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Review Article

A review on molecular aspects of virus-vector relationship to the aphids

Pavithra Pidikiti
School of Agriculture, Lovely Professional University, Phagwara- 144412 (Punjab), India
Chavan Sanket Sudhakar
School of Agriculture, Lovely Professional University, Phagwara- 144412 (Punjab), India
Harkirat Singh
School of Agriculture, Lovely Professional University, Phagwara- 144412 (Punjab), India
Adesh Kumar
School of Agriculture, Lovely Professional University, Phagwara- 144412 (Punjab), India
Shweta Meshram*
School of Agriculture, Lovely Professional University, Phagwara- 144412 (Punjab), India

*Corresponding author. E-mail: Shweta.26662@lpu.co.in

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Abstract
Plant viruses are transmitted through insects, mites, nematodes, and protists. Arthropods as vectors are used by 88% of plant viruses to move from one host to another. Insects are the most prevalent vectors, with aphids accounting for half of all insect-vectored viruses. Aphids have been meticulously developed to serve as vectors. Transforming virions into plant cells is facilitated bypiercing–sucking mouthparts that do not cause irreversible damage. With the ability to reproduce asexually, aphid populations can grow incredibly, amplifying disease epidemics and accelerating the spread of viruses over short and vast distances. Aphids significantly reduce crop productivity by spreading numerous plant viruses. Being obligate intracellular pathogens, viruses rely heavily on vectors to spread and survive. Aphids are responsible for the majority of economically significant plant virus transmission and cause heavy crop loss worldwide. Aphids feed on the plant as insect pathogens and carry plant pathogens such as Viruses. Either persistent circulation, non-circulation or not persistently, they spread viruses. The process of plant virus transmission by insects has changed over time and is significantly impacted by the biology and morphology of insects. Much research during the last century has offered an in-depth understanding of the molecular mechanisms underpinning virus-vector interactions. The present review discusses the molecular interaction of the virus–vector relationship by Aphids. This will provide a clue to the scientific community to successfully combat aphid infestation in agriculture.

Keywords: Aphid, Molecular mechanism, Plant Virus, Transmission, Vector

INTRODUCTION

Climate change, rapid human population increase, food insecurity, and environmental degradation are all socio-economic concerns that adversely affect farming systems, human and cattle health, and vulnerable ecosystems worldwide. At the same time, the world is entering an exciting period of tremendous scientific and technical discoveries that promise to help us overcome these issues. Global food security is a key concern for the twenty-first century due to fast, accelerated population growth, which is anticipated to reach 10 billion by 2050 (Ohlan and Ohlan, 2022). Reducing crop disease risks is critical if humankind is to achieve the 60 per cent increase in food production required by 2050 and meet its future nutritional needs. This necessitates good plant disease control in a variety of cropping systems around the world and achieving this goal without harming natural ecosystems (Chakraborty *et al*., 2011, Ding *et al*., 2023). Viruses are a major source of plant disease, with an annual economic effect of more than $30 billion (Anderson *et al*., 2004, Fuchs *et al*., 2021). They are responsible for over half of the pathogens that cause new and re-emerging plant diseases globally and harm both natural and cultivated plants.
Virus infections endanger farmed plants by reducing their growth and vigour, lowering gross yields, and degrading the quality of the produce, lowering marketable yields. Crop losses occur worldwide, inflicting damage ranging from minor to complete failure (Chakraborty *et*

al. 2011). One of the most significant harmful organisms is the virus. Viruses are necessary, submicroscopic pathogens that spread disease throughout the world. They pose serious risks to plants and are problematic for crop protectionists. It is the root cause of numerous serious plant diseases and significant global agricultural losses. The most common virus infection symptoms include yellowing of leaves, leaf deformation, plant stunting, and flower or fruit production anomalies. Virus infection symptoms vary depending on the severity of the disease (Bragard *et al*., 2013, Acharya and Regmi, 2020, Kumari *et al*., 2022).

Plant viruses are spread from one host to the next by bud wood, seeds, or tubers, as well as arthropods, nematodes, fungi, and plasmodiophorid vectors. Transmission is vital to the virus's biological cycle since it assures its survival and maintenance. Although human activities such as vegetative plant propagation, grafting, global exchange of infected material, changes in cropping systems, and the introduction of novel crops in existing or new agricultural areas effectively disseminate plant viruses, most plant viruses are transmitted by vectors from one host to another (Ander-Link and Fuchs, 2005; Sarwar *et al*., 2020).

The key trait of viruses that ensures their life and continuity is their ability to transmit. Most viruses are bound to a single kind of host. They are transmitted from plant to plant in a variety of ways, including vegetative means, propagation by seed, pollen, insect, mites, and nematodes, and mechanical means through seed, pollen, insect, mites, and nematodes (Singh *et al*., 2020). Around 94 percent of animal species belong to the phylum arthropod, which transmits plant viruses. Insects, on the other hand, are the most important agents of viral illness propagation. Insects feeding on sap, such as the Auchenorrhyncha and Sternorryhncha, are important vectors, transferring over 380 viruses. The aphid family (Aphididae) is by far the most important among these vectors, carrying far more viruses than whiteflies (Aleyrodidae), leafhoppers (Cicadellidae), or planthoppers (Delphacidae). (Sankarganesh *et al*. 2020).

Aphids (Aphididae) are the sucking insects that transfer the most plant viruses, followed by leafhoppers (Cicadellidae), planthoppers (Delphacidae), treehoppers (Membracidae), and other vectors such as whiteflies (Aleyrodidae) and mealybugs (Pseudococcidae). Beetles (Coleoptera) and thrips (Thysanoptera) are also considered to be important pests (Sankarganesh *et al*., 2020).

Aphid-transmitted viruses belong to 19 of the 70 identified virus genera and account for over 275 virus species. Many of these viruses produce large economic losses in crops such as cereals (Jones *et al*., 2021), potatoes and sugar beets (Yi, 2020, Armand *et al*., 2021, Devar, 2022). Aphids have evolved as the most important group of insects to exploit higher plants as food sources and one of the most important vectors of plant viruses, parthenogenetic reproduction, viviparity, polymorphism, host alternation, wide host range in some species, and possession of needle-like mouth parts (Ghosh *et al*. 2017). The present study reviews the molecular aspects of the aphid virus–vector relationship.

VECTORS OF PLANT VIRUSES

Many taxonomic groups, such as arthropods, nematodes, fungi, and plasmodiophorids, are home to plant viral carriers. Most plant viruses are transmitted by arthropod vectors such as aphids, whiteflies, leafhoppers, thrips, beetles, mealybugs, mirids, and mites, with aphids being the most common, with over 200 documented vector species. More than half of the 550 known vector-transmitted viral species are dispersed by aphids (55%) followed by leafhoppers (11%), beetles (11%), whiteflies (9%), nematodes (7%), fungi and plasmodiophorids (5%), and thrips, mites, mirids, or mealybugs (2% each) (Sarwar et al., 2020, Dolja et al., 2020, Wang and Blanc, 2021, Kondo *et al*., 2022).

Phases of transmission

The transfer of virions (viral particles complete with the RNA or DNA core and protein coat) from infected to healthy plants occurs when an aphid (or any other vector) transmits a virus. There are up to four phases in the transmission cycle.

Acquisition: Aphid's procedure of acquiring virions from an infected plant.

Retention: Carrying of virions in or on the vector at specified locations.

Latency: Inability to inoculate immediately after acquiring the virus (the aphid can spread the virus once the 'latent phase' (LP) has passed).

Inoculation: Introduction of retained virions into the tissues of a susceptible plant to initiate a fresh infection.

Aphids have many traits that make them good virus carriers. In virus epidemiology, host selection and feeding behaviour are essential aspects, and the host range and life cycle characteristics of aphid species are also important in influencing virus dissemination rates (Ghosh *et al*., 2017; Singh and Singh, 2021; Li *et al*., 2021).

IMPORTANCE OF APHIDS AS VIRAL VECTORS

Many plant viruses are spread by aphids, which are common in gardens. Because parthenogenetic breeding enables swift, exponential population growth, aphids are common in nature. Aphids' piercing, sucking mouthparts make them effective carriers as well. Although aphids and other hemipterans have similar

Table 1. Categorisation of virus transmission by aphids into three major types based on the vector's retention time

Transmission Type	Character	Example	References
Nonpersistent transmission	Acquisition period is more (from seconds to minutest) No latent period Inoculation period is low (From seconds to minutes) Persistent: -< 4 hours Also called as Stylet borne virus	Caulimoviruses, Cucumoviruses, Potyviruses & Potato virus Y (PVY)).	Tungadi *et al*., 2020, Chesnais *et al*., 2021
Semi-persistent	Acquisition period is more (from minutes to hours) No latent period Inoculation period is low (From minutes to hours) Persistent: 1-100 hours	Closterovirus (Beet yellow virus) & Citrus tristeza virus (CTV)).	Patton *et al*., 2020, LaTourrette *et al*., 2021
Persistent	Acquisition period is more (From minutes to hours) No latent period Inoculation period is low (From minutes to hours) Persistent: >100 hours Also called as Circulative virus	Enamovirus, Luteoviruses & Cereal yellow dwarf virus-RPV (CYDV-RPV).	Ghosh *et al*., 2019, Aradottir *et al*., 2021

mouthpart morphology and feeding strategies, aphids appear to be the only vectors that can transfer viruses after quickly probing a leaf. Additionally, aphids can transmit viruses that circulate in their bodies and grow into new viruses. While many aphid-borne viruses depend on non-virion proteins in addition to the main coat protein, most viruses are thought to spread as complete virions (CP). Several examples of these components include the read-through (RT) protein found in luteovirus capsids, the CPm (a minor CP form) a portion of closterovirus particles, and the helper component (HC) of pot viruses. Common traits include the capacity to create vector specificity and data transmission (Gadhave *et al.,* 2020, Sõmera *et al*., 2021, Agranovsky *et al*., 2021, Li *et al*., 2021) (Table 1 and 2, Fig. 1).

Molecular mechanisms of aphid virus transmission

A variety of plant viruses have been selected for aphid vector transmission. Transmission techniques can differ dramatically, and there is no link between genome type, replication strategy, or particle form. Elucidating the fate of virions within the vector, such as identifying ligands to which virions attach, their courses of movement, and (where relevant) tissue tropisms, is at the forefront of the field of virus–vector connections. Ligands can be simple (or less well-defined) surfaces like the cuticular lining of the stylet and foregut, a matrix of carbohydrates, proteins, and lipids, or complex (or less well-defined) surfaces like the cuticular lining of the stylet and foregut. Early episodes of infection are a relatively untapped area of plant virology research. Aphid vectors are in charge of placing viruses at their infection sites. Because salivation appears crucial in releasing virions, a greater understanding of virus entrance may eventually necessitate a better understanding of salivation. The understanding of viruses will evolve in tandem with our knowledge of vector biology, just as viruses have evolved in tandem with their aphid vectors (Fig. 2).

Nonpersistent virus transmission

Nonpersistent plant viruses infect a healthy plant within a few seconds or minutes after being retained in an insect's stylet. Most of the time, insect vectors pick up the virus from the infected plants within less than a minute of feeding. Epidermal and/or parenchymal cells contain nonpersistent virus replications. These viruses have a very short retention time—just a few minutes to many hours. A few minutes on a single plant will cause a vector to lose its capacity to spread the virus to healthy plants (Shi *et al.,* 2021). Examples include the papaya ringspot virus, which is primarily spread by aphids (Table 2).

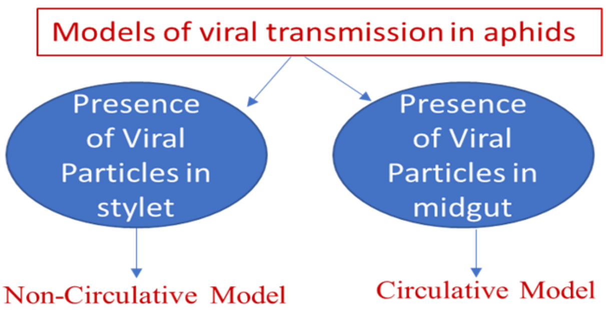

Fig. 1. *Circulative and Non- persistent models of virus transmission in aphids*

Table 2. Plant virus transmitted by different and exclusively by aphid species (Dempsey *et al*., 2017, ICTV, 2020)

General transmission of virus			Viruses exclusively transmitted by aphids	
Taxa of virus	**Number of members**	**Main vector**	**Virus**	**Aphid-Vector Species**
Caulimovirus	17	Aphids	Barley yellow dwarf	*Acyrthosiphon dirhodum*
Alfamovirus	1	Aphids	Ragi mosaic	*Rhopalosiphum maidis*
Carlavirus	55	Aphids	Cowpea mosaic	*Aphis craccivora*
Cucumovirus	3	Aphids	Bean common mosaic	*Acyrthosiphon pisum*
Fabavirus	2	Aphids	Bean yellow mosaic	*Acyrthosiphon pisum*
Machlomovirus	1	Thrips and Beetles	Soyabean mosaic	*Aphis glycines*
Macluravirus	2	Aphids	Soyabean mild mosaic	*Myzus persicae*
Potyvirus	55	Aphids, Mites, and Mechanical	Pea enation mosaic	*Acyrthosiphon pisum*
Badnavirus	16	Mealy bug and Leafhoppers	Peanut rosette	*Aphis craccivora*
Closterovirus	25	Aphids, Whiteflies and Mealy bug	Sugarcane mosaic disease	*Aphis gossypi*
Nepovirus	39	Nematodes	Banana bunchy top	*Pentalomia nigronervosa*
Sequivirus	2	Aphids	Citrus tristeza	*Toxoptera auruntii*
Tobravirus	4	Nematodes	Chilli mosaic	*Aphis gossypi*
Sequivirus	2	Aphids	Cucumber mosaic disease	*Myzus persicae*
Tobravirus	4	Nematodes	Potato leaf roll	*Myzus persicae*
Trichovirus	6	Aphids, Mealybug, and mites	Katte disease of cardamom	*Pentalomia nigronervosa*
Waikavirus	3	Aphids and Leafhoppers	Tobacco mosaic virus	*Myzus persicae*
			Tobbaco streak virus	*Thrips tabaci*

Nonpersistent plant viruses spread via either of two methods

1. Capsid-strategy of aphid (*Myzus persicae*)

Aphid specifically employs this method to spread the cucumber mosaic virus (CMV) . The viral coat protein (CP) and conserved capsid surface regions are required for efficient aphid spread. The CMV 2b protein, an RNA silencing suppressor, has reportedly been discovered to interfere with various stages of the RNA silencing pathway in plants and to indirectly enhance CMV transmission by promoting persistent phloem-feeding and aphid vector survival (Tungadi *et al*., 2020, Rhee *et al*., 2020).

2. Helper-dependent virus transmission strategy

A synthetic viral vector that requires a helper virus to reproduce is called a "gutless virus," also called a helper-dependent virus. For example, it has been shown that the helper-dependent process of the cauliflower mosaic virus (CaMV) requires many viral proteins and virions. CaMV virions are targeted to microtubules for association with P2 (Chesnais *et al.,* 2021; Agranovsky, 2021). It was shown that the aphid stylet and the CP-anchored P3 could engage with CaMV P2. Furthermore, it was found that CaMV-induced microtubule-associated transmission bodies (TBs) reallocate essential viral proteins, like P2, onto cellular microtubules upon "sensing" aphid feeding to promote uptake and enhance acquisition by the vector.

Semipersistent transmission

The most semipersistent viruses transmitted by aphids are the caulimoviruses and closteroviruses. The parent member of the genus Caulimovirus, cauliflower mosaic virus, uses a helper-dependent transmission strategy but adds two virally produced nonstructural proteins, P2 and P3, as an additional requirement. P2 mediates aphid binding, while P3 binds to virions to produce a P2-P3-virion complex, with P2 serving as the "bridge" between the two. Before obtaining P3-virion complexes from other mesophyll or phloem cells, aphids may first receive P2 from infected mesophyll cells (Patton *et al*., 2020, LaTourrette *et al.,* 2021).

In vivo, P2 forms complexes with microtubules, although it is unclear how these interactions affect transmission. Non-persistently and semi-persistently transmitted viruses with RNA and DNA genomes have evolved helper transmission mechanisms. Because Helper component (HC) and viral particles can be acquired in a specific order, one virus can aid in transmitting another virus. This mechanism, known as HC trans complementation, has been found in many plant virus families and has the potential to alter plant viral epidemiology and dissemination (Patton *et al*., 2020, Raja-

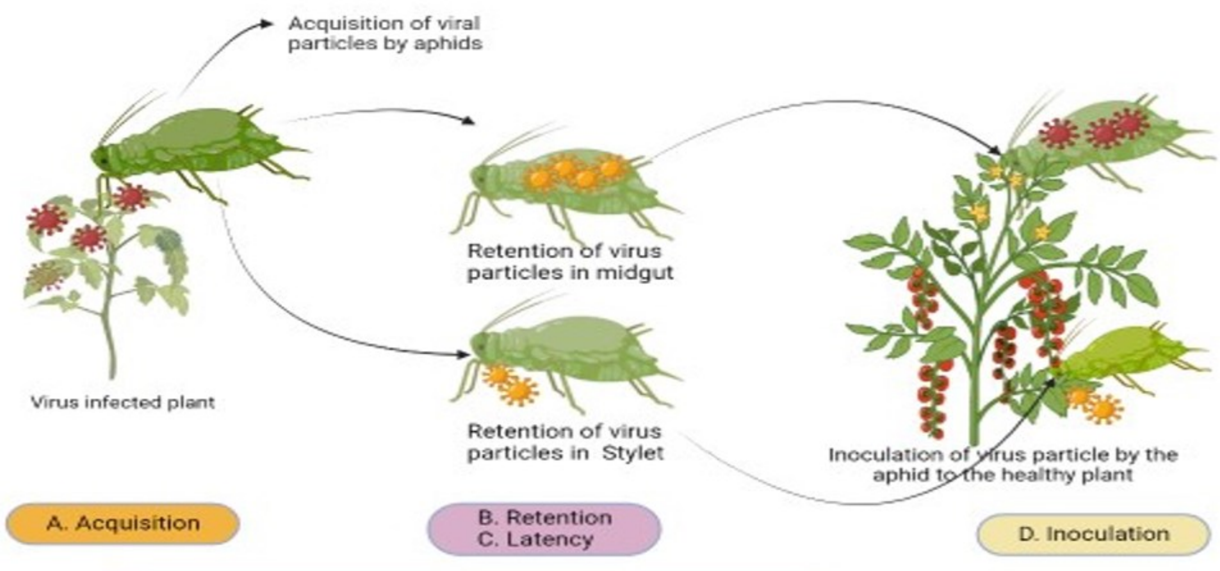

Fig. 2. *Illustration of virus transmission cycle in the vector*

rapu *et al*., 2021, Miller and Lozier, 2022).

Three other families of plant viruses provide examples of intermittent aphid transmission are Secoviridae, Potyviridae and Caulimoviridae. Sequiviruses, such as the Parsnip yellow fleck virus (PYFV), are among them. Although the type of the helper component is unclear, PYFV transmission does not involve encapsidation of its DNA by the helper virus CP. This is in contrast to the helper relationship for umbraviruses . PYFV does not encode the helper, unlike potyviruses and caulimoviruses; instead, the viral Anthriscus yellows virus genus waikavirus is most likely to provide it (Jayasinghe *et al*., 2022, Yoshida, 2020).

Circulative virus transmission

Longer acquisition durations, ranging from days to weeks, are typical in circulative viral transmission. The virus must go to the salivary glands via the aphid digestive system within the vector. The latent phase is the interval between when the virus is first acquired and when it is first successfully inoculated. The retention period describes how long the vector retains its capacity to spread the virus. Depending on the virus's capacity for replication in carrier cells, circulatory viruses are classified as propagative or non-propagative. If a virus is circulatory, non-propagative, and not lost during moulting, its transmissibility may be kept for the remainder of its life. The Enamovirus, Luteovirus, and Polerovirus genera of the Luteoviridae family use this transmission mechanism (Ghosh *et al*., 2019, Krueger *et al*., 2013, Miller and Lozier, 2022) (Table 3).

Luteoviruses are phloem-restricted viruses that can only be contracted by consuming phloem cells that have been affected. Viral particles move through the food tract, the foregut, the midgut, and the hindgut of the insect before passing through a second cellular barrier, which may enforce vector specificity, to enter the hemocoel cavity and circulate towards the accessory salivary gland. The introduction of virions explains the specificity of transmission by aphid species into the hemolymph and these obstacles (Khalili *et al*., 2022). According to trans-encapsidation experiments in double -infected plants, the CP of luteoviruses is a determinant of aphid-specific transmission. It was eventually discovered that a small structural protein in virions corresponded to an RT variation of the CP, which controls transmissibility and vector specificity. The association of a CP-RT protein with symbionin, a protein homolog of the GroEL chaperone produced by endosymbiotic bacteria of the genus Buchnera, was considered crucial in keeping virions stable in the aphid hemolymph's hostile environment (Ryckebusch *et al.*, 2020, Miller and Lozier 2022). However, because luteoviruses bind symbiotically in both vector and nonvector aphids, the interaction's contribution to transmission is debatable, and current investigations on the chaperone's in vivo localisation cast doubt on its availability for interaction.

It is hypothesised that specific insect receptors are needed for the endocytosis, vesicle transfer across cells, and exocytosis of viruses because internalisation of virions in insect cells-with or without replication-is necessary for circulative transmission. In Sitobion avenae, binding experiments have been conducted to identify potential receptors that mediate the transmission of luteoviruses like the Barley yellow dwarf virus (BYDV-MAV) (Choudhury *et al*., 2019, Aradottir *et al*., 2021). These are possible biomarkers that could be used to predict the transmission ability of specific aphid

Table 3. Plant virus genera categorised by insect mode of transmission

Nonpersistent Noncirculative	Semipersistent Noncirculative	Persistent Circulative	Persistent Propagative	References
Alfamovirus	*Badnavirus*	*Begmovirus*	*Tospovirus*	Chakrabarti and Das, 2014, ,Sankarganesh, 2017, Tungadi *et al*., 2020, Patton *et al*., 2020,
Carlavirus	*Caulimovirus*	*Curtovirus*	*Marafivirus*	
Cucumovirus	*Closterovirus*	*Mastrevirus*	*Phytoreovirus*	
Fabavirus	*Sequivirus*	*Enamovirus*	*Fijivirus*	
Machlomovirus	*Trichovirus*	*Nanavirus*	*Oryzavirus*	
Macluravirus	*Waikavirus*	*Umbravirus*	*Phytorhabdovirus*	
Potexvirus		*Bromovirus*	*Cytorhabdovirus*	
Potyvirus		*Carmovirus*	*Nucleorhabdovirus*	
		Comovirus	*Tenuivirus*	
		Sobemovirus *Tymovirus*		

species. Luteoviruses can operate as helper viruses in transmitting viruses from the Umbravirus genus, which does not have CP. The relationship of these viral entities could be much more complicated since it could necessitate the inclusion of satellite molecules that aid in encapsidation and aphid transmission. As the viruses can reproduce in the insect and escape via the salivary glands, the circulative propagative virus transmission is similar to the spread of animal viruses by mosquitoes and other blood-feeding vectors. Plant rhabdoviruses can live for a long time in an infected insect, and the virus can spread to progeny via a transovarial route. Transmission is classified as 'circulative, nonpropagative' or 'circulative, propagative' depending on whether the virus replicates in the vectoring aphid (Gupta *et al.,* 2022). Aphids can remain virulent for extended periods; the virus persists, and this mode of transmission is known as persistent.

Conclusion

Viruses are obligatory and submicroscopic pathogens that create challenges for crop production. Common Symptoms include yellowing, deformation of leaves, stunting, and abnormalities in flower or fruit production, the most prevalent. Viruses use vectors for transmission, and insects are the most important group. They are responsible for many significant plant diseases and massive crop yield losses worldwide. For transmission and survival, most plant viruses that cause crop diseases rely on biotic vectors. Regarding the virus's ability to spread and the economic significance of the afflicted diseases, aphids are the most significant plant virus vectors. This review will aid future researchers in further investigating the aphid virus-vector relationship since viruses are one of the most important pathogenic organisms and put the productivity of food crops in danger. Understanding the virus-vector relationship will be useful in developing effective viral-vector management methods.

Conflict of interest

The authors declare that they have no conflict of interest.

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