



Phytophagous mites transmitting plant viruses: update and perspectives

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With 1 table

Abstract: Plant viruses can be effectively transmitted by phytophagous mites. Many species of mites, mainly eriophyids and tenuipalpids, induce symptoms in infested plants that may be mistaken for viral diseases or may hide infections produced by unidentified putative viruses. The virus-mite interplay and the multitrophic interactions with their host plants are often inadequately described and require further clarifications. Advances in biotechnological methods could enable increasing identification and characterization of viruses transmitted and their potential mite vectors. This review examines the state of knowledge of mites and plant-virus interactions by summarizing the strengths and weaknesses in this research field, thus paving the way for new research directions.

Keywords: Eriophyidae; Tenuipalpidae; plant pathogens; virus transmission; pathosystems

1 Introduction

Amid the relatively sparse data on mite vectors of plant viruses, some species of Eriophyoidea and Tenuipalpidae (Tetranychoidae) are particular reference points in plant-virus transmission (*cf.* Vacante 2016). Even in these instances, however, information on mite-virus relationships remains limited and fragmented. Research on these subjects suffers as a consequence of the tiny size of the mites involved, particularly in the case of eriophyoids. In addition to the peculiarities of niches and microhabitats, the dynamics and behavioural traits of these mites hinder their rearing, as well as experimental assays (Oldfield & Proeseler 1996; de Lillo & Skoracka 2010; de Lillo et al. 2018).

Within the superfamily Eriophyoidea, only mites of the family Eriophyidae have been determined to be plant virus vectors, and most of them do not cause hypersensitive reac-

tions in the pierced plant cells (Stenger et al. 2016). In the superfamily Tetranychoidae, apart from a very few reports suggesting that spider mites are involved in the transmission of plant viruses, most of the current knowledge of virus transmission is derived from studies of *Brevipalpus* species (Tenuipalpidae). Data on *Brevipalpus*-transmitted viruses (BTVs) have increased significantly in recent years (Freitas-Astúa et al. 2018). BTVs are unable to systemically move on their host plants, causing local infections (Childers et al. 2003a; Kitajima et al. 2003a, 2014; Dietzgen et al. 2018a; Freitas-Astúa et al. 2018). As far as is known, infestations by *Brevipalpus* mites trigger a drastic reprogramming of the plant transcriptome to render the host more susceptible to mite colonization, by inducing the salicylic acid-mediated pathway (Arena et al. 2016, 2018). The same mechanism is also presumed to be deployed by eriophyoids (de Lillo et al. 2018).

The current review updates information on mite-virus interactions and critically evaluates the needs, weaknesses, and strengths of the topics covered.

2 Plant viruses transmitted by mites

2.1 Viruses transmitted by eriophyids

Jones (1999) listed at least 26 plant virus diseases that are potentially associated with eriophyid mites. Eriophyid-transmitted viruses (ETVs) are highly specific and vectored only by a single species of mite (Oldfield & Proeseler 1996; Stenger et al. 2016). Conversely, a single eriophyid species can transmit more than one virus belonging to the same or a different genus and family. ETVs and suspected ETVs have a wide range of genomes and expression strategies, and their particle morphologies range from spherical, enveloped (*Fimoviridae*: emaraviruses) or not (*Secoviridae*: nepovirus), to filamentous (*Potyviridae*: tritoviruses, poaceviruses, and rymoviruses; *Betaflexiviridae*: trichoviruses; *Alphaflexiviridae*: allexiviruses), containing single or split RNA molecules as the genome (Stenger et al. 2016; <http://ictv.global>) (Table 1).

Potyviruses are transmitted by aphids, whiteflies, fungi, and eriophyids, and the involvement of spider mites has also been suggested (King et al. 2012). Viral particles are about 700×12 nm and contain a positive (+) single-stranded (ss) RNA genomic molecule, which is expressed as a single polyprotein that is further processed into single functional proteins by viral encoded proteases.

Particles of allexiviruses are around 800×12 nm. Their genome consists of (+) ssRNA molecules coding for six proteins, *i.e.*, replicase (open reading frame 1=ORF1), movement, coat, and nucleic acid-binding proteins (ORF2-3, 5-6); the function of ORF4 is currently unknown (King et al. 2012).

Trichoviruses are around 700×12 nm, with (+) ssRNA. Their genomes contain three overlapping ORFs encoding replicase, movement, and coat proteins (King et al. 2012). Some members also have a fourth ORF, which encodes a nucleic acid-binding protein.

Viral particles of nepoviruses encapsidate two (+) ssRNAs (RNA1 and RNA2), which are translated into polyproteins that are successively processed into structural and functional proteins (Seitonen et al. 2008).

Eriophyid-transmitted emaraviruses induce typical cytopathic effects in their host plants, including the presence of double membrane-bounded bodies (DMBs) (Kim et al. 2001). Virus particles measure 80–200 nm in diameter and possess four to eight segmented negative (–) ssRNAs, each encoding a single ORF (Mühlbach & Mielke-Ehret 2012; Hassan et al. 2017; Kubota et al. 2020). These viruses are localised mainly in the plant parenchymatic tissues.

2.2 Viruses transmitted by tenuipalpid

The first evidence for the involvement of *Brevipalpus* mites in plant virus transmission was reported by Frezzi (1940), who reproduced symptoms of citrus leprosis by transferring viruliferous *Tenuipalpus pseudocuneatus* (Blanchard) (a junior synonym of *Brevipalpus obovatus* Donnadieu) to healthy citrus plants. The same mite species was associated with a leprosis-like disease in *Ligustrum sinense* Lour. (Vergani 1942). Since then, numerous viruses of the genera *Cilevirus* (family *Kitaviridae*) and *Dichorhavirus* (family *Rhabdoviridae*) were found to be transmitted by several *Brevipalpus* spp. (Childers et al. 2003a; Kitajima et al. 2010, 2014; Dietzgen et al. 2018a; Freitas-Astúa et al. 2018) (Table 1). Despite the significant difference in genome organization, it is speculated that cileviruses and dichorhaviruses show signs of convergent evolution, likely determined by their intimate interaction with *Brevipalpus* mites (Freitas-Astúa et al. 2018).

Citrus leprosis virus C (CiLV-C) is the type member of the genus *Cilevirus*. Virions are short bacilliform, $100\text{--}120 \times 60\text{--}70$ nm, membrane-bound particles that are mainly contained in cisternae of the endoplasmic reticulum (ER) in the infected plant cells. A characteristic electron-dense inclusion, referred to as viroplasm, results from cilevirus infections and is believed to be an accumulation of virus-coded proteins. Virion morphogenesis likely occurs by budding of the virion precursor from viroplasm through the ER membrane towards the ER lumen (Kitajima et al. 2003a). The genome of cileviruses consists of two (+) ssRNAs. RNA1 contains genes encoding the RNA-dependent RNA polymerase and P29. RNA2 has four major ORFs (P15, P61, MP, and P24). Proteins P29, P61, and P24 are putative structural proteins, while the function of P15 is unknown (Freitas-Astúa et al. 2018). Although CiLV-C can experimentally infect many plant species (Garita et al. 2014) besides citrus, only the plant species *Swinglea glutinosa* (Blanco) Merr. in Colombia (León et al. 2008) and *Commelina benghalensis* L. in Brazil (Nunes et al. 2012) were found to be naturally infected by the virus. Citrus leprosis virus C2 (CiLV-C2) (Roy et al. 2013, Melzer et al. 2013; Roy et al. 2018), passion fruit green spot virus (PfGSV) (Kitajima et al. 2007; Ramos-González et al. 2020) and the tentative cilevirus *Solanum violifolium* ringspot virus (SvSRV) (Ferreira et al. 2007) are other identified cileviruses (Table 1).

Viruses of the genus *Dichorhavirus* have non-enveloped bacilliform particles measuring 100–110 nm in length and 40 nm in width. Orchid fleck virus (OFV), the type member of the genus, was the first to be described and molecularly characterized as a dichorhavirus (Doi et al. 1969; Kondo et al. 2006). OFV has been detected worldwide in orchids and other ornamental plants (Table 1) and its widespread distribution is likely a consequence of the intense trade in orchids.

Table 1. List of plant viruses transmitted by mites.



| Virus (Acronym) | Viral genus | Plant host/s | Geographical distribution | Mite species vector | Main reference/s |
|---|--------------------|---|--|---|--|
| Family Alphaflexiviridae | | | | | |
| garlic mite-borne filamentous virus (GarMbFV) | <i>Allexivirus</i> | <i>Allium sativum</i> L. | Argentina, Brazil, Korea, Japan | <i>Aceria tulipae</i> | Yamashita et al. 1996, Melo-Filho et al. 2004; Lee et al. 2007; Oliveira et al. 2014 |
| garlic virus A (GarVA), B (GarVB), C (GarVC), D (GarVD), E (GarVE), X (GarVX) | <i>Allexivirus</i> | <i>Allium cepa</i> L., <i>A. sativum</i> , <i>Tulipa</i> sp. | probably occurring wherever the host plants grown | <i>Aceria tulipae</i> | Chen et al. 2001; Melo-Filho et al. 2004; Lee et al. 2007; Gieck et al. 2009; Wylie et al. 2012; Gawande et al. 2015; CABI/EPPO 2021; Nurulita et al. 2020 |
| shallot virus X (ShVX) | <i>Allexivirus</i> | <i>A. sativum</i> , <i>A. cepa</i> , <i>A. caeruleum</i> Pall. | China, Ecuador, India, Italy, New Zealand, Poland, Sudan, USA | <i>Aceria tulipae</i> | Ward et al. 2009; Wang et al. 2019; CABI/EPPO 2021 |
| Family Betaflexiviridae | | | | | |
| cherry mottle leaf virus (ChMLV) | <i>Trichovirus</i> | <i>Prunus emarginata</i> (Dougl. Ex Hook.) Eaton | China, Europe, North America, South Africa | <i>Eriophyes inaequalis</i> | Németh 1986; Ma et al. 2014 |
| fig latent virus-1 (FLV-1) ¹ | <i>Trichovirus</i> | <i>Ficus carica</i> L. | China, Europe, Iran, Saudi Arabia, Syria, Tunisia, USA | <i>Aceria ficus</i> | Shahmirzaie et al. 2012; Preising et al. 2021 |
| grapevine berry inner necrosis virus (GINV) | <i>Trichovirus</i> | <i>Vitis vinifera</i> L. | China, Japan | <i>Colomerus vitis</i> | Yoshikawa et al. 1997; Fan et al. 2017 |
| grapevine pinot gris virus (GPGV) | <i>Trichovirus</i> | <i>V. vinifera</i> | Worldwide | <i>Colomerus vitis</i> | CABI/EPPO 2021 |
| peach mosaic virus (PcMV) | <i>Trichovirus</i> | <i>Prunus hortulana</i> L. Bailey, <i>P. mexicana</i> Watson, <i>P. munsoniana</i> Wight & Hedrick, <i>P. persica</i> (L.) Batsch, | Mexico, USA | <i>Eriophyes insidiosus</i> | CABI/EPPO 2021 |
| Family Fimoviridae | | | | | |
| actinidia chlorotic ringspot-associated emaravirus (AcCRaV) | <i>Emaravirus</i> | <i>Actinidia</i> sp. | China | Eriophyidae ² | Zheng et al., 2017  |
| blackberry leaf mottle associated emaravirus (BLMaV) | <i>Emaravirus</i> | <i>Rubus</i> sp. | USA | Not identified Eriophyoidea | Hassan et al. 2017 |
| chrysanthemum mosaic-associated emaravirus (ChMaV) ¹ | <i>Emaravirus</i> | <i>Chrysanthemum</i> sp. | East Asia | <i>Paraphytoptus kikus</i> ³ | Kubota et al. 2021 |
| european mountain ash ringspot-associated emaravirus (EMARaV) | <i>Emaravirus</i> | <i>Sorbus aucuparia</i> L., <i>Amelanchier</i> sp. | Czech Republic, Germany, Norway, Poland, Sweden, UK | <i>Eriophyes pyri</i> | CABI/EPPO 2021 |
| fig mosaic Emaravirus (FMV) | <i>Emaravirus</i> | <i>Ficus carica</i> , experimentally <i>Catharanthus roseus</i> (L.) Don, <i>Cyclamen persicum</i> Mill. | worldwide | <i>Aceria ficus</i> | Chiumenti et al. 2013; Preising et al. 2021 |
| high plains wheat mosaic emaravirus (HPWMoV) | <i>Emaravirus</i> | <i>Triticum aestivum</i> L., <i>Avena sativa</i> L., <i>Bromus tectorum</i> L., <i>Hordeum vulgare</i> L., <i>Secale cereale</i> L., <i>Zea mays</i> L. | Argentina, Australia, Brazil, Canada, Chile, Denmark, Ukraine, USA | <i>Aceria tosichella</i> | CABI/EPPO 2021 |

Table 1. continued.

| Virus (Acronym) | Viral genus | Plant host/s | Geographical distribution | Mite species vector | Main reference/s |
|---|---------------------|--|--|---|--|
| perilla mosaic emaravirus (PerMV) | <i>Emaravirus</i> | <i>Perilla frutescens</i> var. <i>crispa</i> (Thunb.) Deane | Japan | <i>Shevtchenkella</i> sp. | Kubota et al. 2020 |
| pigeonpea sterility mosaic emaravirus 1 (PPSMV-1) | <i>Emaravirus</i> | <i>Cajanus cajan</i> L. | Bangladesh, India, Myanmar, Nepal, Sri Lanka, Thailand | <i>Aceria cajani</i> | CABI/EPPO, 2021 |
| pigeonpea sterility mosaic emaravirus 2 (PPSMV-2) | <i>Emaravirus</i> | <i>Cajanus cajan</i> | India | <i>Aceria cajani</i> | Elbeaino et al. 2015 |
| pistacia emaravirus B (PiBV) | <i>Emaravirus</i> | <i>Pistacia</i> sp. | Turkey | Eriophyoidea ² | Buzkan et al. 2019 |
| raspberry leaf blotch emaravirus (RLBV) | <i>Emaravirus</i> | <i>Rubus idaeus</i> L., <i>Rubus fruticosus</i> x <i>Rubus idaeus</i> | probably widely distributed in Europe | <i>Phyllocoptes gracilis</i> | Bi et al. 2012; Ciešlińska & Tartanus 2014; Pleško et al. 2014; Zindović et al. 2015; McGavin et al. 2012; Delić et al. 2020; Paunović & Jevremović 2020 |
| redbud yellow ringspot-associated emaravirus (RYRaV) | <i>Emaravirus</i> | <i>Cercis</i> spp. | USA | Not identified Eriophyoidea | Di Bello et al. 2016 |
| rose rosette emaravirus (RRV) | <i>Emaravirus</i> | <i>Rose multiflora</i> Thunb., <i>Rosa</i> spp. | Canada, India, USA | <i>Phyllocoptes fructiphilis</i> | CABI/EPPO 2021 |
| Family Kitaviridae | | | | | |
| citrus leprosis virus C (CiLV-C) | <i>Cilevirus</i> | <i>Arabidopsis thaliana</i> (L.) Heynh., <i>Citrus</i> sp., <i>Commelina benghalensis</i> L., <i>Swinglea glutinosa</i> Merr. | Central America, Mexico, South America | <i>Brevipalpus yothersi</i> <i>Brevipalpus papayensis</i> ⁴ | Locali-Fabris et al. 2006; León et al. 2008; Nunes et al. 2012a, 2018; Ramos-González et al. 2016a; Arena et al. 2017 |
| citrus leprosis virus C2 (CiLV-C2) | <i>Cilevirus</i> | <i>Citrus</i> sp., <i>Hibiscus</i> sp. | Brazil , Colombia, USA | <i>Brevipalpus yothersi</i> | Melzer et al. 2013; Roy et al. 2013, 2018 |
| passion fruit green spot virus (PfGSV) | <i>Cilevirus</i> | <i>Passiflora edulis</i> Sims | Brazil | <i>Brevipalpus yothersi</i> | Kitajima et al. 2003b; Ramos-González et al. 2020 |
| Solanum violaeifolium ringspot virus (SvRSV) ¹ | <i>Cilevirus</i> | <i>A. thaliana</i> , <i>Solanum violaeifolium</i> hott | Brazil | <i>Brevipalpus obovatus</i> | Ferreira et al. 2007; Arena et al. 2017 |
| Family Potyviridae | | | | | |
| potato virus Y (PVY) | <i>Potyvirus</i> | <i>Capsicum</i> spp., <i>Nicotiana tabacum</i> L., <i>Solanum lycopersicum</i> L., <i>S. tuberosum</i> L. | Worldwide | <i>Tetranychus urticae</i> | McDonald et al. 1996; CABI/EPPO 2021 |
| agropyron mosaic virus (AgMV) | <i>Rymovirus</i> | <i>Elymus repens</i> (L.) Gould, <i>T. aestivum</i> | Bulgaria, Canada, Hungary, Finland, Germany, UK, USA | <i>Abacarus hystrix</i> | CABI/EPPO 2021 |
| hordeum mosaic virus (HoMV) | <i>Rymovirus</i> | <i>H. vulgare</i> | Canada | Eriophyoidea ² | Slykhuis & Bell 1966 |
| ryegrass mosaic virus (RGMV) | <i>Rymovirus</i> | <i>Festuca perennis</i> Lam., several grasses | Czech Republic, UK, Australia, Victoria, New Zealand | <i>Abacarus hystrix</i> | CABI/EPPO 2021 |
| brome streak mosaic virus (BrSMV) | <i>Tritimovirus</i> | <i>Bromus hordeaceus</i> L.; <i>B. sterilis</i> L., <i>Cyperus esculentus</i> L., <i>Hordeum murinum</i> L., <i>H. vulgare</i> | Worldwide | <i>Aceria tosichella</i> | CABI/EPPO 2021 |
| oat necrotic mottle virus (ONMV) | <i>Tritimovirus</i> | <i>A. sativa</i> | USA | Eriophyoidea ² | Stenger & French 2004 |

Table 1. continued.

| Virus (Acronym) | Viral genus | Plant host/s | Geographical distribution | Mite species vector | Main reference/s |
|--|----------------------|---|---------------------------|---|---|
| tall oatgrass mosaic virus (TOgMV) | <i>Tritimovirus</i> | <i>Arrhenatherum elatius</i> (L.) P.Beauv. | Czech Republic | Eriophyidae ² | Hassan et al. 2014 |
| wheat eglid mosaic virus (WEqMV) | <i>Tritimovirus</i> | <i>T. aestivum</i> | Iran | Eriophyidae ² | Rastegar et al. 2008 |
| wheat streak mosaic virus (WSMV) | <i>Tritimovirus</i> | <i>T. aestivum</i> , <i>A. fatua</i> L., <i>A. sativa</i> , <i>Eragrostis cilianensis</i> (All.) Janch., <i>Hordeum</i> spp., <i>Lolium rigidum</i> Gaudich., Zea mays, <i>Panicum</i> spp., <i>Tragus australianus</i> S.T. Blake | Worldwide | <i>Aceria tosichella</i> | Navia et al. 2013a |
| yellow oat grass mosaic virus (YOgMV) | <i>Tritimovirus</i> | <i>Trisetum flavescens</i> L. | Czech Republic, Hungary | Eriophyidae ² | Hassan et al. 2009; Hassan 2014; Pasztor et al. 2020 |
| triticum mosaic virus (TriMV) | <i>Poacevirus</i> | <i>Triticum aestivum</i> , several grasses | Canada, USA | <i>Aceria tosichella</i> | Byamukama et al. 2013; McMechan et al. 2014; Bennypaul et al. 2021 |
| Family Rhabdoviridae | | | | | |
| citrus chlorotic spot virus (CiCSV) | <i>Dichorhavirus</i> | Citrus sp., <i>Agave desmettiana</i> Jacob, <i>Talipariti tiliaceum</i> L. | Brazil | <i>Brevipalpus yothersi</i> | Chabi-Jesus et al. 2018, 2019 |
| citrus leprosis virus N (CiLV-N) | <i>Dichorhavirus</i> | <i>Citrus sinensis</i> Macfad. | Brazil | <i>Brevipalpus phoenicis</i> | Ramos-González et al. 2017 |
| clerodendrum chlorotic spot virus (CICSV) | <i>Dichorhavirus</i> | <i>Clerodendrum</i> spp. | Brazil | <i>Brevipalpus yothersi</i> | Kitajima et al. 2008; Ramos-González et al. 2018 |
| coffee ringspot virus (CoRSV) | <i>Dichorhavirus</i> | <i>Coffea</i> spp. | Brazil, Costa Rica | <i>Brevipalpus papayensis</i> | Rodrigues et al. 2002; Ramalho et al. 2014 |
| Cestrum ringspot virus ¹ | <i>Dichorhavirus</i> | <i>Cestrum</i> sp. | Brazil | <i>Brevipalpus obovatus</i> | Kitajima 2020 |
| orchid fleck virus (OFV) | <i>Dichorhavirus</i> | Several orchid species, <i>Alcea rosea</i> L., <i>Citrus</i> spp., <i>Cordyline fruticosa</i> (L.) Chev., <i>Dieffenbachia</i> sp., <i>Liriope spicata</i> (Thunb.) Lour., <i>Swinglea glutinosa</i> (Blanco) Merr. | Worldwide | <i>Brevipalpus californicus</i> | Kondo et al. 2006; Peng et al. 2017; Ramos-González et al. 2016b; Sauvêtre et al. 2018; Cook et al. 2019; Bratsch et al. 2021; Read et al. 2021; Olmedo Velarde et al. 2021; Otero-Colina et al. 2021 |
| Family Secoviridae | | | | | |
| blackcurrant reversion virus (BRV) | <i>Nepovirus</i> | <i>Ribes nigrum</i> L. | Europe, New Zealand | <i>Cecidophyopsis ribis</i> | CABI/EPPO 2021 |
| Family Sobemoviridae | | | | | |
| papaya lethal yellowing virus (PLYV) | <i>Sobemovirus</i> | <i>Carica papaya</i> L. | Brazil | <i>Tetranychus urticae</i> ⁵  | Loreto et al. 1983; Fernando et al. 2015 |
| Unassigned | | | | | |
| barley yellow streak mosaic virus (BaYSMV) | Unassigned | <i>Hordeum vulgare</i> | Canada, USA | <i>Petrobia latens</i> | Robertson & Carroll 1988; Smidansky & Carroll 1996; Robertson & Brumfield 2000 |

¹ tentative species² supposed to be involved an eriophyoid mite, but not looked for³ supposed to be involved an eriophyoid mite, but not proved⁴ under experimental conditions⁵ able to be acquired by *T. urticae* but not to be transmitted

Certain strains of OFV also naturally infect *Citrus* spp. (Cook et al. 2019; Olmedo Velarde et al. 2021). Citrus leprosis, originally described in Florida in the early 1900s (Fawcett 1911), disappeared after the 1960s (Childers et al. 2003c). The suspicion that it could be caused by a dichorhavirus, based on the symptoms (Kitajima et al. 2011), was supported by molecular analysis of leaf samples preserved in an herbarium (Hartung et al. 2015). The causal agent seems to be most closely related to the OFV-citrus isolate found in several *Citrus* spp. in Mexico (Roy et al. 2015). Other dichorhviruses, e.g., coffee ringspot virus (CoRSV), citrus leprosis virus N (CiLV-N), citrus chlorotic spot virus (CiCSV), clerodendrum chlorotic spot virus (ClCSV), and cestrum ringspot virus are also transmitted by *Brevipalpus* spp. and have so far been detected mainly in Brazil (Table 1).

2.3 Viruses transmitted by tetranychids

In general, the possibility of viral transmission by mites of the family Tetranychidae has been generally accepted but remains in need of experimental evaluation.

A few reports have suggested that *Tetranychus urticae* Koch is involved in transmitting viruses (Oldfield 1970; Fernando Basso et al. 2015) (Table 1). The still-unclassified barley yellow streak mosaic virus (BaYSMV) (Robertson & Brumfield 2000) was experimentally transmitted by *Petrobia latens* (Muller), likely in a persistent circulative replicative manner, with possible transovarial passage (Smidansky & Carroll 1996) (Table 1). BaYSMV particles appear to be very long (64 × up to 4,000 nm), encapsidate an ssRNA of 11–13 kb (Robertson & Carroll 1991), and occur in cavities of ER elements, resembling cytorhabdoviruses (Robertson & Carroll 1988).

3 Mites involved in virus transmission and virus-mite pathosystems

3.1 Eriophyidae

The true number of eriophyid species serving as virus vectors is unknown. Eleven species were first indicated by Stenger et al. (2018), and additional species were recently associated with the transmission of new emaraviruses (Di Bello et al. 2016; Kubota et al. 2020, 2021; Von Bargen et al. 2020) (Table 1). Eriophyids show a high degree of specificity and efficacy in the transmission of a given virus (Oldfield & Proeseler 1996). Exceptionally, *Aceria tosichella* Keifer and *Abacarus hystrix* (Nalepa) transmit viruses of more than one viral family (Navia et al. 2013a). Moreover, transmission efficiency depends on the mite biotype, as observed for *A. tosichella*, *Aceria cajani* Channabasavanna, and *A. hystrix*, as well as on the plant susceptibility and mite developmental stage (Kumar et al. 2001; Harvey et al. 2005; McMechan et al. 2014). Therefore, plant genotypes that are only slightly susceptible to the viruses can serve as reservoirs for the mite when preferred host-plant species are unavailable. Eriophyid

mites are strictly associated with the epidermal cells and parenchymatic tissues of green, watery, and soft plant organs (de Lillo et al. 2018). Particularly, feeding of virus-vector mites does not kill the pierced cells but does induce a wide range of effects (Petanović and Kielkiewicz 2010) that can positively affect viral transmission.

The cereal rust mite, *Abacarus hystrix*, is a vagrant polyphagous species of Phyllocoptinae (Skoracka et al. 2010) that inhabits the leaf lamina and prefers grooves on the adaxial (upper) side, where it feeds on the watery bulliform cells of the epidermis. These mites cause leaf discoloration, reduce seed production, and lead to withering and stunting (Frost & Ridland 1996). They transmit ryegrass mosaic virus (RGMV), mainly to perennial ryegrass (*Lolium multiflorum* Lam.), and to a wide range of pasture grasses as well (Salm et al. 1994; Webster et al. 2005), and agropyron mosaic virus (AgMV) to quackgrass (*Elymus repens* (L.) Gould) and occasionally to wheat (Oldfield & Proeseler 1996). RGMV causes mild or severe mottling and streak chlorosis, necrosis of leaves followed by ryegrass stunting, and decreased biomass yield in ryegrass (Slykhuis 1980; Heard & Chapman 1986). AgMV induces mild to severe light-green or yellow chlorosis in leaves, stunting, and yield losses in wheat (Oldfield & Proeseler 1996). The colonization rate of the cereal rust mite depends on the host-plant species and mite biotype. The varied efficiency in virus dissemination to a wide range of grasses suggests the existence of races and/or sister species (Skoracka & Dabert 2010; Laska et al. 2018). The minimum acquisition access period (AAP) for RGMV was assessed at 2 hours of feeding on infected plants, and the infectivity was lost after 24 hours (Mulligan 1960; Slykhuis 1980).

Aceria cajani is a vagrant member of Eriophyinae and infests *Cajanus cajan* (L.) Millsp., one of the most important protein sources for South Asian populations. Mites of this species also survive on the wild leguminous *Cajanus scarabaeoides* (L.) Thouras and other volunteer pigeon-pea plants (Reddy et al. 1989, 1990; Manjunatha et al. 2013). They colonise mainly the underside (abaxial side) of young leaves and the stem apices, which are well protected by dense trichomes. These mites transmit pigeon-pea sterility mosaic emaravirus (PPSMV-1 and 2) (Elbeaino et al. 2015). PPSMV-1 causes the sterility mosaic disease in pigeon-pea. Symptoms of *A. cajani* overlap those induced by PPSMV-1: stunting of branches, yellowing and hyper-proliferation of leaflets, which remain smaller, together with mosaic mottling and partially or completely sterile flowers (Seth 1962). The symptoms are more severe after early infections, usually in plants less than 45 days old. A semi-persistent mode of transmission of PPSMV-1 is suggested because of the lack of both a latent period of infectivity and transovarial transmission. The minimum AAP and the inoculation access period (IAP) were estimated as 10 and 60 minutes, respectively (Latha et al. 2004). Mite-VPPSMV-2 interactions need to be investigated.

The fig mottle mite, *Aceria ficus* (Cotte), is a vagrant species, occurring worldwide and strictly associated with *Ficus carica* L. The mite overwinters mainly in the terminal buds and tends to colonize the underside of the youngest and densely pubescent leaves, which provide good micro-environmental conditions and protection from predators (Monfreda & de Lillo 2007). The mite induces chlorosis, distortion, russetting and premature dropping of leaves as well as bud stress, and affects stem growth (Ebeling & Pence 1950; Çağlayan et al. 2012). Symptoms caused by infestations of fig mottle mite and fig mosaic emaravirus (FMV) (Table 1) can closely overlap. Fig mosaic disease is characterized by a consistent variability in symptom form and severity, which might be associated with certain fig genotypes and virus haplotypes, as well as with viral loads (Martelli et al. 2013). Virus-infected plants can show chlorotic spots or ringspots on leaves, often bordered by a rust-coloured band and vein banding. Leaves are smaller and are sometimes deformed or blistered, where the chlorosis gradually extends to veins and other foliar areas. Fruits can also show yellow mosaic spots, smaller size, and potentially early drop, and in the worst cases the tree declines. Viral acquisition is more efficient when the mites feed on terminal buds; the virus may also be transmitted by a single individual after moulting, although no transovarial transmission has been documented (Martelli et al. 2013; Proeseler 1969, 1972). A persistent-circulative transmission mode is presumed, based on the minimum AAP (5 minutes), latency (6–7 hours), and retention time (10–20 days), which seem to depend on temperature (Proeseler 1972; Martelli et al. 2013). *Aceria ficus* is likely involved in the transmission of filamentous viral particles that resemble those of the trichovirus fig latent virus 1 (FLV-1) (Table 1) (Çağlayan et al. 2012).

The wheat curl mite, *A. tosichella*, is a vagrant and refuge-seeking mite that infests a wide range of species of Poaceae worldwide and transmits a few viruses (Table 1). Mite colonization of hosts from other plant families is quite unusual. Mites that likely belong to genetically distinct lineages with uncommon host preferences are currently under molecular and biological investigation (Tatineni & Hein 2018). Some mite lineages can be generalists and colonize susceptible volunteer wheat plants and alternate host species, which can grow at the field edges, fallow fields, along roadsides, and in natural environments. These plants can offer ‘green bridge’ refuges for mites and viruses during the non-growing periods of elective host-plant species (Slykhuis 1980; Malik et al. 2003; Skoracka & Kuczyński 2006). *Aceria tosichella* inhabits mainly deep sites within leaf whorls, where micro-environmental conditions are more favourable because of the watery tissues, high humidity, and protection from predators (Orlob 1966). Dense mite populations on susceptible wheat cause yellow spotting, curling, and rolling of leaves, and occasional trapping of growing leaf tips (flag leaves) by the older unexpanded and tightly rolled leaf, lending a stunted appearance to the plant (Oldfield 1996; Richardson

et al. 2014). The effects on corn plants can be ‘distortive’ or ‘non-distortive’ depending on the infested organs and mite density. Leaves appear spotted, curled, and rolled; sweet, pop, dent, and flint corns can show reddish discolouration of the kernels, which are presumed to be induced by toxins in the injected mite saliva (Nault et al. 1967; Oldfield 1996). Streaks extend from the base of the pericarp to the crown and are red or pink/purple in the yellow and white varieties, respectively. *Aceria tosichella* can directly reduce wheat yield by up to 30% (Harvey et al. 2002), but the main injury is caused by transmission of the more severely yield-reducing wheat streak mosaic virus (WSMV) and high plains wheat mosaic emaravirus (HPWMoV), in single or mixed infections (Oldfield & Proeseler 1996; Coutts et al. 2008; Dumón et al. 2013; Richardson et al. 2014) (Table 1). The effectiveness of the mite in transmitting these viruses depends on the mite lineage (Stenger et al. 2016; Tatineni & Hein 2018). In general, infections by WSMV seem to be more severe in winter wheat infected in autumn. WSMV infection induces light-green to yellow streaks and dashes on leaves, followed by diffuse yellowing. These symptoms are associated with more or less severe stunting of the plants, which produce small, light, poorly filled seed heads and shrivelled kernels (Slykhuis 1980; Navia et al. 2013a). Infected plants have poor root development with consequently lower grain and forage yields (Velandia et al. 2010). The minimum AAP for WSMV was assessed as 15 minutes and the transmission efficiency was directly related to the feeding time of mites on viruliferous plants (Orlob 1966). The retention time was 6–9 days at 20–25°C and 61 days at 3°C (Slykhuis 1955; Orlob 1966). Virus filaments continued to be observed in the midgut 5 days after the mites were removed from the virus source, and the mite infectivity continued after moulting, suggesting a circulative mode of transmission (Orlob 1966; Paliwal 1980).

HPWMoV causes a severe disease in wheat and corn and also infects other grasses and weeds (Seifers et al. 1998) (Table 1). The symptoms of HPWMoV overlap those caused by WSMV. In wheat, initial chlorotic spotting or ring spot can evolve to wide and severe yellowing, necrosis, stunting and, sometimes, plant death (Styer & Nault 1996), whereas red striping is usual in corn. The retention time for transmission of HPWMoV was assessed as 8 days (Nault & Styer 1970; Slykhuis 1980), but no other data on the infective parameters are available. Several studies have reported seed-mediated transmission of WSMV and HPWMoV in wheat, corn, and other grass species, although at low rates (0.07–1.5%) (Jones et al. 2005; Sagadin & Truol 2006, 2008; Lanoiselet et al. 2008). This pathway is important in virus-free areas, where once introduced, the virus could be further spread by its vector.

Symptoms caused by triticum mosaic virus (TriMV) overlap those caused by WSMV and include streaking or striped leaf yellowing along with stunting when wheat is infected early in the season (Bockus et al. 2010). Mixed

TriMV-WSMV infections may induce synergic effects in wheat, causing severe leaf deformations, bleaching, and stunting (Tatineni et al. 2019). TriMV-infected plants hamper the reproduction of *A. tosichella*, likely indicating a short co-evolutionary path between mite and virus. The low rate of mite reproduction is a consequence, for instance, of lower nutritional quality of the host or an increase in the production of secondary plant metabolites, with detrimental effects to the mite (McMechan et al. 2014).

Finally, brome streak mosaic virus (BrSMV) has been detected in some grasses, causing chlorotic leaf streaks (Navia et al. 2013a) (Table 1).

The dry bulb mite, *Aceria tulipae* (Keifer), is a refuge-seeking mite, infesting bulbous plants such as garlic, onion, shallot, tulip, leek, and other species of Alliaceae and Liliaceae. *Aceria tulipae* was proposed to be a complex of species, meaning that its biology, behaviour, induced symptoms, and virus relationships require careful revision (Perring 1996; Skoracka et al. 2014). In the past, *A. tulipae* was considered a synonym of *A. tosichella*, contributing to a misunderstanding of the mite-plant relationships. *Aceria tulipae* feeds on the scales and leaves of fleshy bulbs, causing their collapse and scarification of the bract surface. Infestation of garlic bulbs may reduce emergence by up to 20% and yield by up to 23% (Larrain 1986). *Aceria tulipae* has been related to viruses (including the former onion mite-borne latent virus and shallot mite-borne latent virus) (Table 1), whose accumulation in tissues is favoured by the vegetative propagation of garlic. The symptoms of new vegetation of *Allium* species resemble those of garlic virus (GarV) infections and consist of stunted, twisted, and discoloured leaves and stems. Typical symptoms of infection by garlic virus (GarV), shallot virus X (ShVX), and garlic mite-borne filamentous virus (GarMbFV) in garlic plants consist of retarded growth, curled yellow-strip mosaic, and distortion of leaves, and the severity of symptoms is associated with the presence of the mites (Kang et al. 2007), although infections by ShVX can be asymptomatic (*cf.* Ostojca Strazewski & Matthews 2009).

Cecidophyopsis species have been suggested to transmit black currant reversion virus (BRV) (Table 1) (Lemmetty et al. 2004). The black currant bud mite or big bud mite, *Cecidophyopsis ribis* (Westwood), is a gall-making member of Cecidophyinae that causes serious infestations in black currant. The mite is bud-confined for most of the year and migrates from dried-brown buds to newly formed buds in early spring to early summer, mainly around the blossoming time (de Lillo & Duso 1996). In black currant, *Cecidophyopsis ribis* causes galling mainly of basal and apical cane buds, which become ovoid to spherical. The mite induces retardation of bud growth, development of asymmetrical and malformed leaves from infested buds, drying of the buds in spring, and loss of fruit yield (de Lillo & Duso 1996). The virus causes a reversion of the plant to its wild phenotype, inducing several symptoms: fewer, smaller, and distorted leaves with tiny marginal serrations, fewer main veins, and

less clearly defined sines at the petioles; flower buds that are markedly less hairy and more intensely coloured in spring; fewer, smaller and abnormal fruits; and blossom drop before fruit production. This syndrome is linked to an increase in plant susceptibility to mite infestation (Thresh 1964, 1967). The involvement of *C. ribis* in transmitting BRV was proved by transferring mites from symptomatic plants to healthy ones after the mites fed for about 4 days (Thresh 1963). The minimum AAP was assessed as 3–4 hours (optimum of about 50 hours) and the retention period was calculated as 25 days (Jacob 1976). These data indicate a semi-persistent transmission mode. Other species of *Cecidophyopsis*, morphologically similar to *C. ribis*, were found on other *Ribes* spp., and symptoms of reversion disease were recognized also in *Ribes alpinum* L. and *R. spicatum* Robson (Bremer & Heikinheimo 1980).

Colomerus vitis (Pagenstecher) is a gall-making member of Cecidophyinae. It occurs worldwide and causes varying degrees of harm in grape-growing regions, depending on the grapevine cultivars, environmental conditions, and mite density and strain (Javedi Khederi et al. 2014, 2018a, 2018b). Three strains are distinguished based on the symptoms induced: bud strain, leaf erineum strain (the most common grapevine erineum mite, GEM), and the leaf curl strain (Smith & Stafford 1948). The most evident symptom induced by GEM is the development of white felt-like patches (erineum) that later change to brown, usually on the abaxial (lower) surface of leaves, which appear blister-like on the adaxial surface. GEM also affects the amount of chlorophyll in leaves, weight and size of leaves, length of canes, amount of sugar in grapes, and yield (Avgin & Bahadiroğlu 2004; Javedi Khederi et al. 2014, 2018a, 2018b). Kunugi et al. (2000) demonstrated that GEM is involved in transmission of grapevine berry inner necrosis virus (GINV) (Table 1), through field trials with net-confined potted plants to which potential vectors were applied. GINV induces a delay in bud breaking, shortening internodes, plant weakening, and sparse growth, discoloured leaves with wide chlorotic line, ring and zigzag patterns, inner necrosis in young shoots and berries, delay in ripening, and small berries (Yoshikawa et al. 1997). GINV seems to be limited to some areas in Japan and China (Fan et al. 2016a, b). The genetic closeness between grapevine pinot gris virus (GPGV) (Table 1) and GINV led to investigation of the involvement of GEM in transmitting GPGV (Malagnini et al. 2016). GPGV is responsible for chlorotic mottling, crumpling and deformation of leaves, stunting of plants, and loss of grape quality and yield (Martelli 2014). Laboratory assays suggested a minimum of 24 hours for both AAP and IAP (Valenzano, pers. comm.).

Eriophyes inaequalis Wilson & Oldfield is a refuge-seeking and galling member of Eriophyinae. It inhabits the lateral buds of wild bitter cherry, *Prunus emarginata* (Douglas), and moves from dried buds to new ones in early summer. The mite induces swelling of buds, which turn reddish and then burst, producing retarded shoots. It transmits the cherry

mottle leaf virus (ChMLV) in sweet and wild bitter cherries, and in peach, where it is symptomless (Table 1) (Oldfield 1970; James & Mukerji 1993). The mite reproduces only in the swollen buds of *P. emarginata*, where it can develop dense populations. Although the transmission of ChMLV to sweet cherry and peach by mites has been observed in laboratory conditions, vectoring of ChMLV in these stone-fruit trees and in apricot might be performed in the field by another, unknown vector, especially in areas where *P. emarginata* is absent (Hansen 1978; Oldfield & Proeseler 1996). The mite has never been collected in sweet cherry orchards infected by ChMLV. Symptoms of ChMLV consist of irregular chlorotic mottling, edge tattering, and reduction in the size of leaves, particularly the youngest leaves, while the fruits appear normal but tend to lack flavour and often ripen late (Oldfield & Proeseler 1996). Some cherry cultivars can also show shortening of internodes.

Eriophyes insidiosus Keifer & Wilson is a refuge-seeking mite inhabiting the buds of commercial and ornamental peach, nectarine, and wild species of *Prunus* (Keifer & Wilson 1956; Gispert et al. 1998). The mite is protected beneath the bud scales and its population is barely exposed on the young leaf surface of new blossoms. *Eriophyes insidiosus* feeds on bud tissue and causes bud swelling and twisting, delay in blossoming of peach, and/or, more severely, only partial opening of buds, which fail to develop leaves or shoots. This mite was found to transmit the peach mosaic virus (PcMV) to ornamental and commercial peach trees (Table 1) (Wilson et al. 1955; Oldfield & Proeseler 1996). PcMV can induce vein and leaf chlorosis, smaller and deformed leaves, colour breaking and deformation of petals, discolouration of blossoms, fruit deformities, dwarfing, and rosetting of stems and twigs (Gispert et al. 1998). Gispert et al. (1998) demonstrated that a single mite is sufficient to transmit PcMV. The virus requires a minimum IAP of 6 hours with about 10 mites, even though the infested-infected plant samples and mite specimens were cold-stored (4°C) for 11 days, and a minimum AAP of 3 days with 5–10 mites, while infectivity increased within 5 days of acquisition. Wilson et al. (1955) demonstrated that the mite is not able to transmit the virus transovarially.

The pear leaf blister mite, *Eriophyes pyri* (Pagenstecher), is a galling species. It has been reported on several species of Pomoidea, raising the question of whether sister species exist under the same name (Easterbrook 1996). The *Eriophyes pyri* blister strain affects mostly leaves, in which coloured spots progressively develop on blisters. These deformations of the leaf lamina contain large lacunae in the mesophyll and formed by intercellular spaces in which the mites live. Necrosis can gradually appear from the borders of these lacunae and extend through the entire blister, which becomes a dark-brown area (Easterbrook 1996). *Eriophyes pyri* (site) is suspected to be the vector of European mountain ash ringspot-associated emaravirus (EMARaV) in *Sorbus aucuparia* L. in Norway (Table 1) (von Barga et al. 2014). This

virus was identified as the causal agent of a ringspot disease characterised by leaf mottling and ringspots (Mielke-Ehret & Mühlbach 2007; Mielke-Ehret et al. 2010). Nucleocapsid protein P3 and the viral genomic and antigenomic forms of the viral RNA3 were detected in the body of the mite, using immunofluorescence microscopy and reverse transcriptase-polymerase chain reaction (RT-PCR) assays (Mielke-Ehret et al. 2010).

The bud and fruit mite of the wild rose, *Phyllocoptes fructiphilus* Keifer, is a refuge-seeking species of Phyllocoptinae (Diakaki et al. 2019). It is commonly found in the youngest tissues of roses, in the angles between leaf petioles and axillary buds during the growing season and under bud scales during winter and spring (Allington et al. 1968). The rose rosette disease (RRD) was detected in numerous cultivated, wild, native, and introduced rose species (Vazquez-Iglesias et al. 2020) in the western and central USA and Canada (Manitoba). The mite was considered of interest because of its potential as a biological control agent against wild multiflora rose, as well as its economic impact on ornamental roses (Amrine et al. 1988; Amrine 1996). Recently, rose rosette emaravirus (RRV), the causal agent of RRD, was detected in India, although the mite vector could not be determined (Chakraborty et al. 2017). *Phyllocoptes fructiphilus* can efficiently transmit the virus to rose species and multiflora roses (Table 1) only when feeding on rapidly growing plant organs, which are more sensitive to the mite and more receptive to the virus (*cf.* Vazquez-Iglesias et al. 2020). Infected multiflora roses can show smaller, wrinkled, and deformed leaves that become reddish on part of or the entire surface and the veins, and often assume a rosette appearance, as well as reduced flowering (Doudrick 1983). Infected plants show premature breaking of axillary buds, with the development of stunted, shorter, and thicker secondary shoots, assuming a witches' broom or rosette appearance, especially on the terminal part, or causing dwarfism of young plants (Allington 1968; Doudrick 1983). Usually, RRD plants require about 3–5 years to fully decline. Symptoms in other rose species can differ slightly with respect to leaf mottling, shoot development, and thorn density (Allington 1968), and their sensitivity to RRD varies widely depending on the genotype (Amrine 2002). Di Bello et al. (2018) demonstrated that the mite must feed for at least 5 days on virus-infected roses before transmitting the virus, whereas the minimum IAP was 1 hour, and the virus infectivity increased within 14 days of inoculation.

The raspberry leaf and bud mite, *Phyllocoptes gracilis* Nalepa, is a refuge-seeking species. It causes the most severe symptoms on raspberry and blackberry, but can also infest dewberry and other closely related species. This mite has been associated with raspberry leaf blotch disorder (RLBD). The symptoms of mite infestation and viral disease overlap and consist of yellow blotching and development of necrotic patches on leaves, abnormal leaf-hair development on the abaxial surface and a pale-green appearance, as well

as twisted and distorted margins of the lamina (Gordon & Taylor 1976). Also, the growing tip of raspberry canes as well as the plant growth and development can be affected, along with irregular ripening and poor quality of fruits. The raspberry leaf blotch emaravirus (RLBV) (Table 1) was identified in symptomatic raspberry plants and in the mite body by RT-PCR (McGavin et al. 2012; Tartanus et al. 2015). Although transmission assays are needed, preliminary observations have suggested that *P. gracilis* is likely involved in virus transmission.

Still-undescribed or unidentified eriophyid species have been associated with some additional viruses (Table 1). This is the case for *Shevchenkella* sp., a vagrant member of Phyllocoptinae, which transmits perilla mosaic emaravirus (PerMV) (Kubota et al. 2020). The mite causes rust symptoms in *Perilla frutescens* var. *crispa* (Thunb.) when it proliferates at a high density, whereas the virus induces severe mosaic and deformations of leaves. Laboratory assays ascertained that the virus could be acquired after at least 30 minutes of feeding on infected leaves, and no transovarial transmission occurred. A second unknown eriophyid species was shown to transmit blackberry leaf mottle associated emaravirus (BLMaV) to blackberry (Hassan et al. 2017), and a third species transmits redbud yellow ringspot-associated emaravirus (RYRaV) to *Cercis* plants (Di Bello et al. 2016). A few other eriophyid mites are merely presumed to be involved in virus transmission (Table 1) (Zheng et al. 2017; Buzcan et al. 2019; Kubota et al. 2021) but no evidence of this role has been provided until now and these hypotheses stem from the similarity of these viruses to other ETVs.

3.2 Tenuipalpidae

Of the 292 known valid species of *Brevipalpus* (Castro et al. 2020), only *Brevipalpus californicus* (Banks), *B. obovatus*, and *B. phoenicis* (Geijskes) were recognized as vectors of plant viruses before 2015 (Childers et al. 2003a; Beard et al. 2015). Several incongruences between molecular and morphological data suggested the presence of cryptic diversity within *Brevipalpus*, which was later confirmed by the revision of *B. phoenicis* (Rodrigues et al. 2004; Navia et al. 2013b; Beard et al. 2015). Morphological characteristics historically used for the identification of tenuipalpid species, such as dorsal and ventral patterns, design of microplates, and size and shape of spermathecae, were analysed, and *B. phoenicis sensu lato* was split into *B. phoenicis sensu stricto*, *B. azores* Beard & Ochoa, *B. feresi* Beard & Ochoa, *B. feraguti* Ochoa & Beard, *B. hondurani* Evans, *B. papayensis* Baker, *B. tucuman* Beard & Ochoa, and *B. yothersi* Baker (Beard et al. 2015). This new arrangement was also supported by mitochondrial (COI) and nuclear (28S gene) markers (Alves et al. 2019). Similar work is being carried out with *B. californicus*, *B. obovatus*, and *B. yothersi* (R. Ochoa, J. Beard, ADT, pers. comm.). As a consequence, the adjustment of these taxa has generated many questions regarding the virus-vector-host associations (Table 1) and led to

the need for further revision of BTV-vector relationships, as already begun with several experiments summarized by Tassi et al. (2019).

Brevipalpus species commonly infest several plant species belonging to different families. Childers et al. (2003b) listed nearly 1,000 species of host plants for *B. californicus*, *B. obovatus*, and *B. phoenicis*. In many instances, a single plant species may be co-infested by more than one *Brevipalpus* species, with densities depending on the season (ADT, personal observations). *Brevipalpus* mites infest mainly the abaxial surface of the leaves, twigs, flowers, and fruits. Mite species that transmit viruses reproduce by thelytokous parthenogenesis and were found to be feminised if infected by the endosymbiont '*Candidatus Cardinium*' (Weeks et al. 2001), which invades most of the mite's organs (Kitajima et al. 2007). Males are rare and seem to be sterile, although they behave actively in copulation. High infestations are rare, but when they occur may result in silvery-white areas, chlorosis, bronzing, blistering or necrotic areas on leaves, premature leaf and fruit drop, necrotic lesions on branches and twigs, and formation of roughness, russetting and cracking on fruits (Childers et al. 2003a, 2003b). The diseases caused by BTVs result in localised lesions on leaves, fruits, and stems (Kitajima et al. 2010). Symptoms include ring, necrotic, and green spots on green and/or senescent leaves; chlorotic and/or necrotic spots on stems; chlorotic or brown spots on fruits, along with premature drop; brown spots on flowers; and a high incidence of dieback in citrus trees (Childers et al. 2003a; Kitajima et al. 2003a).

Brevipalpus yothersi is widely spread and transmits the largest number of known BTVs (Table 1) (Kitajima et al. 1997, 2003; Roy et al. 2015; Ramos-González et al. 2017, 2018, 2020; Ferreira et al. 2020). The replication of these viruses in the vectors has not been ascertained, though some evidence indicates a persistent-circulative type of virus-vector relationship for the cileviruses (Kitajima & Alberti 2014). All active instars of *B. yothersi* can acquire and inoculate CiLV-C: the inoculation access period was estimated as 2 hours and the acquisition access period as 4 hours, the transmission efficiency ranged from 25% to 60%, and no transovarial transmission was observed (Tassi et al. 2017). A persistent-circulative-replicative transmission mode is suggested for the dichorhavirus CICSV to *Clerodendrum* spp. (Ramos-González et al. 2018). Preliminary evidence based on transmission experiments shows that the ability of *B. yothersi* to transmit these different viruses seems to depend on still-unassessed peculiarities of the mite populations (ADT, personal observations). A mixture of *B. yothersi* and its close relative *Brevipalpus* aff. *yothersi* (a new species under description) was found on infected sweet orange trees showing leprosis-type symptoms in Piauí, Brazil. The disease was caused by citrus chlorotic spot dichorhavirus (CiCSV) (Table 1) (Chabi-Jesus et al. 2018), which was also found infecting beach hibiscus (*Talipariti tiliaceum* (L.)) and

agave (*Agave desmettiana* Jacobi) plants (Chabi-Jesus et al. 2019).

Brevipalpus phoenicis s.s. was identified as a vector of citrus leprosis virus N (CiLV-N), a dichorhavirus involved in the citrus leprosis syndrome, which was found infecting backyard orange plants in cooler climates, at higher-altitude sites in the state of São Paulo (Ramos-González et al. 2017). No data on the virus-vector relationship have been reported.

Initial studies on mite transmission of the coffee ringspot dichorhavirus (CoRSV) identified *B. phoenicis* as its vector (Chagas 1978), but a taxonomic re-evaluation of *Brevipalpus* (Beard et al. 2015) and experimental assays have indicated that *B. papayensis* was the actual vector (Table 1) (Nunes et al. 2018). This species also transmitted CiLV-C under experimental conditions, although with low efficiency (Nunes et al. 2018). A persistent replicative transmission mode is suggested for CoRSV, based on electron microscopy observations of cytopathic effects in the mite tissues (Kitajima & Alberti 2014). Under experimental conditions, transmission efficiency was about 24% for adult females; no transovarial transmission was observed (Chagas et al. 2003).

Knorr (1968) first reported *B. californicus* as a vector of BTV, after a successful transmission of the causal agent of citrus leprosis in Florida. Later, *B. californicus* was found to vector OFV between orchids in Japan (Maeda et al. 1998) and between *Citrus* species in Mexico and Colombia (Table 1) (Roy et al. 2015; Garcia-Escamilla et al. 2018). *Brevipalpus californicus* was also associated with an outbreak of leprosis symptoms in navel sweet orange orchards in South Africa (Cook et al. 2019). A long latent period, no transmission by immatures, retention of infectivity for three weeks in a virus-immune host, and cytopathic effects on mite tissues similar to those observed in OFV-infected plant cells suggested a persistent propagative transmission (Kondo et al. 2003; Kitajima & Alberti 2014).

Brevipalpus obovatus was the first tenuipalpid associated with BTV (Frezzi 1940) and was used to experimentally transmit the causal agent of citrus leprosis (Knorr 1968). According to recent surveys, this mite is rarely found on citrus in Argentina, in contrast to *B. yothersi*, which is prevalent (Cáceres et al. 2013). The tentative cilevirus, SvRSV (Ferreira et al. 2007), and the tentative dichorhavirus, *Cestrum* ringspot virus (Guidotti et al. 2006) are also transmitted by *B. obovatus*, but no data on virus-vector relationships have been reported (Table 1).

4 Mode of virus transmission, methods of study, and related weak points

The interactions between mites and transmitted plant viruses are highly specific, necessitating complex and integrated laboratory and greenhouse experiments to explain them. The mode of transmission of almost all mite-borne viruses is unknown. This is due mainly to the tiny size of the mites and

difficulties in their manipulation, colony establishment, and management as a consequence of unsuitable food, micro-environmental conditions, predators, etc. (Stenger et al. 2016). A ready and constant supply of virus-free mites is needed to conduct assays determining pathways and parameters of transmission (Gispert et al. 1997). An exception is the pathosystem composed of *A. tosichella* and WSMV: the transmission mode of this ETV is better understood than the others, mainly because of the relative ease in managing annual wheat test plants, mite populations, and WSMV transmission (Skare et al. 2003; Tatineni & Hein 2018).

4.1 Transmission trials: how to transfer mites

Transmission trials are carried out by transferring individual or several mites from infected plants, or their parts, to healthy ones, usually seedlings. Mites can be transferred by coiling, clipping, or apposing pieces of infected plant organs (usually leaves) infested by mites to the test seedlings. The mites tend to move to the receptive healthy plants as the detached donor pieces dry, making them inhospitable. This protocol, less stressful for both mites and operators, can also be used for non-mechanically transmitted viruses but does not allow assessment of AAP, IAP, or the minimum population density for infection (Çaglayan et al. 2009, 2010).

A more stressful procedure involves transfer of single mites from infected to healthy plants or leaf discs. This protocol is a necessarily microscope-assisted procedure to check for successful transfer of the mites. It is largely operator-dependent and necessitates manipulating the mite with a needle, eyelash, or fine brush. This procedure allows a confident evaluation of AAP and IAP as well as the population density needed for plant inoculation, and drastically reduces the risk of mechanical transmission of the virus during the mite handling (Gispert et al. 1997, 1998; Tassi et al. 2017).

Another protocol consists of transferring the mite by blowing it from infested-infected sources toward healthy target plants inside a protected and confined space such as a cabinet, screen-house, or greenhouse. This protocol is certainly less stressful for the operators but not for the mites, which might be exposed to the wind and be passively dispersed over a short distance. It does not allow contact between healthy and infected plants or the assessment of AAP, IAP, and minimum population density. This protocol was used to determine the involvement of *A. hystrix* in transmitting AgMV (Slykhuis 1969; Catherall & Chamberlain 1975).

An important step in mite-transmission experiments is the development and rearing of lines formed from a single individual (isolines) of a given species or population. Although arduous for eriophyid mites, it is potentially feasible (de Lillo & Skoracka 2010), especially for species related to Poaceae (Karpicka-Ignatowska et al. 2019; Laska et al. 2019). Isolines of a few species of *Brevipalpus* were developed on plants of common bean (*Phaseolus vulgaris* L.) (Groot 2006). Isolines of *B. yothersi* have been main-

tained on orange fruits or leaves of jack bean (*Canavalia ensiformis* (L.) DC.) in Brazil. These mites have been used for experimental transmission of CiLV-C (Arena et al. 2016, 2018, 2020; Ramos-González et al. 2016a) and other BTVs (M.A. Nunes, V.M. Novelli, and ADT, pers. comm.). Colonies of *B. papayensis* and *B. obovatus* have been maintained on detached leaves of coffee (*Coffea arabica* L.) and *S. violifolium* for transmission assays of CoRSV and SvRSV, respectively (Ferreira et al. 2007; Nunes et al. 2018).

4.2 Transmission trials: where mites must be transferred

Feeding of eriophyid mites can influence the physiology and morphology of the pierced plant organs. The alterations induced by refuge-seeking and gall-making species are the result of intimate and specific reactions of the plant tissues to certain salivary chemicals injected into the wounds and of the plant defense mechanisms triggered upon piercing (de Lillo et al. 2018). This means that the successful, stable plant colonization by the mites depends on the presence of suitable organs of the host plant to be infested. Consequently, the selection of plant parts to which mites are to be transferred during transmission assays is crucial to allow the mites to establish, and the transfer must be done at the time when the plant organs are most receptive. For example, successful transmission of PcMV by *E. insidiosus* occurs only in buds (Gispert et al. 1997, 1998). However, mite probing on discs of mature leaves is useful in ETV trials and allows virus transmission in the laboratory, as recently observed for GPGV transmitted by *C. vitis* (DV, personal observations). Finally, it has been observed that cold storage of viruliferous mites on infected plant samples for 11 (*E. insidiosus*, by Gispert et al. 1998) and 61 days (*Aceria tosichella*, by Orlob 1966) did not reduce the transmission rate, which can allow storage and prolonged use of mites.

Brevipalpus species are less critical in transferring trials, due to their wide range of host-plant species and their lower requirements for specific states of plant tissue. In BTV transmission trials, single individuals or groups of mites, after accessing the source of the virus, are then transferred to leaves. If infection occurs, local lesions are produced around the feeding sites. *Brevipalpus* mites can be also transferred to fruits, twigs, and flowers, or to leaves of potted plants. Alternatively, leaves can be removed and kept with the abaxial surface upwards on moistened filter paper. Experiments with CiLV-C using common bean resulted in the appearance of small necrotic lesions about 5 days after inoculation, much faster than on sweet orange leaves, in which the initial chlorotic lesions appeared only after 3 weeks (Garita et al. 2013).

4.3 Transmission mode: involved mite instars

ETVs are not known to have been transmitted by neonate larvae. This excludes transovarial transmission, whereas

transtadial transmission is well documented (Slykhuis 1955, 1980; del Rosario & Sill 1965; Orlob 1966; Oldfield 1970; Gispert et al. 1998; Oldfield & Proeseler 1996). The vectoring efficiency may depend on the mite life stage and may be higher in adults than in immatures (Gispert et al. 1998). Transmission of viruses may be inefficient when the mite acquires and transmits them as an adult (Slykhuis 1955; Del Rosario & Sill 1965; Orlob 1966). WSMV vectoring appeared to be unaffected by moulting of *A. tosichella* immatures, suggesting that it was not internalized on the intima cuticle-like surfaces (Orlob 1966). McMechan et al. (2014) provided further support for this hypothesis, demonstrating that TriMV can be transmitted by moulted individuals of *A. tosichella* transferred at the quiescent stage on the host plant.

The instars of species of *Brevipalpus* can be identified with a stereomicroscope. Although the instars can be manipulated, the larvae and nymphs are highly delicate and require special care in manipulation. All developmental stages of these mites (larva, proto- and deutonymph, and adult female and male) transmit CiLV-C, although no transovarial passage of this virus has been recorded (Tassi et al. 2017).

4.4 Transmission mode: virus internalisation

Studies of the entry of plant viruses into their vectors are essential to understand the pathway of translocation of the virus into the vector body and its mode of transmission (non-persistent, semi-persistent, persistent, circulative non-propagative, or circulative propagative).

By means of the current diagnostic molecular procedures, the presence of virus particles around the mouthparts of the eriophyids or inside their body can be easily established. In these cases, a positive response may merely indicate uptake of the cell sap containing the virus that is not yet ingested or promptly degraded by digestive enzymes, as observed by Paliwal (1980) for WSMV in the midgut of *A. hystrix* and for barley stripe mosaic virus (BSMV) in *A. tosichella*. How and where the viruses are internalized is not understood. Some studies on ETVs have documented that WSMV persists in the mite gut for several days and that the virus is present in the hemocoel and salivary glands (Slykhuis 1955; del Rosario & Sill 1965; Orlob 1966; Paliwal & Slykhuis 1967; Stein-Margolina et al. 1969; Paliwal 1980). Sinha & Paliwal (1976) detected the virus in body fluids, using an antigen, although Mahmood et al. (1997) failed to detect viruses by immunofluorescence and dot-immunobinding assays. Orlob (1966) artificially inoculated WSMV into plants by using homogenates of viruliferous *A. tosichella*, but no positive infection resulted from mechanical inoculation of homogenates of non-vector species such as *Aculodes mckenziei* (Keifer) and *A. hystrix* that had been reared on WSMV-infected leaves. Taken together, these data partially support the hypothesis advanced by Takahashi and Orlob (1969) that the *A. tosichella*-WSMV relationship is circulative and that the virus might be transmitted via saliva into the plant, even

though there is no direct evidence (Paliwal 1980). Because BSMV was also detected in the hemocoel and gut of *A. tosi-chella*, but not in the salivary glands, and the mite was unable to transmit this virus, Paliwal (1980) concluded that the virus was unable to pass through the salivary-gland barriers of the mite. Finally, nothing is known about the process used by putatively circulative ETVs in crossing cell barriers during their translocation from the mite gut to the salivary glands.

Transmission electron microscopy of viruliferous *Brevipalpus* mites detected cileviruses and dichorhaviruses in their tissues (Kitajima & Alberti 2014). Virions of CiLV-C were consistently found between membranes of adjacent cells of the midgut epithelium, anterior prosomal glands, muscles, and epidermis in the prosoma, but not in the cytoplasm. Also, the viroplasms seen in the cytoplasm of infected plant cells could not be found in the mite tissues. These observations seem to be consistent with a virus-vector relationship of the persistent-circulative type. This hypothesis is further supported by the short latent period (7 hours) of CiLV-C in the vector and by the short acquisition and inoculation periods (2–4 hours) of larvae and protonymphs (Tassi et al. 2017). In contrast, ultrastructural observations of *Brevipalpus* transmitting dichorhaviruses provided shreds of evidence that the viruses replicate in the midgut epithelium and anterior prosomal gland cells. Nuclei of these cells contained electron-lucent viroplasm, and rod-like particles were abundant in both the nucleoplasm and cytoplasm, as observed in cells of the plant leaf lesions. Viral replication in mites is consistent with the information that the latent period of OFV in the vector *B. californicus* extends up to 10 days (Kondo et al. 2003).

The mechanism by which cileviruses reach the intercellular space is unknown, and a paracellular route is suspected. It is hypothesised that septate junctions, formed by a complex of transmembrane proteins that keep the epithelial cells tightly together, could open temporarily, leaving a narrow extracellular passage for virions. This mechanism could involve epithelial-cell membrane receptors and viral-membrane glycoproteins in both the midgut lumen and the apical part of the anterior prosomal glands. This process would permit cileviruses to move from the midgut lumen to the median salivary duct and up to the interchelicer channel, and then be injected into the plant cell together with saliva. For dichorhaviruses, the internalization of virions may involve endocytosis. Both para- and intracellular routes require the mediation of putative cell surface receptors that recognize the virions. Analysis of the recently obtained *B. yothersi* genome sequence (Navia et al. 2019) may contribute to clarifying the mechanisms involved in virus internalization.

4.5 Transmission mode: plant tissues/organs pierced by mites and infected by viruses

The main animal vectors of plant viruses (aphids, hoppers, whiteflies, and nematodes) have long and, in some cases,

flexible stylets that allow these animals to feed on vascular tissues of plants.

The short cheliceral stylets (commonly 20–30 μm long) of eriophyid mites enable them to feed mainly on epidermal cells of plants (Oldfield 1996; de Lillo et al. 2002). In many eriophyid species, these cells remain viable as the cell contents are ingested (Petanović & Kielkiewicz 2010). Through this means, the eriophyids successfully acquire the disease agents and inoculate them into the most superficial tissues of leaves, buds, and other green organs, preferably soft watery tissues, as evidenced by microscopic analysis of *C. ribis* (Jones 2000). This suggests that these agents might also be experimentally transmitted by mechanical inoculation of sap extracts and that the mode of transmission by eriophyid mites may be non-persistent or semi-persistent (Jones 2000). In agreement with this suggestion, PPSMV and FMV could be mechanically transmitted to *Nicotiana clevelandii* Gray, *N. benthamiana* Domin, and *Chenopodium quinoa* Willd. (Kumar et al. 2003; Serrano et al. 2004), even though some information may indicate a persistent (circulative) mode for certain other viruses (Jones 1999; Gray & Banerjee 1999).

Species of *Brevipalpus* have relatively short stylets, around 50 μm long (de Lillo et al. 2002; Alberti & Kitajima 2014), that cannot reach the plant vascular bundles. *Brevipalpus* stylets pierce the epidermis and adjoining parenchymal cells of leaves, stems, fruits, and flowers. After the stylet reaches the desired cell, the mite injects saliva, possibly initiating pre-digestion, and BTVs would be injected together with the saliva. Because the interchelicer channel is not connected to the digestive duct (de Lillo et al. 2002; Alberti & Kitajima 2014), the mite withdraws its stylet after initially piercing the plant, maintaining the infracapitular tip firmly around the remaining opening. The cell contents would be passively expelled by cell turgor and also be actively ingested by the action of the pharyngeal pump (Alberti & Kitajima 2014).

4.6 Transmission mode: protocols for virus detection in mites

Viruses in mite tissues (eriophyids and *Brevipalpus* spp.) are usually detected by means of a reverse-transcriptase reaction (RT) followed by a PCR or real-time PCR (RT-qPCR) and sequencing (Mielke-Ehret et al. 2010; Çaglayan et al. 2012; Lommen et al. 2012; Ramos-González et al. 2017, 2018, 2020).

Extraction of viral RNA could require a specialized procedure (Druciarek et al. 2019), depending on the characteristics of both the mite and virus; it is possible to detect the virus in a single individual (ADT and DV, pers. comm.). Viruses can also be detected by using a virus-specific antibody conjugated with a fluorescent dye in crude mite homogenates (Sinha & Paliwal 1976), and by analysis of protein extracts from mite homogenates, using immunosorbent electron microscopy (ISEM) and a specific antiserum (Kang et al. 2007). Immunofluorescence microscopy along

with confocal laser scanning have been used for whole mites. The accumulation of putative EMARaV N-protein P3 was detected in the body of *E. pyri* after the mite fed on EMARaV-infected *S. aucuparia* (Mielke-Ehret et al. 2010). This procedure appears promising, although the results may be inconclusive because several tissues and organs of mites may be naturally fluorescent and the mite anatomy may be inadequately identified. The subcellular localization of the virus inside the mite body has been successfully assessed through transmission electron microscopy, which is a time-consuming procedure (Paliwal 1980; Kitajima & Alberti 2014). Besides virions, transmission helper factors involved in the retention of WSMV have been detected in mite bodies (Tatineni et al. 2018).

5 Final remarks (future directions and perspectives)

Knowledge of mite-plant virus pathosystems has far advanced since the most recent reviews dealing with eriophyid (Oldfield & Proeseler 1996; Stenger et al. 2018) and *Brevipalpus* mites (Beard et al. 2015; Dietzgen et al. 2018; Freitas-Astúa et al. 2018). With the development of novel and more sensitive biomolecular tools and protocols, new mite-borne viruses or viruses presumed to be transmitted by mites have been discovered and characterized (Table 1) (Roy et al. 2013, 2015; Hassan et al. 2017; Ramos-González et al. 2017, 2018; Zheng et al. 2017; Chabi-Jesus et al. 2018; Buzkan et al. 2019; Olmedo-Velarde et al. 2019; Kubota et al. 2020). Notably, despite the use of innovative biotechnologies, the mere detection of a virus in the body of a mite must be carefully analysed rather than taken as a direct validation of vectorial activity. Positive results may indicate the presence of viral genomes, viral transcripts, or partially degraded viral genomes in undigested food in the digestive tract.

Mite transmission of viruses is often species-specific (Oldfield & Proeseler 1996; Hogenhout et al. 2008), and therefore accurate identification of the mite species is vital to understand the spread of mite-transmitted viruses. In some cases, accurate mite identification may be challenging due to the existence of cryptic speciation. Misidentification of species hidden within cryptic complexes may lead to inappropriate diagnoses of pests and pathogens (Bickford et al. 2007). Characterization of the mite species transmitting a virus is crucial to define the bio-ecology of the mite and its epidemiological impact. Potential sibling species, such as those in *A. hystrix*, *A. tosichella*, *A. tulipae*, *C. ribis*, *C. vitis*, and *E. pyri*, among eriophyids, as well as in *B. californicus*, *B. phoenicis*, *B. yothersi*, and *B. obovatus*, among flat mites, can hide smaller but divergent pathosystems. Essentially, morphological and genetic characterization of complexes of multiple lineages and identification of their primary and elective host-plant species could help to understand, for

instance, the true dimensions of a given mite-virus pathosystem, the need for new research projects on mite biology, and the implementation of more effective control measures. In parallel, better comprehension of virus populations, e.g., symptomatic and asymptomatic GPGV, may contribute to identifying viral lineages involved in the development of distinct pathosystems.

The role of some mite life strategies, i.e. deutogyny in the eriophyid mites, in the efficiency and other aspects of virus transmission have not been adequately investigated. Also, the ecological relationships between mite vectors, the pathogens that they transmit, and their hosts are still poorly understood for most pathosystems involving mites. Although some hints are available, the contribution of the mite-virus symbiosis to the fitness of both eriophyids and tenuipalpids needs to be further evaluated (Freitas-Astúa et al. 2018). Likewise, the responses of mites to virus-infected plants and the potential changes in the biology of mites on virus-infected plants have not been fully investigated. The mites may gain certain advantages, such as in the cases of *A. cajani* and *P. fructiphilus*, which develop denser and more persistent populations on PPSMV- and RRV-infected plants, respectively (Epstein & Hill 1999; Jones et al. 2004; Solo et al. 2019). Another example is *A. tosichella*, which increases in fecundity when feeding on WSMV-infected plants (Murugan et al. 2011). In the case of the citrus leprosis pathosystem, the interaction between CiLV-C and *B. yothersi* has been examined in some details. CiLV-C infection triggers the SA-mediated pathway in *Arabidopsis thaliana* (L.) Heynh. and *Citrus sinensis* (L.) Osbeck (Arena et al. 2016). Infected leaves accumulate reactive oxygen species (ROS) and areas of dead cells around the local lesions, suggesting a hypersensitive-like response (Arena et al. 2016). Besides activating the SA pathway, the infection causes progressive reprogramming of the plant transcriptome, including down-regulation of the jasmonic acid (JA)/ethylene (ET)-mediated pathways and processes involved in primary metabolism, including photosynthesis (Arena et al. 2020). During infestation with non-viruliferous *Brevipalpus* mites, plants also accumulate ROS around the mite feeding sites, and at the transcription level display a drastic up-regulation of defensive responses involving salicylic acid (SA) and JA, as well as down-regulation of growth-related processes (Arena et al. 2016, 2020). These findings suggest that *Brevipalpus* mites manipulate the host defensive response to render the plant more susceptible to their colonization. It is hypothesized that CiLV-C might act as an effector used by the mites to modulate the plant metabolism, contributing to reduction of the anti-herbivore defenses controlled by the JA pathway. Mites oviposit less on mutant plants with defective SA biosynthesis and signaling, confirming that the SA pathway functions to improve mite fitness (Arena et al. 2018). In biological assays using two sets of *Arabidopsis* plants infested with non-viruliferous and viruliferous *B. yothersi*, the number of mites on the CiLV-C-infected *Arabidopsis* plants increased significantly

in comparison to the plants infested with non-viruliferous mites. Furthermore, the viruliferous mites preferentially laid eggs on CiLV-C-infected leaves (Arena et al. 2016).

Some information suggests that the mode of transmission of several mite-borne viruses may be persistent or semi-persistent. However, many pieces of this complex puzzle are missing and most of the current research models do not provide satisfying explanations. Innovative biomolecular tools and procedures (*i.e.*, next-generation sequencing), advances in mite genomics with the discovery of genes involved in membrane transfers, virus translocation among tissues, or coat-absorbance may be useful for this study. The recent completion of *B. yothersi* genome sequencing (Navia et al. 2019) may yield insights regarding the specificity of BTV and species/populations of *Brevipalpus* mites, as well as the mechanisms of viral internalization and transmission. The role of traditional and applied acarologists remains essential to provide supportive biological and ecological confirmations.

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