent in the rest of the world. Pepper viruses that are prevalent in the Mediterranean area belong to two main categories. The first one consists of viruses that are particularly stable and/or that are seed-borne, like tobamoviruses, since they are easily introduced and spread in new areas by human activities and trade. The second category consists of viruses that have a broad host range, particularly if this host range includes vegetatively-propagated crops. These viruses could have been introduced into the Mediterranean area through other crops, like PVY that could have been introduced with potato tubers and could have adapted secondarily to pepper (Moury, 2010). Others like CMV or TSWV may have been present in the Old World before the introduction of pepper and may have jumped and adapted to this crop afterwards. Viruses that have narrower host ranges and that are not transmitted vertically by seeds in pepper were less likely to be introduced or to emerge in the Mediterranean area. For example, only two *Potyvirus* species of ten described worldwide in pepper are present in the Mediterranean basin.

The second explanation to the apparent stasis of viral diseases in pepper in the Mediterranean region compared to other crops is the lower susceptibility of this plant species to whiteflies and notably to *Bemisia tabaci*, which was recently responsible for the emergence of a large number of virus species from the genus *Begomovirus* and to a lower extent from the genera *Crinivirus*, *Ipomovirus* and *Torradovirus*, in other vegetable crops such as tomato or cucurbits (Hanssen *et al.*, 2010).

The most recent viral emergences in pepper crops in the Mediterranean area correspond to tospoviruses and/or to isolates breaking down specific resistances of pepper cultivars. Phylogenetic arguments suggest that some TSWV variants could have been introduced in Spain, Italy, France and Algeria from Northern America whereas other TSWV variants have probably re-emerged in the Old World following the worldwide spread of the thrips species *F. occidentalis* (Tentchev *et al.*, 2011). Recent resistance breakdowns include the tobamovirus resistance gene L^3, estimated to have occurred between 24 and 56 years ago (Fraile *et al.*, 2011), and the TSWV resistance gene *Tsw*

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which was broken down only a few years after being deployed (Roggero *et al.*, 2002; García-Arenal and McDonald, 2003; Thomas-Carroll and Jones 2003; Margaria *et al.*, 2004; Sharman and Persley, 2006). No alternative resistance gene is available yet against TSWV, making of this virus the primary constraint on pepper production in some areas.

Future viral threats to pepper production in the Mediterranean area could include CMV isolates from subgroup IB, which have been introduced probably from Asia and have been observed in pepper crops in Spain (Bonnet *et al.*, 2005), poleroviruses that have so far been isolated from pepper crops in the Eastern part of the Mediterranean area only, but can induce severe outbreaks and, potentially, the tospovirus *Polygonum ringspot virus* that is confined to wild plants in several areas in Italy but has the potential to infect many pepper cultivars. In addition, the risk that begomoviruses that affect severely pepper crops in other areas of the world (Torres-Pacheco *et al.*, 1996; Ala-Poikela *et al.*, 2005; De Barro *et al.*, 2008; Tiendrebeogo *et al.*, 2011) could be introduced, for example with whiteflies, and spread in the Mediterranean area should not be underestimated.

Finally, pepper has also been a model plant for the study of plant resistances to viruses. Natural eIF4E-mediated recessive resistances against viruses were first characterized in pepper (Ruffel *et al*., 2002). Pepper is also a model plant for the study of polygenic resistances against viruses (Palloix *et al.,* 2009; St Clair, 2010). Finally, two series of virus resistance alleles in pepper correspond to the two main plant-parasite co-evolutionary models: resistance to tobamoviruses controlled by the *L* locus fits the "gene-for-gene" model of interaction and the resistance to potyviruses controlled by the *pvr2* locus rather corresponds to the "matching-allele" model of interaction (Sacristán and García-Arenal, 2008).

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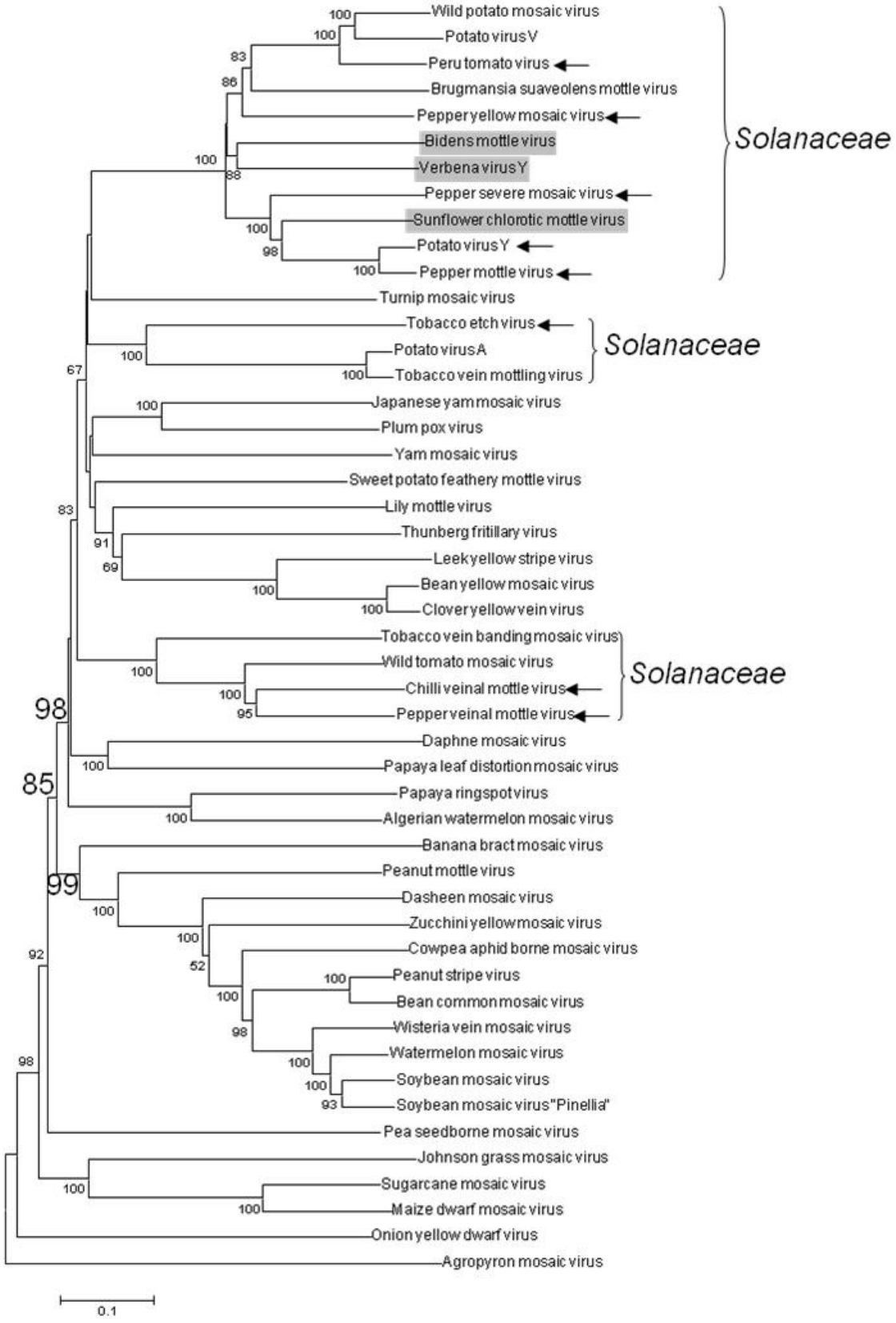

Figure 1: Unrooted neighbor joining phylogenetic tree of full-length genomes of potyviruses. The arrows indicate pepper-infecting potyviruses and potyviruses that do not infect solanaceous plants but cluster with *Solanaceae* groups are underlined in gray. Bootstrap percentages above 50% are shown. The scale bar indicates branch lengths in substitutions per nucleotide.

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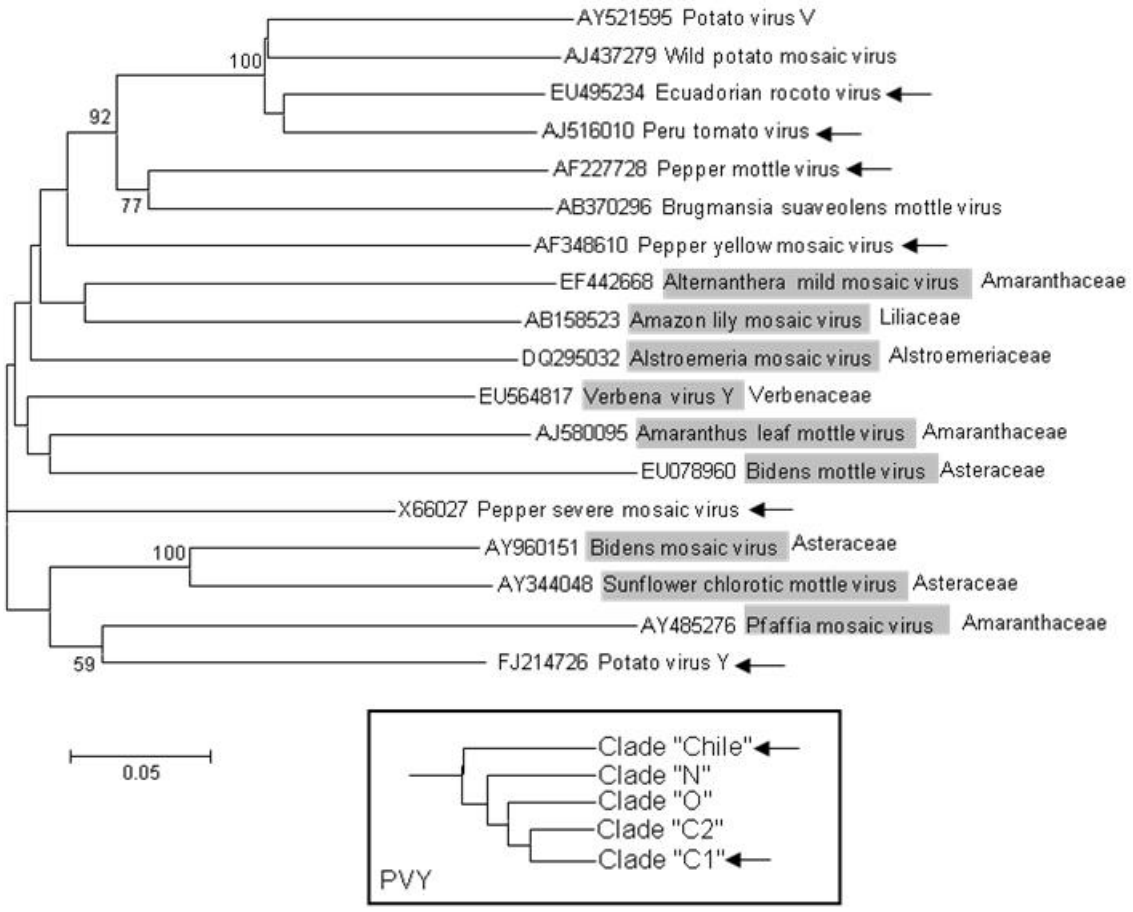

Figure 2: Unrooted neighbor joining phylogenetic tree of the coat protein (CP) coding region of potyviruses in the *Potato virus Y* (PVY) cluster. The arrows indicate pepper-infecting potyviruses and potyviruses that do not infect solanaceous plants but cluster with *Solanaceae* groups are underlined in gray. The tree topology of the PVY clades is boxed (see Moury, 2010). Bootstrap percentages above 50% are shown. The scale bar indicates branch lengths in substitutions per nucleotide.

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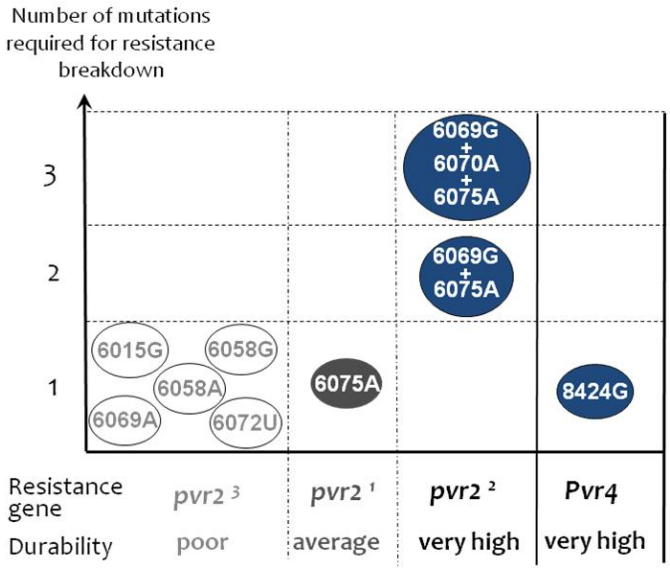

Figure 3: Nucleotide substitutions in the *Potato virus Y* (PVY) genome (numbered according to isolate SON41p; accession number AJ439544) involved in the breakdown of pepper resistances at the *pvr2* or *Pvr4* loci and durability level of these resistances. For breakdown of *pvr2*^{2}, the two combinations of mutations correspond to French (two nucleotide substitutions) or Tunisian (three nucleotide substitutions) isolates with VPg sequences closest to SON41p, the only *pvr2*^{2}-breaking PVY isolate characterized).

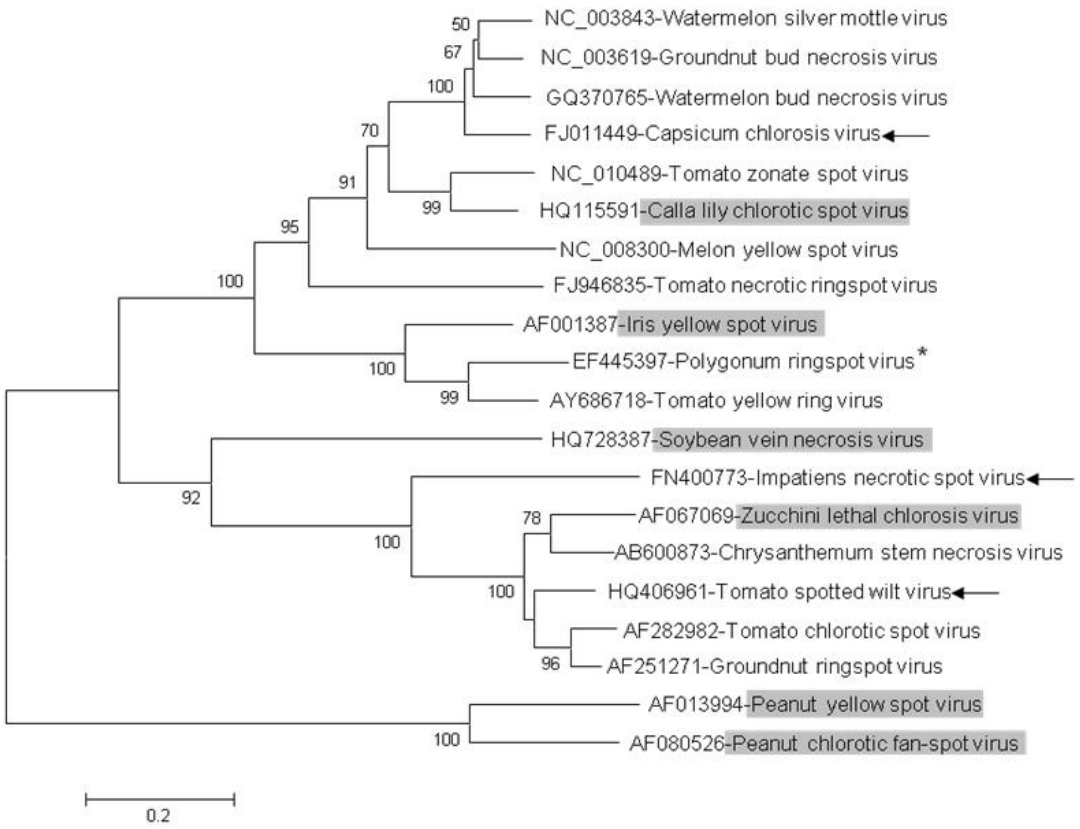

Figure 4: Unrooted neighbor joining phylogenetic tree of the coat protein gene of tospoviruses. The arrows indicate pepper-infecting tospoviruses and tospoviruses that do not infect solanaceous plants are underlined in gray. Bootstrap percentages above 50% are shown. The scale bar indicates branch lengths in substitutions per nucleotide.

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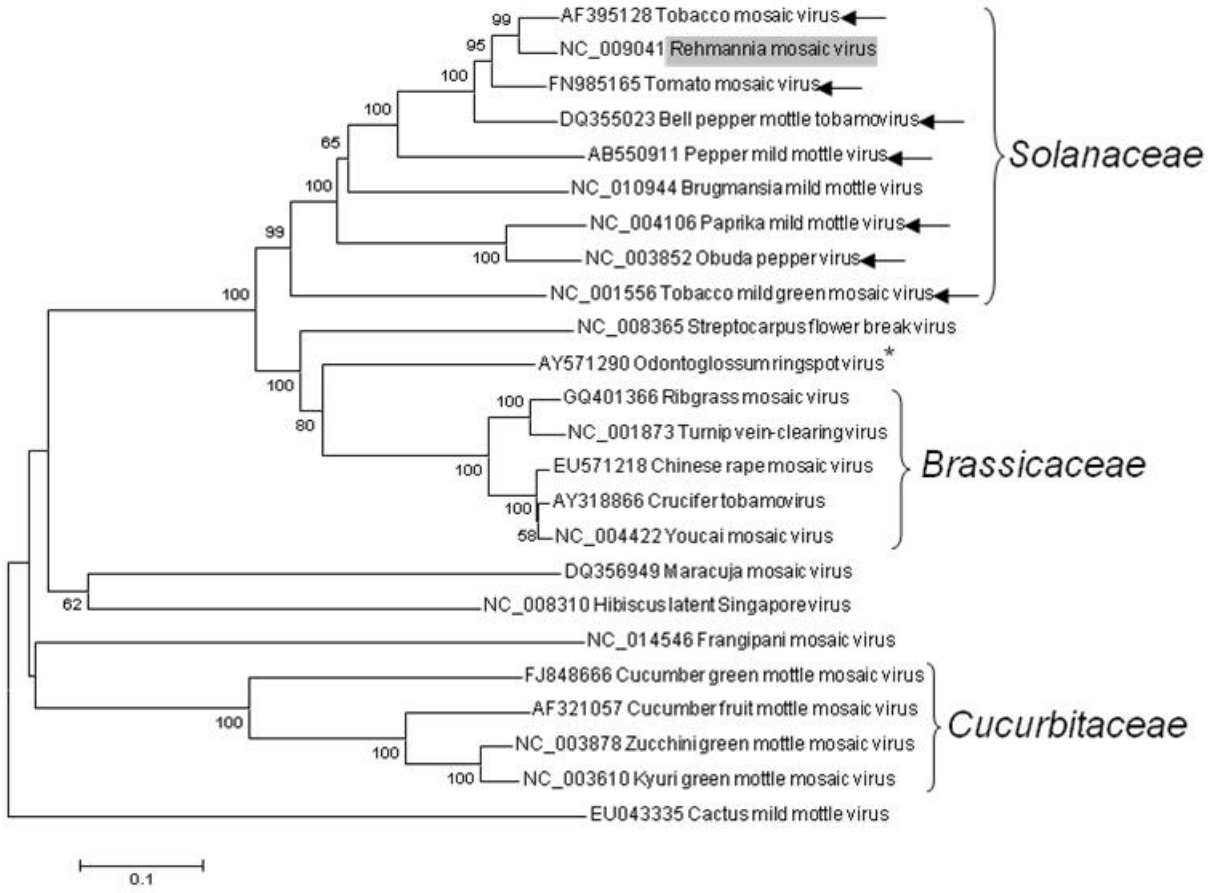

Figure 5: Unrooted neighbor joining phylogenetic tree of the replicase coding region of tobamoviruses. The arrows indicate pepper-infecting tobamoviruses and a tobamovirus that does not infect solanaceous plants but clusters with a *Solanaceae* group is underlined in gray. The asterisk indicates that *Odontoglossum ringspot virus* is an interspecific recombinant tobamovirus that clusters with different groups depending on the genome region examined. Bootstrap percentages above 50% are shown. The scale bar indicates branch lengths in substitutions per nucleotide.

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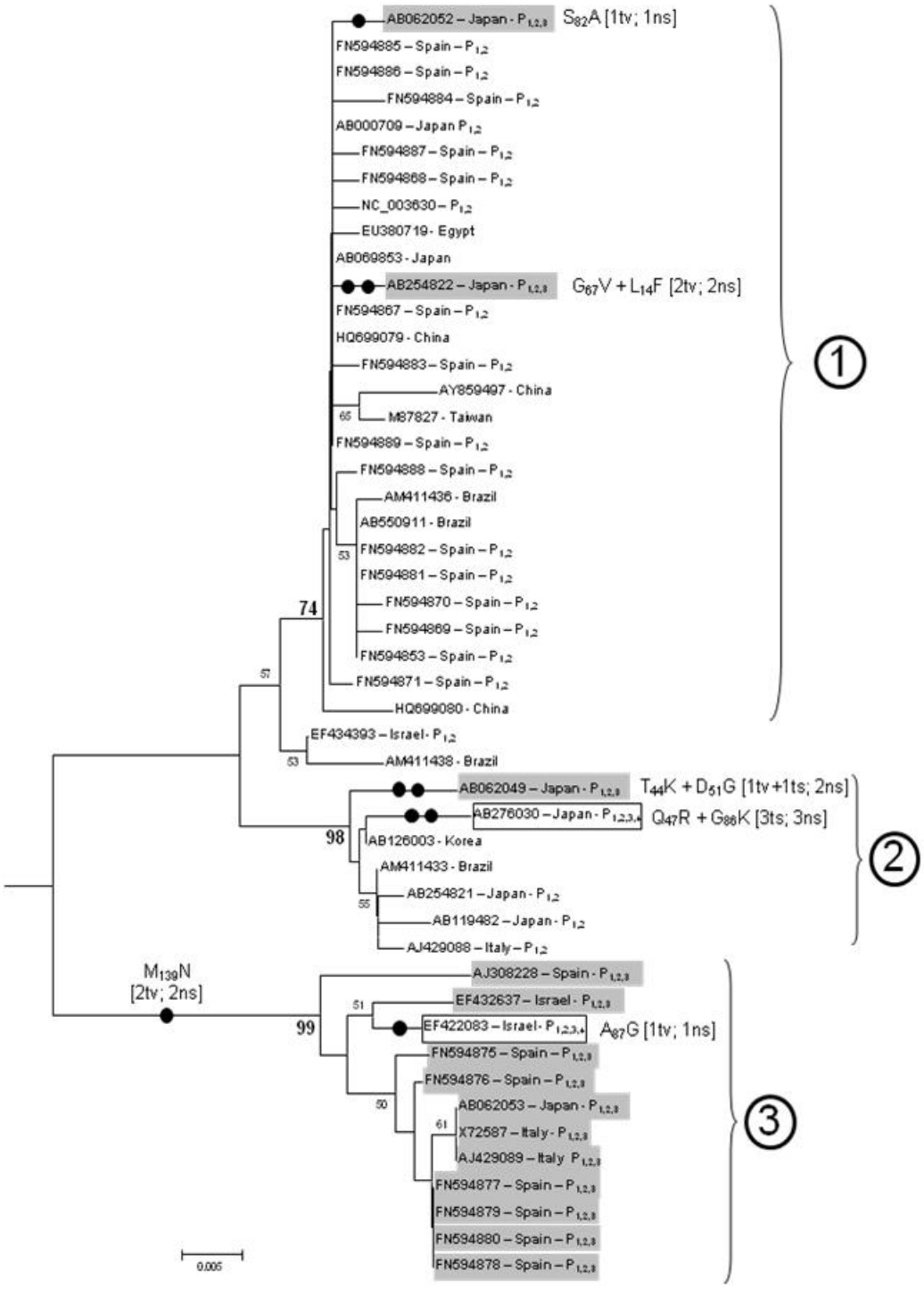

Figure 6: Rooted neighbor joining phylogenetic tree of the coat protein (CP) coding region of *Pepper mild mottle virus* (PMMoV). PMMoV pathotypes defined according to the behaviour against pepper resistance genes at the *L* locus are indicated when known (see Table 1). Pathotype $P_{1,2,3}$ PMMoV isolates are underlined in gray and pathotype $P_{1,2,3,4}$ PMMoV isolates are boxed. The number of amino acid changes in PMMoV CP involved in the breakdown of the L^3 and L^4 resistance genes are indicated (black circles), together with the corresponding number of transitions (ts), transversions (tv) and nonsynonymous (ns) nucleotide substitutions. Bootstrap percentages above 50% are shown. The scale bar indicates branch lengths in substitutions per nucleotide.

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Table I : Reaction of different tobamovirus species (see Fig. 5) and pathotypes towards *Capsicum* spp. genotypes carrying different alleles at the *L* locus.

		Pepper species and genotype				
Virus	Pathotype	*C. annuum* L^+/L^+	*C. annuum* $L^1/-$	*C. frutescens* $L^2/-$	*C. chinense* $L^3/-$	*C. chacoense* $L^4/-$
TMV, ToMV, TMGMV, BPeMV	P_0	S	R	R	R	R
PaMMV, ObPV, BPeMV?	P_1	S	S	R	R	R
PMMoV	$P_{1,2}$	S	S	S	R	R
PMMoV	$P_{1,2,3}$	S	S	S	S	R
PMMoV	$P_{1,2,3,4}$	S	S	S	S	S

S: susceptibility, *i.e.* systemic infection; R, resistance, *i.e.* necrotic local lesions without systemic infection.
TMV: *Tobacco mosaic virus*; ToMV: *Tomato mosaic virus*; TMGMV: *Tobacco mild green mosaic virus*; BPeMV: *Bell pepper mottle virus*; PaMMV: *Paprika mild mottle virus*; ObPV: *Obuda pepper virus*; PMMoV: *Pepper mild mottle virus*.