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Mechanism of Arthropod-mediated Transmission of Plant Viruses - A Review

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Abstract

In the intricate world of botanical life, an often-overlooked menace lurks – plant viruses. Viruses invade their target and hijack the plant cell's mechanisms to multiply and reproduce. The impact of these microscopic assailants is profound, affecting food security, food safety, national economies, biodiversity, and the rural environment. Plant viruses, although small in stature, wield immense influence in the plant kingdom. They are sub-microscopic entities comprised of genetic material, either DNA or RNA, encased within a protective protein coat. They need a medium of transmission for survival and spread, which can be air, water, contaminated tools, or certain other organisms known as vectors. These vectors, often insects, fungi, or nematodes, serve as intermediaries between the virus and its plant host, facilitating transmission and infection. Understanding the intricate interactions between plant viruses and their vectors is vital for developing effective control strategies that can mitigate the devastating impact of these diseases on crops. This relationship between a plant virus and a vector is a testament to the complexity of the natural world, where microscopic organisms wield enormous influence over the health and fate of plants, impacting ecosystems and even human agriculture. This review delves into the world of plant virus vectors, un-ravelling their roles in disease transmission, their biological mechanisms, and the pivotal role they play in shaping agricultural landscapes worldwide. It also explores the types of virus transmission and their effects on vector behaviour. This knowledge is essential for developing strategies to mitigate the impact of plant viruses and protect global food security.

Keywords: *Insect, Plant, Transmission, Vector, Virus*

1. Introduction

In the intricate world of botanical life, an often-overlooked menace lurks – plant viruses. Viruses invade their target and hijack the plant cell's mechanisms to multiply and reproduce (Garcia-Ruiz, 2019). The impact of these microscopic assailants is profound, affecting food security, food safety, national economies, biodiversity, and the rural environment (Wilkinson et.al. 2011). Plant viruses, although small in stature, wield immense influence in the plant kingdom. They are sub-microscopic entities comprised of genetic material, either DNA or RNA (Chaitanya, 2019), encased within a protective protein coat (Taylor, 2014). This unseen warfare between plants and viruses is an ongoing battle that has shaped the evolution of both parties. While plants have developed intricate defence mechanisms to fend off viral attacks, viruses have evolved sophisticated strategies to evade detection and exploit their hosts' vulnerabilities (Wu et al.2019; Liu et al., 2017). Once inside their host, plant viruses initiate a molecular hijacking, subverting the plant's cellular machinery to replicate and propagate themselves (Masayoshi et al. 2016).

Viral particles are destructive but cannot harm unless they enter their host (Louten, 2016). They need a medium of transmission, that can be air, water, contaminated tools etc (Fermin, 2018) are some of the medium of transmission, however certain other organisms also help in their transmission, known as vectors (Brault et al. 2010). These vectors, often insects, fungi, or nematodes, serve as intermediaries between the virus and its plant host, facilitating transmission and infection (Jones and Naidu 2019).

Understanding the intricate interactions between plant viruses and their vectors is vital for developing effective control strategies that can mitigate the devastating impact of these diseases on crops.

In the web of ecological relationships, a fascinating and often elusive partnership exists between plant viruses and their vectors (Wang et. al. 2022). This synergy between viruses and vectors represents a remarkable example of coevolution and adaptation, with profound implications for plant health, crop productivity, and ecosystem dynamics (De Filippis and Villarreal 2000). Exploring this dynamic partnership provides valuable insights into the world of plant pathology and the interconnectedness of life forms within our planet's diverse ecosystems.

This relationship between a plant virus and a vector is a testament to the complexity of the natural world, where microscopic organisms wield enormous influence over the health and fate of plants, impacting ecosystems and even human agriculture. In an era where agriculture plays a pivotal role in feeding the ever-growing global population, the consequences of viral infections in crops are far-reaching. Devastating diseases like the Tobacco Mosaic Virus and Potato Leaf-roll Virus possess serious crop threats, responsible for considerable agronomical losses, global food problem, and human life overall all over the world (Nicaise 2014). In this review, we delve into the world of plant virus vectors, unravelling their roles in disease transmission, their biological mechanisms, and the pivotal role they play in shaping agricultural landscapes worldwide.

Transmission of plant viruses

Transmission is the basic step for the survival and spread of viruses. Most viruses are restricted to a particular type of host (Clémence et al. 2013), often causing the death of their host and transmitted from plant to plant in numerous methods, which can be by vegetative propagation or by some mechanical means, which can be through seed, pollen, insect, mites, nematodes etc. (Pagán 2022). Among the animal species approximately 94% belongs to the phylum arthropod which transmits plant viruses (Singh et al., 2020). However, the most important agents of spread or dispersion of viral diseases are by insects. Insects are the most important group of vectors of plant virus both in terms of virus transmission and economic importance of the diseases concerned. The insect which carries the disease is known as vector. More than 400 diseases have been reported to be transmitted by insect vectors (Agrios 2009). Insect's viz., aphids, leafhoppers, white flies, thrips, flea beetles and scale insects are such important species play a major role in the dissemination of plant viruses (Sarwar 2020).

Among the sucking insects, aphids, belonging to family Aphididae transmit a greater number of plant viruses than any other insects (Purcell and Almeida 2004; Agrios 2009) which are followed by whiteflies belonging to family Aleyrodidae, followed by leafhoppers, belonging to family Cicadellidae, followed by planthoppers belonging to family Delphacidae (Purcell and Almeida 2004). The beetles (Coleoptera) and thrips (Thysanoptera) are also considered to be a significant importance. There are existences of more than 2000 virus species and those affecting plants includes virus of at least 21 families (Whitfield et al. 2015).

Plant viruses are unable to penetrate the plant surfaces which are lined with substances like cuticle or lignin (Savatin et al., 2014) and infection can only be initiated or entry through the wound in the tissues (Gergerich and Dolja 2006). The insect obtains virus through its mouth parts, that might be biting and chewing, as in beetles, or piercing and sucking, as in hemipteran bugs and nematodes, at the time of feeding on the diseased plant and then inoculated in the healthy plant by means of feeding of certain plant parts, tissue or upon young leaves (Smith 1924; Gray and Banerjee 1999). The period of development of infectivity for the virus within the vector is called the incubation period (Louten 2016). The incubation period of different viruses varies from a few hours to days. There is some relationship exist between the plant viruses and the insect vectors. Mostly the plant viruses transmitted by one group of vectors are not transmitted by other groups (Whitfield et al. 2015). For example, the peach aphid is the vector of sugar beet mosaic virus (Laurent et al. 2023) but the leafhopper feeding on the same crop does not transmitting this virus (Walkey 1991).

Virus vector interactions/relationship

Virus transmission through insect vectors involves the movement of mature virus particles (virions) from infected plants to healthy ones. This transmission process can be classified as either persistent or non-persistent, depending on how the virus is acquired, retained, and inoculated by the vector (Cunniffe et al. 2021).

Acquisition: This marks the initial step in the infection cycle when the vector encounters the virus within an infected plant and acquires it (Ng and Perry 2004).

Retention: In the second stage, the vector carries virions at specific locations on or within itself. The duration of virion retention determines the classification of vectors as non-persistent (lasting from minutes to hours), semi-persistent (retaining virions for a few days), or persistent (holding virions for a lifetime and potentially passing them to their offspring). For non-persistent and semi-persistent viruses, the virions are primarily retained in the vector's stylet and foregut, respectively, (Ng and Falk 2006; Hogenhout et al. 2008).

Inoculation: This final step involves the release of retained virions into the tissues of a susceptible plant in a manner that allows them to establish a new infection. The act of inoculating viruses by the vector also has the effect of altering the virus's accumulation within plants, regardless of whether one or both viruses were cultivated in new hosts. These findings underscore the intricate nature of interactions between vectors, viruses, and plants that impact the spread and replication of viruses, both as single infections and co-infections (McLaughlin et al. 2022).

The virus transmission cycle

The virus transmission cycle involves host-finding, feeding and acquisition of virus, transport, and delivery of virus to a new host plant (Whitfield and Rotenberg 2016). Plant virus transmission by insects can be classified into two categories: non-circulative and circulative transmission (Table 1). The non-circulative-externally borne viruses associate with specific cuticular structures of the insect stylet or foregut and the attached virus particles are lost during the insect molt (Ng and Falk, 2006; Whitfield and Rotenberg 2016). The circulative transmission involves the viruses moving from the foregut further towards the mid- and hindgut, followed by their movement into the haemolymph and further to the salivary gland, from where they are released into the plant tissue at the time of feeding. The different modes of viral transmission by vectors include non-persistent, semi-persistent (non-circulative) and persistent (circulative), whereby the transmission window to disseminate the virus to a new host plant after feeding on an infected plant by the vector lasts from seconds to minutes, hours to days, or days to weeks, respectively (Dietzgen et al. 2016).

Non-circulative transmission

Viruses categorized as non-circulative are transmitted either in a non-persistent or semi-persistent fashion, implying that they are swiftly acquired, usually within seconds to minutes of feeding, and also quickly transmitted. In the case of semi-persistent viruses, a more extended acquisition and transmission period is necessary, typically taking a few minutes to a few hours (Whitfield and Rotenberg 2016).

Non-persistent

Most plant viruses carried by aphids are transmitted through a non-persistent method. It is marked by brief periods for both acquiring and inoculating the virus, typically lasting seconds to minutes, and by short retention periods. Papaya ring-spot virus is one of the examples of non-pesrsistent transmission of virus which is transmitted by aphid (Pidikiti et al. 2023). Usually, the insect vectors pick up the virus from the infected plant in less than a minute which retains for very short period. The replications of these non-cirulative viruses are reserved in epidermal or parenchymal cells of the infected plants (Shi et al. 2021). There are two approaches to the transmission of non-circulative viruses by aphids: one involves only the capsid, as seen in cucumoviruses, and the other relies on helpers, as exemplified by caulimoviruses and potyviruses (Pirone et al. 2002). In capsid strategy, virus particles bind to aphid receptors on the maxillary stylet cuticle using their coat protein, virus particles bind to a helper component. CaMV (Caulimovirus) requires the binding of a non-structural protein to the virion before it can attach to a receptor found in the common canal, formed through the fusion of the food canal (FC) and the salivary canal (SC). This binding event ultimately leads to fusion between FC and SC, facilitating the virus's attachment to the receptor. The virus can be inoculated both in superficial and in deeper tissues during the feeding process of aphids. Thus, aphids are organisms that can acquire and inoculate any viral taxon within plants, whatever their tissue specificity (Brault et al. 2010).

Semi-persistent

Insect vectors can acquire virus in minutes, but the efficiency increases with prolonged feeding. Generally, 12-24 hours are enough to increase the efficiency of vector to infect the other healthy palnts. Vectors need to acquire the virus from the phloem of the infected plant. The virus binds to the specific protein sites at the anterior gut of the insect vector. Once the virus is acquired, it retains in vector body for longer duration. Aphids, whiteflies, leafhoppers etc. transmit the semi-persistent viruses (Singh et al. 2020). Semi-persistent is mostly transmitted by leafhoppers and whiteflies (NG and Perry 2004).

Circulative transmission

Viruses that are considered circulative or internally transmitted necessitate a more extended period for both acquisition and transmission, typically spanning from hours to days. To successfully facilitate transmission, these viruses must navigate the insect's digestive system and ultimately reach the salivary glands (Figure 1). Unlike other types of viruses, these circulative viruses are not shed during insect moulting, and there exists a latent period between their initial acquisition and the actual transmission event. This mode of transmission is characterized as persistent (Whitfield and Rotenberg 2016).

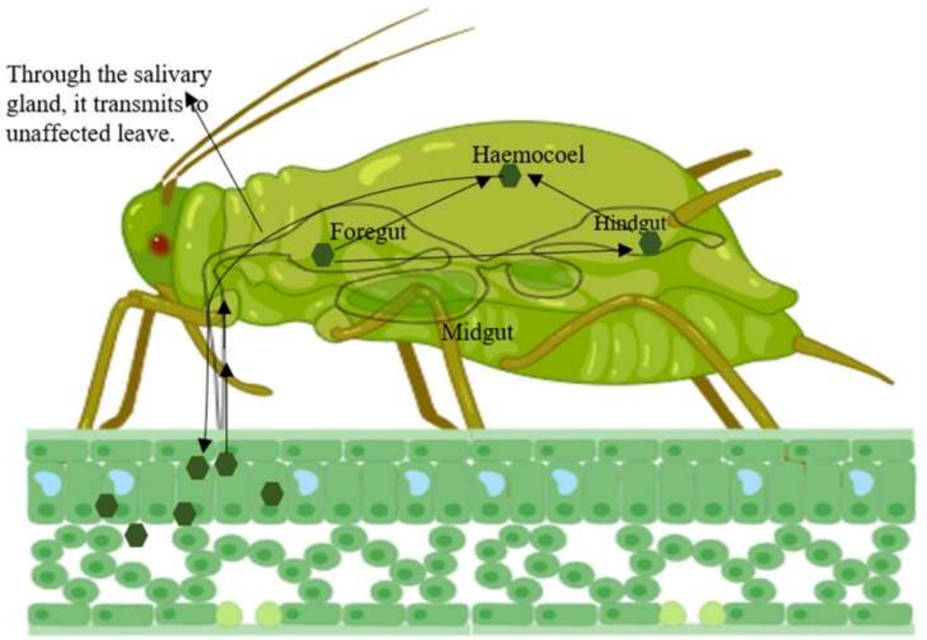

***Figure 1*: Plant virus circulative route in insect**

Persistent

Persistent viruses can be categorized as either persistent propagative or non-propagative/persistent circulative. Circulative viruses do not replicate often in their vectors but the propagative virus do (Hogenhout et al. 2008). In the case of viruses transmitted circulatively in a non-propagative manner, their ability to be transmitted can be sustained throughout their entire lifespan, and the virus is not eliminated during moulting. This transmission method is observed in the Enamovirus, Luteovirus, and Polerovirus genera within the Luteoviridae family (Gray et al. 2003). Tomato leaf curl virus (TLCV) transmitted by whitefly, *Bemisia tabaci* and tomato spotted wilt virus (TSMV) transmitted by thrips, *Frankliniella occidentalis* are some of the examples of persistently transmitted plant virus (Chen et al. 2018). The propagative virus is transmitted to the vector progeny due to the infection in the embryo or germ cell in the female vector (Hogenhout et al. 2008). Persistent viruses cannot spread between plant cells or be transmitted through grafting; instead, they are distributed to all plant cells during host cell division. There is no evidence for their horizontal transmission by a vector, whereas they are vertically transmitted to seeds at rates close to 100% (Boccardo et al. 1987; Blanc 2007; Roossinck 2010).

Table 1: An overview of non-circulative (non-persistent and semi-persistent type) and circulative manner of insect-mediated plant virus transmission

Name of Plant Virus	Crop	Family	Genome	Transmission	Reference
Non-persistent Manner					
Alfalfa Mosaic Virus (AMV)	Pea	Genus Alfamovirus, Family Bromoviridae	+ive sense ssRNA	Several species of Aphids and mechanically by grafting	Wang et al. (2023)
Brome Mosaic Virus (BMV)	Monocotyledonous cereal crops	Genus Bromovirus, Family Bromoviridae.	+ive sense ssRNA	Spotted cucumber beetles, *Diabrotica undecimpunctata*	He et al. (2021)
Broad bean wilt virus-1	More than 200 plant species	Genus Favavirus, Family Comoviridae	+ive sense ssRNA	Aphids, *Myzus*	Carpino et al. (2020)

				persicae and *Aphis gossypii*	
Cauliflower/Turnip Mosaic Virus	Cauliflower, mustard and turnip	Genus Caulimovirus, Family Caulimoviridae	circular, double-stranded DNA	More than 27 aphid species	Bak and Emerson (2020)
Cowpea Mosaic Virus (CPMV)	Cowpea, *Nicotiana benthamiana* and other legumes	Genus Comovirus, Family Comoviridae	+ive sense ssRNA	Leaf-feeding beetles, thrips and grasshoppers	Lomonossoff (2008); Shukla et al (2020)
Cucumber mosaic virus (CMV)	Safflower	Genus Cucumovirus, Family Bromoviridae	+ive-sense ssRNA	Mechanical inoculation of plant sap, through seeds and more than 80 species of aphids	Mochizuki and Ohki (2012)
Maclura Mosaic Virus (MacMV)	Plant species of family Chenopodiaceae and Solanaceae	Genus Macluravirus, Family Potyviridae	+ive-sense ssRNA	Aphids, *Myzus persicae*	Turina et al. (2006)
Papaya Ring Spot Virus (PRSV)	Papaya	Genus Potyvirus and the family Potyviridae	+tive-sense single-stranded RNA (ssRNA)	Numerous aphid species such as *Myzus persicae*	Medina-Salguero et al. (2021)
Pea Seedborne Mosaic Virus (PSbMV)	Pea	Genus Potyvirus, Family Potyviridae	+ive sense ssRNA	More than 20 aphid species, and by mechanical means. The most efficient vector of PSbMV worldwide is the pea aphid (*Acyrthosiphon pisum*)	Beck-Okins et al. (2022)
Pea Streak Virus (PSV)	Pea	Genus Carlavirus, Family Betaflexiviridae	Linear +ive sense ssRNA	*Aphis craccivora, A. spiraecola* and *Myzus persicae*	Navrátil M, Šafářová D (2019); Gaafar et al. (2020)
Peanut Mottle Virus (PeMoV)	Pea	Genus Potyvirus, Family Potyviridae	+ive sense ssRNA	Infected seeds and aphids	Soumya et al. (2014)
Peanut Stunt Virus (PSV)	Pea	Genus Cucumovirus Family Bromoviridae	+ive sense ssRNA	seed-transmitted and is vectored by several aphid species	Wrzesińska et al. (2018)
Potato/Tomato Virus Y	Potato and Tomato	Genus Potyvirus and the family Potyviridae	+tive-sense ssRNA	Through grafting, plant sap inoculation and through several species of aphids	Prigigallo et al. (2019)
Potato/Tomato Virus S	Potato and Tomato	Genus Carlavirus and family Betaflexiviridae	+tive-sense ssRNA	transmitted both by contact between diseased and healthy plants (e.g., by farm implements) and by aphids	Bettoni et al. (2022)
Plum Pox Virus (PPV)	Apricot, cherry, nectarine, peach and plum	Genus Potyvirus, Family Potyviridae	+ive-sense ssRNA	Aphids, *Aphis spiraecola* and *Myzus persicae*	Ilardi and Tavazza (2015)
Soybean Mosaic Virus (SMV)	*Glycine max* (cultivated soybean) and *G.*	Genus Potyvirus, Family Potyviridae	+ive-sense ssRNA	Aphid, *Aphis glycines*	Domier et al. 2011

	soja (wild soybean)				
Sunflower Mosaic Virus (SMV)	Sunflower	Genus Nepovirus, Family Potyviridae	+ive-sense ssRNA	Mechanically sap transmitted and by several aphids *viz.*, *Aphis gossypii, A. malvae, A. craccivora, Rhopalosiphum maidis* and up to some extent it is seed-borne	Gulya et al. (2002)
Turnip mosaic virus (TuMV)	All Brassica species, lettuce, watercress, radish and rocket	Genus Potyvirus, Family Potyviridae	+ive-sense ssRNA	40–50 species of aphids	Nellist et al. (2022)
Zucchini yellow mosaic virus (ZYMV)	All cultivated cucurbits	Genus Potyvirus, Family Potyviridae	+ive-sense ssRNA	Several species of aphids	Simmons et al. (2013)
Semi-persistent Manner					
Agropyron Mosaic Virus (AMV)	Weedy grass species	Genus Rymovirus, Family Potyviridae	Monocistronic, +ive sense ssRNA	Eriophyid mite, *Abacarus hystrix*	Hodge et al. (2018)
Anthriscus Yellows Virus (AYV)	*Anthriscus sylvestris* (cow parsley)	Genus Waikavirus, Family Sequiviridae	+ive sense ssRNA	Aphid, *Cavariella aegopodii*	Jiménez et al. (2021)
Bean Golden Mosaic Virus (BGMV)	*Phaseolus vulgaris*	Genus Begomovirus, Family Geminiviridae	ssDNA	Whiteflies, *Bemisia tabaci*	De Freitas-Vanzo et al. (2021)
Beet Yellow Virus (BYV)	Plants of crucifer and composite families	Genus Closterovirus, Family Closteroviridae	+tive-sense ssRNA	23 aphid species, *Myzus persicae* and *Aphis fabae* being the main natural vectors	Hossain et al. (2021)
Citrus Tristeza Virus (CTV)	Citrus and related species	Genus Closterovirus, Family Closteroviridae	+tive-sense ssRNA	Brown citrus aphid, *Toxoptera citricida*	Herron et al. (2006)
Commelina Yellow Mottle Virus (CoYMV)	monocot weed, *Commelina diffusa* (day flower)	Genus Badnavirus, Family Caulimoviridae	dsDNA	Mealybug	Medberry et al. (1990)
Lettuce Infectious Yellow Virus (LIYV)	Beet, lettuce and cucurbits	Genus Crinivirus, Family Closteroviridae	+tive-sense ssRNA	Whiteflies, *Bemisia tabaci*	Ng et al. (2021)
Maize Chlorotic Dwarf Virus (MCDV)	species of the Poaceae family	Genus Waikavirus, Family Sequiviridae	Monopartite positive-sense ssRNA	Leaf hopper (*Graminella nigrifrons*)	Gingery (1988); Chatterji and Fauquet (2000)
Oat Necrotic Mottle Virus (ONMV)	Oat and some wild/cultivated grasses	Genus Tritimovirus, Family Potyviridae	Monocistronic, positive sense ssRNA	Eriophyid mite	Stenger and French (2004)
Parsnip Yellow Fleck Virus (PYFV)	Parsnip	Genus Sequivirus, Family Sequiviridae	Monopartite ssRNA	Aphid, *Cavariella aegopodii* (dependent on a helper virus, Anthriscus yellows virus)	Turnbull-Ross et al. (1993)
Pigeonpea Sterility Mosaic Virus (PPSMV)	Pigeonpea	Genus Emaravirus, Family Fimoviridae	negative-sense ssRNA	Eriophyid mite, *Aceria cajani*	Sayiprathap et al. (2022)
Piper Yellow Mottle Virus (PYMoV)	Black pepper	Genus Badnavirus, Family Caulimoviridae	dsDNA	Citrus mealy bug, *Planococcus citri* and Foliar mealy bug,	Ahamedemujtaba et al. (2021)

				Ferrisia virgata	
Rice Tungro Virus (RTV)	Rice	Two particles are there- ➢ Rice tungro spherical virus (RTSV) is a plant pathogenic virus of the family Sequivirida e and genus Waikavirus. ➢ Rice tungro bacilliform virus (RTBV) is a plant para-retrovirus of the family Caulimoviri dae and genus Tungrovirus.	➢ Rice tungro spherica l virus (RTSV) has a single-stranded RNA ➢ Rice tungro bacillifo rm virus (RTBV) contains double stranded DNA	Green leafhopper, *Nephotettix virescens* transmits only RTSV	Kumar and Dasgupta (2020)
Ryegrass mosaic virus (RMV)	*Lolium multiflorum, Lolium perenne,* and *Dactylis glomerata*	Genus Rymovirus, Family Potyviridae	Monocistronic, positive ssRNA	Eriophyid mite, *Abacarus hystrix*	Dąbrowska et al. (2020)
Southern Bean Mosaic Virus (SBMV)	Cowpea and common bean	Genus Sobemovirus, Family not assigned	+ive sense ssRNA	Striped cucumber beetle, *Acalymma vittata*	Hacker and Fowler (2000)
Wheat Streak Mosaic Virus (WSMV)	Wheat	Genus Tritimovirus, Family Potyviridae	+ive sense ssRNA	wheat curl mite, *Aceria tosichella*	Paliwal (1980)
Persistent					
Persistent Circulative					
Barley Yellow Dwarf Virus (BYDV)	Wheat	Genus Luteovirus, Family Luteoviridae	+ive sense ssRNA	Aphids, *Sitobion avenae* and *Rhopalosiphu m padi*	Nancarrow et al. (2021)
Beet Curly Top Virus (BCTV)	Sugar beet	Genus Curtovirus, Family Geminiviridae	single-stranded circular DNA	Beet leafhopper, *Circulifer tenellus*	Anabestani et al. (2017)
Bean Leaf Roll Virus (BLRV)	Bean, alfalfa, chickpea, pea, lentil	Genus Luteovirus, Family Luteoviridae	+ive sense ssRNA	Several species of aphids, like pea aphid (*Acyrthosipho n pisum*) is the principal vector	Agindotan et al. (2019)
Bunchy top / Curly top / Cabbage top /Strangles disease Banana Bunchy Top Virus (BBTV)	Banana	Genus Badnavirus, Family Caulimoviridae/ Nanoviridae	Circular ssDNA	Banana aphid, *Pentalonia nigronervosa*	Wickramaarach chi et al. (2016)
Carrot Red Leaf Virus (CtRLV)	Carrot	Genus Polerovirus, Family Luteoviridae	positive-sense ssRNA	Willow-carrot aphids, *Cavariella aegopodii*	Gungoosingh-Bunwaree et al. (2009)

Carrot mottle virus (CMoV)	Carrot	Genus Umbravirus, Family Tombusviridae	positive-sense ssRNA	Willow-carrot aphids, *Cavariella aegopodii*	Adams et al. (2014)
Chickpea Chlorotic Dwarf Virus (CCDV)	Chickpea	Genus Mastrevirus, Family Geminiviridae	single-stranded circular DNA	Leafhopper, *Orosius albicinctus*	Kanakala and Kuria (2018)
Groundnut Rosette Assistor Virus (GRAV)	Groundnut	Genus unassigned, Family Luteoviridae	satRNAs are linear single-stranded RNA	Aphid, *Aphis craccivora*	Anitha et al. (2014)
Fiji Disease Virus (FDV)	Maize, sorghum and sugarcane	Genus Fijivirus, Family Reoviridae	dsRNA	Delphacid planthoppers, *Perkinsiella saccharicida, P. vituensis, P. vastatrix*	Zhang et al. (2021)
Maize Streak Virus (MSV)	Maize	Genus Mastrevirus, Family Geminiviridae	single-stranded circular DNA	Leafhopper species in the Genus *Cicadulina*, but mainly by *C. mbila* and *C. storeyi*	Tembo et al. (2020)
Papaya Leaf Curl Virus (PaLCuV)	Papaya	Genus Begomovirus, Family Geminiviridae	Bipartite circular ssDNA	Whitefly (*Bemisia tabaci*)	Soni et al. (2022)
Pea Enation Mosaic Virus (PEMV)	Pea, chickpea, broadbean and lentil	PEMV-1, Genus Enamovirus and PEMV-2, Genus Umbravirus, Family Luteoviridae	positive-sense ssRNA	Aphids, pea aphid (*Aphis pisum*) and the green peach aphid (*Myzus persicae*) are the most common aphid species	Doumayrou et al. (2016)
Potato Leafroll Virus (PLRV)	Potato	Genus Polerovirus, Family Luteoviridae	positive-sense ssRNA	Green peach aphid, *Myzus persicae*	Kumar et al. (2020)
Subtarranean Clover Stunt Virus (SCSV)	Legumes	Genus Nanovirus, Family Nanoviridae.	Multipartite ssDNA	Several species of aphids	Chatzivassiliou (2021)
Tomato Yellow Leaf Curl Virus (TYLCV)	Tomato	Genus Begomovirus and the family Geminiviridae	Bipartite circular ssDNA	Whitefly (*Bemisia tabaci*)	Yan et al. (2021)
Bhendi Yellow Vein Mosaic Virus (BYVMV)	Okra	Genus Begomovirus and the family Geminiviridae	Bipartite circular ssDNA	Whitefly (*Bemisia tabaci*)	Venkataravanappa et al. (2017)
Persistent Circulative Propagative					
Barley Yellow Striate Mosaic Virus (BYSMV)	Wheat, maize, oat, rye and *Agropyron repens*	Genus Cytorhabdovirus, Family Rhabdoviridae	negative-sense ssRNA	Small brown planthopper, *Laodelphax striatellus*	Cao et al. (2018)
Groundnut Bud Necrosis Virus (GBNV)	Arange of solanaceous and fabaceous hosts including groundnut	Genus Tospovirus, Family Bunyaviridae	small RNA genome (S RNA)	*Thrips palmi*	Singh et al. (2014)
Iranian Maize Mosaic Virus (MIMV)	Maize and several other grass species	Genus Nucleorhabdovirus, Family Rhabdoviridae	dsRNA	Small brown planthopper, *Laodelphax striatellus*	Moeini et al. (2020)
Lettuce Necrotic Yellows Virus (LNYV)	Lettuce, *Sonchus oleraceus*	Genus Cytorhabdovirus, Family Rhabdoviridae	Monopartite, negative-sense ssRNA	Sowthistle aphid, *Hyperomyzus lactucae*	Ibrahim et al. (2020)
Potato Leaf Roll Virus (PLRV)	Potatoes and other members of the family Solanaceae	Genus Polerovirus, Family Solemoviridae	+ive sense ssRNA	Green peach aphid, *Myzus persicae*	Kumar et al. (2020)
Potato Yellow Dwarf Virus (PYDV)	Potato	Genus Nucleorhabdovirus, Family Rhabdoviridae	negative-sense ssRNA	Either by leafhoppers or plant- hoppers or by aphids	Bandyopadhyay et al. (2010)

Maize Rayado Fino Virus (MRFV)	Maize	Genus Marafivirus, Family Tymoviridae	Monopartite ssRNA	Leafhoppers including *Dalbulus maidis* and *Graminella nigrifrons*	Mlotshwa et al. (2020)
Maize Stripe Virus (MSpV)	Maize, sorghum, and itchgrass	Genus Tenuivirus, Family Bunyaviridae	negative-sense ssRNA	Delphacid planthoppers, *Peregrinus maidis*	Bolus et al. (2021)
Rice Grassy Stunt Virus (RGSV)	Rice	Genus Tenuivirus, Family Bunyaviridae	negative-sense ssRNA	Brown plant hopper, *Nilaparvata lugens*	Satoh et al. (2013)
Rice Ragged Stunt Virus (RRSV)	Plants belong to Graminae family	Genus Oryzavirus, Family Reoviridae	dsRNA	Delphacid brown planthoppers, *Nilaparvata lugens*	Zhang et al. (2018)
Rice Hoja Blanca Virus (RHBV)	Rice	Genus Tenuivirus, Family Bunyaviridae	negative-sense ssRNA	Planthopper, *Tagosodes orizicolus*	Romero et al. (2014)
Sonchus Yellow Net Virus (SYNV)	Sowthistle plant	Genus Nucleorhabdovirus, Family Rhabdoviridae	negative-sense ssRNA	Aphid, *Aphis coreopsidis*	Martins et al. (1998); Deng et al. (2007)
Tobacco Streak Virus (TSV)	Sunflower necrosis	Genus Ilarvirus of Bromoviridae	+tive-sense single-stranded RNA (ssRNA)	Thrips (*Scirtothrips dorsalis*) or Thrips-mediated pollen transfer	Vemana and Jain (2010)
Tomato Spotted Wilt Virus (TSWV)	Tomato	Genus Tospovirus of the family Bunyaviridae	negative-sense ssRNA	Various species of thrips, *Thrips tabaci, Scirtothrips dorsalis* and *Frankliniella occidentalis*	Nachappa et al. (2020)
Wound Tumor Virus (WTV)	More than 50 species of plants; firstly reported on yellow sweet clover	Genus Phytoreovirus, Family Reoviridae	dsRNA	Leaf hopper, notably *Agallia constricta*	Peterson and Nuss (1986)

Plant virus effect on vector behaviour

The virus-induced changes in vector behaviour are adaptive and vary among viruses, hosts, and vectors (Mauck et al. 2014). The best-characterized plant viral insect vectors are aphids, thrips, leafhoppers, planthoppers and whiteflies (Bragard et al. 2013). Viruses that are only acquired during sustained vector feeding in the phloem tend to increase host palatability and quality for vectors, which results in increased settling and uptake of virions, while viruses that are only acquired during short bouts of cellular content ingestion from non-vascular tissues tend to decrease palatability, which enhances dispersal immediately following virion acquisition (Mauck et al. 2012, 2016; Eigenbrode et al. 2018).

In nature most viruses are capable of infecting multiple host species. Adaptations that result in manipulation of one host should, at minimum, have neutral effects on the phenotypes of other commonly infected hosts so as not to reduce the overall probability of transmission by vectors, but this has rarely been explored (Mauck et al. 2012, 2016). Volatile organic compounds emissions from Cucumber mosaic virus (CMV)-infected plants are more attractive to aphids than those from uninfected plants (Mauck et al. 2010, 2014; Safari et al. 2019). Acute plant viruses influence aphid vectors to aid in their transmission, benefiting themselves, whereas PCV-1, a long-lasting plant virus that doesn't spread horizontally, shields its host plant from aphids by diminishing the plant's appeal and its suitability as a host for aphids. This has the secondary effect of protecting the plants from aphid herbivory, which can also cause significant damage (Safari et al. 2019). Wu et al. (2014) reported congruent aphid behavioral responses to infection of cultivated peas by either of two members in the Luteoviridae family (Bean leafroll virus [BLRV] and Pea enation mosaic virus [PEMV]) alongside divergent virus effects on host quality. Aphids were attracted to plants infected with both viruses and exhibited settling preferences for infected plants over sham-inoculated plants. But PEMV infection resulted in lower aphid survivor-ship and no benefits to fecundity, while BLRV enhanced almost all aphid performance metrics.

Barley yellow dwarf virus [BYDV] and Potato leafroll virus, both belonging to Leutoviridae, are also known to change the developmental and reproduction behavior of their vector, aphid. This virus tends to increase the feeding of aphid on infected plants which results in high reproduction and dispersal of the vector (Montllor and Gildow, 1986; Eigenbrode et al., 2002; Jiménez-Martínez et al., 2004a; Jiménez-Martínez et al., 20024b; Srinivasan et al., 2006).

Chesnais et al. (2019) did a study to find that whether the plant viruses manipulate the host plant to increase the vector transmission. In their studies, they found that the host with the highest tolerance for infection i.e. wild *Camelina microcarpa* exhibited phenotypic changes in response to turnip yellow virus (TuYV) infection that were at least equivalent (in terms of benefits for the virus) to changes induced in the less tolerant domesticated host, *Camelina sativa*. They found that F1 hybrid of these two species was the least tolerant of infection and exhibited phenotypic changes that were also the least beneficial for virus transmission. It showed that aphid (*Myzus persicae*) behavior and performance are strongly influenced by both soluble sugar and starch levels. The nature of virus effects on these metabolites, and aphid preferences, potentially depend on genetically controlled variation in host carbon fixation efficiency and allocation strategies. However, the factors responsible for the variability in how viruses affect the performance of aphids remain uncertain, (Hodge and Powell 2010; Wu et al. 2014).

Table 2: A list of virus families transmitted by different insect vectors and their symptoms.

Virus family	Common symptoms	Vector	References
For single stranded DNA virus			
Geminiviridae	Twisted/distorted growth, leaf curling and enation	White fly and leaf hopper	Hanley et al. (2013); Hassan et al. (2016)
For double stranded DNA virus			
Caulimoviridae	Chlorotic and necrotic spots	Aphid	Then et al. (2021)
For double stranded RNA virus			
Reoviridae	chlorotic spots, distortion, and galls on rice leaves.	Leaf hopper	Wei and Li (2016)
For single stranded RNA virus (Negative sense genome)			
Bunyaviridae	Necrotic or chlorotic rings or ring patterns on many hosts	Thrips, ticks, mosquitoes and sand flies	Adkins et al. (2005); MacLachlan and Dubovi (2017)
Rhabdoviridae	Stunting, vein clearing, mosaic and mottling of leaf tissue, to tissue necrosis	Aphids, thrips, plant hopper	Dietzgen et al. (2017)
For single stranded RNA virus (Positive sense polarity)			
Betaflexiviridae	Mosaic, mottle, ring-spot, necrosis and pitting	Aphids	Brault et al. (2010)
Bromoviridae	mottling and discoloration on the leaves	Aphid, beetles	Brault et al. (2010); Koch et al. (2020)
Closteroviridae	leaves become thick, leathery, and brittle	White fly, aphids, pseudococcid mealybugs and soft scale insects	German-Retana et al. (1999)
Comoviridae	Mosaics, stunting, and malformations	Beetle, aphids and nematodes	Lomonossoff (2008)
Luteoviridae	The blockage of sieve tubes and degeneration of vascular tissue	Aphid	Miller (1999)
Potyviridae	Yellowing, mottling and ring spotting	Aphid, whitefly, eriophyid mite, mealybug, scale insects	King et al. (2012); Revers and García (2015)
Sequiviridae	Mosaic and mottling	Aphid, leafhopper	Brault et al. (2010)

4. Conclusion

Vectors and viruses are related in the context of vector-borne diseases. Different types of viral diseases are transmitted by different vectors in plants, in different manners. Viruses rely on host-specific transmission for survival. They transferred between plants via seeds, pollen, insects, and more. Insects are vital vectors for plant viruses. Viruses can't penetrate plant surfaces but enter through wounds carried by insect vectors. This transmission is categorized as non-circulative or circulative, based on how the vector acquires and transmits the virus. Non-circulative viruses transmit quickly, either nonpersistently or semi-persistently, acquired and transferred within seconds to minutes. In non-persistent transmission, insects swiftly acquire the virus but retain it briefly, with replication in plant cells. Semi-persistent transmission takes minutes, with peak efficiency after 12-24 hours. The virus, acquired from plant phloem, binds to gut proteins in insects and stays longer. Circulative viruses require hours to days to acquire and transmit. They pass through the insect's digestive system to reach the salivary glands. Unlike other viruses, they are not shed during insect molting, causing a delay in transmission, known as "persistent" mode. The plant virus-vector relationship is a complex and pivotal aspect of plant pathology, influencing disease transmission and management. Understanding vector behaviour and interactions with viruses is crucial for effective disease control strategies. Further research in this field holds promise for improving crop health and global food security.

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