Effect of aphid biology and morphology on plant virus transmission

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Abstract

Insects severely affect crop production by direct feeding and transmitting many plant viruses. Viruses are obligate intracellular pathogens mostly depend on insects for their transmission and survival. Majority of economically important plant viruses are transmitted by aphids. They transmit viruses either persistently (circulative or non-circulative) or non-persistently. Plant virus transmission by insects is a process evolved over time and strongly influenced by insect morphological features and biology. Certain groups of insects are favourable for some particular viruses. Over the past century, large body of research has provided detailed knowledge of the molecular process underlying virus-vector interactions. In this review, we discuss how aphid biology and morphology can affect plant virus transmission.

Key words: mode of virus transmission, persistent and non-persistent viruses, aphid behaviour, capsid strategy and helper strategy

Introduction

Viruses invades all forms of life and viral infection cause physiological changes in host which express as a symptom resulting the significant yield loss of important crop plants. Viruses are undoubtedly the challenging pathogens to control, as they are non-sensitive to chemicals and unlikely to be controlled by application of chemicals. Although, it is very complicated to estimate overall crop loss due to viral diseases, but it was thought to be more than 100 billion/ year. Recently, [1] reviewed significant yield losses in economically important crop due to plant viral disease infection. Being an obligate intracellular pathogen, viruses are exclusively depending on insect vectors for their transmission and survival.

In the life of a plant virus, it should make two kinds of movements: ‘short-distance movement’ to adjacent cells to infect and colonize host plants from its initial infection point. Secondly, the ‘long-distance movement’ which is from one host or place to another to spread and ensure its survival in nature. Plant viruses are compelled to deal with the characteristics of the plant kingdom such as their sessile nature and their impermeable cell walls [2]. The viruses cannot expect transmission from the plant itself except through pollen, seeds or infected parts of plants in the case of vegetatively propagated plants. Further, the cell wall is made of cellulose, hemicellulose and pectin, which preclude the entry and exit of the viruses [3]. Thus, for the long-distance movement, the virus must break the cellular barriers to enter into a new plant cells and often but not always, viruses seek the assistance of insects in this regard and often Hemipteran insects have become the choice of majority of viruses. Aphids play a key role in viral transmission and have become by far the most important plant virus vector, being able to transmit nearly one third of all known plant viruses (Raccah et al., 2001; Whitfield et al., 2015; Dietzgen et al., 2016). Transmission from plant to plant is a *sine qua non* for virus survival and therefore viruses have developed many strategies to accomplish this task. Unlike to other disease-causing organisms, plant viral disease cannot manage by using chemicals in field conditions. Hence, vector control one of the strategies to minimize viral disease for sustainable crop production. However, aphids have been considered as a one of the most effective vectors for plant viruses' transmission, so it is important to know morphology and biological features of aphids that favoured by certain group of viruses for survival and transmission. The understanding of molecular mechanism will greatly help designing sustainable management practices to control aphid-borne virus diseases.

Taxonomy of aphids

More than 5000 aphid species are described, out of which about 100 are considered as agricultural pests, merely due to their ability to transmit plant viruses. *Myzus persicae*, *Macrosiphum euphorbiae*, *Aphis craccivora* and *Aphis gossypii* are some of the well-known aphid species, which, each can transmit more than 20 plant viruses (according to CABI datasheets). Aphids belong to the order Hemiptera, suborder Sternorrhyncha and infraorder Aphidomorpha. Aphidomorpha has two superfamilies namely Aphidoidea and Phylloxeroideam [7]. Majority of plant virus transmitting aphids belongs to the family Aphididae [8].

Mechanisms of virus transmission by aphids

The mechanism of virus transmission by aphids can be divided into several categories based on the time taken for virus acquisition, retention and inoculation by their vectors. [9,10]. Figure 1 provides the detailed classification of plant viruses transmitted by insects and by extension aphids. As classified in the figure 1, viruses can be broadly categorized in to two groups; circulative and non-circulative. The circulative viruses are occasionally classified as persistent viruses as they persist in the insect body long after acquisition and the virus acquisition, retention and inoculation by their vectors normally take many days. The persistent viruses are further divided into circulative- propagative and circulative-non-propagative based on virus's ability to replicate within the insect body or not [11–13].

Non-circulative viruses are also known as stylet-borne/cuticle-borne viruses as those viruses bind to the cuticle of the vector and never passes through cellular barriers. Classification of non-circulative viruses can be done in two ways. One based on the time taken by the virus acquisition, retention and inoculation by the vector. This brings two distinct categories, namely; non-persistent and semi-persistent. Two, based on the molecular data on virus and vector interactions, these viruses can be classified into "capsid strategy" and "helper strategy" [14,15]. The later classification has a better sense as it explains the molecular interaction between the vector and the virus. Viruses in the genus *Cucumovirus*, for example, have adopted a "capsid strategy" while the members of the genera *Potyvirus* and *Caulimovirus* have adopted "helper strategy". Supp. table 1 lists the aphid transmitted plant virus families, an example virus species from each genus and its mode of transmission.

Morphological characters influencing plant virus transmission

Aphid stylet: acquisition apparatus of viruses and the binding site of the non-persistent viruses

The sap-feeding insects such as aphids ingest fluid along a pressure gradient in its mouthparts through proboscis. Aphids' proboscis, also known as stylet, is a long flexible tube made out of two maxillary-stylets enclosed by a pair of mandibular-stylets. The stylet possesses two main ducts, food canal and salivary canal. These two ducts are formed by interlocking of the two maxillary stylets (Figure 1a). The stylets are enclosed by the labial sheath and protracted out during puncturing of the plant tissue. The mandibular-stylets are used to puncture the tissue and then the maxillary-stylets are inserted into the plant tissue. Piercing the plant cell needs mechanical activity and is provided by moving the two mandibular stylets which are capable of moving independently of each other. As the stylet bundle advances in the plant tissue, the head is bent down toward the surface, and the labium shortens by telescoping at the proximal joints. The stylet bundle is protracted and retracted to penetrate the tissue [16]. They penetrate the plant tissue intercellularly or may pierce the cell walls by longitudinal antiparallel movements of the stylets. The piercing canal can have a branched shape within the host's tissue (Bing et al. 1991; Tjallingii and Esch 1993). The feeding habit of aphids is less injurious to plant cells compared to other biting and chewing insects (Figure 1b). In fact, this makes aphids best suited to transmit plant viruses as the feeding may go unnoticed by plant's resistance mechanisms against injury by insects.

The stylet bundle is typically 400–700 µm long and slightly enlarged at the base coming from the head capsule [19]. The mandibular-stylets which interlock and form the outer tube also has a small internal duct with two dendrites which supply nerves to the mandibular-stylets. The two maxillary-stylets are sculpted by longitudinal ridges and grooves which form the inner tube with large food canal and smaller salivary canal once interlocked [20]. These two channels are separated along the stylet except at the very end of the stylet where both canals merge into a one common canal [21] (Figure 1c).

As shown in figure 1c, the most distant end of the aphids stylet is identified to be the binding site for the non-persistently transmitted viruses and found that this specific stylet region containing specific non-glycosylated proteinaceous receptors embedded in chitin (Uzest et al., 2007; Uzest et al., 2010). It is also evident that this ultrastructure is conserved among aphid spp. and referred it as "acrostyle" [22,23]. The P2 of *Cauliflower mosaic virus* (CaMV, genus *Caulimovirus*) bind to receptors present at the surface of the acrostyle named Stylin-01 and Stylin-02, belong to the RR-1 cuticular protein subfamily [24]. A list of plant virus receptor candidates in the tip of maxillary stylet has been revealed in the pea aphid [25]. Binding of non-circulative virus into aphid receptors can be either by direct interaction of coat protein (CP) and stylet receptors or via a helper component (HC).

Cucumber mosaic virus (CMV, genus *Cucumovirus*), the CP solely determine the aphid transmission as CMV CP directly interacts with stylet receptors [26]. Contrary, poty and caulimoviruses produce an HC which is a non-structural protein which can interact with both virus CP and stylet receptor, thus create a molecular bridge allowing the virus retention in the stylet [14,15] .

Aphid mid gut and salivary glands: the two barriers circulative viruses need to cross

Circulative viruses are actively transported across the gut epithelial cells and released into the haemocoel of the aphid [27,28]. The virions then have to pass through the extracellular basal lamina and the underlying plasmalemma of the accessory salivary gland (ASG) to enter into salivary canal [29] (Figure 1d and e).

Figure 1d shows how virions may enter the hemocoel by passing the epithelial cells in mid- or hind-gut areas [30,31]. Membrane alanyl aminopeptidase N has been identified in the pea aphid as responsible for the entry of the *Pea enation mosaic virus* (PEMV, genus *Enamovirus*) into the aphid gut [29]. It was predicted that the endocytosis and exocytosis in aphid gut involved in specific interactions with capsid proteins [27,32]. This was later confirmed in luteoviruses, which entered by endocytosis using clathrin-coated vesicles in epithelial cells of the gut and passes to the haemocoel via exocytosis at the basal side [27,33,34]. It was also observed that although many luteoviruses can penetrate aphid gut, only few are transmittable by the aphid due to the inability to enter in to ASG, suggesting that the movement of virions through gut epithelium is to be relatively non-specific [30,35]. *Barley yellow dwarf virus* (BYDV, genus *Luteovirus*), *Cereal yellow dwarf virus*-RPV (CYDV, genus

Polerovirus) [36] and *Soybean dwarf virus* (SbDV, genus *Luteovirus*) [35] use the hindgut of its aphid vector while *Potato leaf roll virus* (PLRV, genus *Polerovirus*) [34] used the posterior midgut as the site of internalization. *Faba bean necrotic stunt virus* (FBNSV, genus *Nanovirus*) and *Alfalfa leaf curl virus* (ALCV, genus *Capulavirus*) enter the aphid haemocoel through cells of the anterior midgut and cross principal salivary gland cells which is a different route compared to luteoviruses [37,38].

For transmission to occur, the virions must cross the extracellular basal lamina surrounding the ASG and transported through the underlying plasmalemma and enter into salivary canal. Aphid salivary glands are composed of a pair of primary glands (PG) and a pair of ASGs [39]. Studies based on luteoviruses, the basal lamina surrounding the ASG of aphids thought to be a selective barrier [40]. The virions must attach to the basal lamina, which changes the permeability of the basal lamina to allow the virions to pass [28] (Figure 1e). The variation of the efficacy of virus particles binding to the basal lamina of ASG determines the calculative virus transmission efficiency by different aphid species.

Biological characters aiding virus transmission

Intrinsic rate of increase

Aphid's biological characters have enabled them to become very efficient transmitters of plant viruses. The ability of parthenogenesis has given a clear advantage in allocating energy for reproduction. The aphids show nearly a two times faster population increase by having higher degree of intrinsic rate (r_m) compared to that of other similar size sexually reproducing species. The r_m of aphids is also increased by the "telescoping of generations", which means that the growing embryos in embryonic-mothers also have the ability to form embryos [41]. Thus, a single embryonic-mother carries several generations of growing embryos within her body. Subsequently this shortens the time between birth and reproductive maturity. Therefore, when conditions are favourable, aphids will grow exponentially and promote long-term persistence of plant viruses within a plant community [42]. Under favourable condition an insect of the similar size of an aphid which does not show telescoping of generations would take around four weeks to develop from birth to maturity where aphids only take one week. Thus aphids have a threefold reproductive advantage and have achieved the reproduction rate of much smaller organism [41].

Polyphenism

Another important biological character is the evolution of polyphenism. Many aphid species produce winged (alate) and non-winged (apterous) adults within the same species. Producing winged adults requires a considerable amount of energy and by producing alate and apterous morphs separately aphids have evolved to invest the energy cleverly [43]. When the aphid population density increases, host nutritional quality and other host factors influence the production of alate offspring [44]. *M. tanacetaria* will produce around ten times higher winged morphs under crowding stress which is an already known fact to influence wing production in other aphid species such as *Myzus persicae, Aphis craccivora*, *Megoura viciae* and *Rhopalosiphum padi* [45,46] . All alate adults taking flight from the infected host plants will promote onward transmission of the plant viruses [42].

A typical life cycle of an aphid is presented based on *M. persicae* in supplementary figure 1. *M. persicae* is a well-studied, highly efficient plant virus vector. It also produces both alate and apterous morphs in its life cycle.

Aphid behaviour and virus transmission

Host plant colonization and feeding behaviour

Effective transmission of a plant virus, aphid must complete three distinct steps: acquisition, retention and inoculation. Aphids must land on a virus-infected plant to acquire the virus, retain the acquired virus in its body and finally inoculate back in to a new healthy host [2,24,47–50]. Viruses have evolved mechanisms to influence the above steps to secure maximum possibility to spread to new hosts.

Aphids landing on a host plant may or may not colonize the plant or transmit viruses infecting it. Therefore, aphids landing on a host plant can be divided into four categories 1. transient non-vectors (land on host but neither colonize nor transmit virus); 2. transient vectors (cannot colonize but transmit virus); 3. colonizing non-vectors (colonize but do not transmit virus); and 4. colonizing vectors (both colonize and transmit virus). Transient vectors are the main vectors of non-persistent and some semi-persistent stylet-borne viruses, these pose a serious threat to crops as these require short feeding periods and rapid movement of aphids between the visiting plants. Colonising vectors are the main vectors of viruses of persistent and some semipersistent foregut-borne viruses and these require longer feeding times [51].

Powell *et al.* (2006) described a six step processes of host plant selection by aphids. Here we have proposed a modified six step processes of aphid’s feeding behaviour with special interest to plant virus transmission. Winged aphids are adapted to disperse and to locate new hosts [52], yet for ease of experimenting, both forms have been used to describe the following sequence of behaviours. It is also evident that the aphid transmitted plant viruses have evolved to influence one or more stages to attract aphids to virus-infected plants.

Step 1: Pre-alighting behaviour

Pre-alighting behaviour of aphids involves phototactic response to visual cues from the host plant [53] and by plant volatiles detected by antennal olfactory sensilla [54,55]. A detailed review on visual ecology of aphids has been presented before [56]. *M. persicae* have been found to possess three types of photoreceptors in the compound eye [57]. Thus the aphids are most sensitive to 530 nm, 490 nm and near UV (330–340 nm) wavelengths [57]. When winged aphids are subjected to leave from an air stream, they land on yellow-green objects or highly saturated yellow targets [58,59]. This usual preference of aphids to select yellow objects may not be a true colour preference but due to the outcome of brightness [56]. The preference of aphids for yellowing and mottling of virus infected leaves into yellow colours seems likely to be caused by a positive visual response [58–60].

It is unlikely that visual cues can provide host-specific information [58,61] compared to aphids responding to volatile organic compounds (VOCs) from their host plant [62]. However, the effect of VOCs may limit to short range response. It has been evident that the composition of the VOC blend is more important than the quantity, to change the aphid behavioural responses [63,64]. Mauck and colleagues (2010) found that the VOC blend emitted by CMV-infected squash appeared to increase the attractiveness of infected plants to *M. persicae* and *A. gossypii.* In contrast, CMV infection in tobacco did not increase the preference of aphids, despite the changes in the VOC composition [65]. It is also important to note that aphids also select suitable hosts after landing on a plant and this discrimination appears to be made after probing [66], which leads to the next step of host plant selection.

VOCs emitted by host plants encourage the attraction of *M. persicae* than non-host plants [67]. Infection of PLRV modify the composition or concentration of headspace of infected plants which act as stronger attractant to *M. persicae* [64].

Step 2: Initial plant contact and pre-probing period

During this stage aphids make a decision to stay on the landed plant or to move to a new plant. Aphids tend to walk while moving their antennae from side to side searching for desired cues before stylet penetration. Aphids look for odour cues [68], gustatory cues [69], plant texture [70,71], topology [72], as well as olfactory cues [73] before deciding to probe. However, they also attempt stylet penetration as a reflex to the tarsal contact with leaf surfaces [70]. Upon landing, aphids tend to move to different places of plants as each aphid species has preferred sites to colonize. *M. euphorbiae* prefer to colonize older leaves of lettuce while *Nasonovia ribisnigri* prefers younger leaves and absent in the old leaves [74]. *M. persicae* prefers to settle on the under surface of the leaves rather than the upper side [75].

Step 3: Test probing: acquisition and inoculation of stylet-borne viruses

The first few stylet probes are brief usually less than 1 min and limited to epidermal cells. Winged aphids land on the host plant and make test probes before either move to a new host [76,77] or a different location of the plant [78]. This behaviour is well observed in electrical penetration graphs (EPG). Supp. figure 2a shows a simplified illustrates the EPG set up and in supp. figure 2b, a simplified example of different wave forms generated during aphid feeding is presented. Assuming that a non-viruliferous aphid has landed on a plant infected with an aphid transmittable virus, this brief probing will enable the acquisition of the viruses, such as CMV or *Potato virus* Y (PVY, genus Potyvirus) and semipersistent viruses such as CaMV [79]. In EPG studies this step is identified by "potential drop" (pd) and has divided into three subphases: II-1, II-2 and II-3 [69,80] (Supp. Figure 2c). These pds are also known as "standard-pds" [81].

In a situation where a viruliferous aphid has landed on a healthy host plant, subphase II-1 will enable the inoculation of viruses such as PVY and CMV by their aphid vector [80]. The watery salivation occurs during subphase II-1 (Supp. Figure 2c) is responsible for the inoculation of PVY, CMV [80] and PEMV [82]. PEMV accumulates in the accessory salivary glands and does not retain in the stylet [82] showing that the watery salivation flushes out virus particles from the acrostyle (common duct at the end of the stylet) .

The function of subphase II-2 (Supp. Figure 2c) in aphid feeding is not well understood [81]. However, subphase II-2 has been related to the inoculation of CaMV which is a semi-persistent virus [83].

Subphase II-3 (Supp. Figure 2c) represents the ingestion phase of cell contents which is correspondent to the acquisition of nonpersistent viruses. It has been proposed that the subphase II-3 plays a critical role in virus acquisition and when subphase II-3 is sufficiently short, the probability of virus acquisition is also reduced [80,84,85].

Step 4: Stylet penetration beyond the epidermis (stylet pathway activity)

This is the phase between probing epidermis and phloem. Aphids primarily feed on the phloem sap and hence upon successful test probing, the aphid will extend its stylet deeper through the intercellular spaces [76,86]. This stage can last for few minutes to several hours and can be observed as the waveform C in EPGs (Supp. Figure 2b). This stage has less importance with respect to virus transmission.

Step 5: Phloem puncture: inoculation of phloem restricted viruses

Some viruses transmitted by aphids are unable to move outside phloem element (viruses included in the genera *Luteovirus*, *Polerovirus*, *Enamovirus* and *Closterovirus*). Phloem puncture is initially followed by injection of watery saliva which is likely inoculate the virus into the phloem (eg., BYDV) [87]. This is the beginning of "phloem sieve element phase" (PSEP) which occurs when the stylet is in a phloem sieve element or companion cell [88,89]. The initial puncture is newly classified as "phloem pd" (Supp. Figure 2b). Phloem pds always occur shortly before PSEP and has less voltage drop of standard-pds and similar voltage drop as PSEP. The watery saliva during this phase may be responsible for the inoculation of phloem limited viruses as virions retained in the acrostyle possibly be dislodged and flushed out by salivation [81,90].

Step 6: Sustained feeding: acquisition of phloem restricted viruses

If aphids are feeding on the phloem for longer periods (usually more than 10 min) it is represented as phloem acceptance and sustained ingestion. This phase can be identified in EPG as E2 wave form and it is always preceded by the E1 wave form (phloem salivation phase) (Supp. Figure 2d). The watery salivation is continued during the feeding on phloem yet saliva do not enter into the phloem canal due to the high hydrostatic pressure [91]. Watery saliva produced mix with the ingested sap in the acrostyle and flow through the food canal. This was seen with significant increase in acquisition efficiency of BYDV during longer phloem ingestion (E2 > 10 min) [87].

Retention of the virus in aphid body

When the aphid acquires a virus, the virus must be retained in the aphid body until it moves to feed on a new host plant. This retention time and the retention place of the virus depends on virus type. These two criteria have widely used in the characterisation of the aphid transmission modes. The retention time can be from a few seconds to several days and this determines the persistency of the virus in the vector [23,80,82]. The virus's ability to circulate determines the retention place either to be in stylets or salivary glands [92,93].

Non-calculative viruses are further divided as non-persistent and semi-persistent viruses, mostly based on the retention time. A ''capsid strategy'' and the ''helper strategy'' are also proposed, which explains the retention of non-calculative viruses in the aphid stylet [4,14,94]. Some viruses require a virus-encoded HC protein to facilitate the retention of the virion in the stylet i.e., helper strategy. P2 protein, the helper component of CaMV binds directly to the acrostyle [23]. The helper component links the virions with the receptors in the acrostyle in a very specific manner [22]. *Parsnip yellow fleck virus* (PYFV, genus: *Sequivirus*) also employs a helper strategy in its transmission. In fact, PYFV unusually uses the HC of another virus, *Anthriscus yellows virus* (AYV, genus: *Waikavirus*) for its transmission [95]. HC can sometimes work *in trans* as a platform that interlinks two viruses with the aphid stylet [96]. In the capsid strategy, the virus interacts directly with the vector via its CP. *M. persicae* transmits intact CMV (with conserved capsid surface) [97] but not the isolated RNA [98] proposing that the CMV capsid binds to the receptor(s) in the stylet of aphid.

Viruses belonging to family *Rhabdoviridae* and *Luteoviridae* are transmitted in a circulative manner through aphids must have the ability to cross several apical and basal barriers in the midgut/hindgut to reach the ASG. These barriers are often selective and possess virus specific receptors [28]. Aphids use the ASG to filter any waste from the haemolymph as they lack a malpighian tubule system [99].

Effects of plant viruses on their aphid vector

The aphids' interactions with the host and its biology is greatly influenced by plant viruses. This is mainly due to indirect effects of the virus-induced changes in the host plant such as nutritional quality, symptomatology and changers in VOCs. These indirect behavioural and performance changes also can be categorized as plant-mediated effects of viruses on aphid. From the existing literature it is evident that these plant-mediated effects can be host plant and vector specific [42,100]. Furthermore, it can also be virus strain-specific [101]. In this review we have compiled a total of 37 pathosystems where different species of aphids are involved. The effects to the aphid in each pathosystem are summarized in the Table 1. Among viruses transmitted by aphids, indirect effects on aphid tend to be positive with understandable positive effects from plant viruses.

In addition, it has been evident that the presence of virus in vector's body also affects the biology and performance of the vector (the direct effect). The viruliferous aphids can change the preference of the host plant from infected plant to a healthy plant and may have physiological changes such as tolerance to heat (Table 2). These direct changes in vector may have an obvious response to ensure the spread of plant viruses.

Concluding remarks

A majority of plant viruses have adapted for transmission by aphids. In this review we discussed the aphid biological, morphological and behavioural aspects influencing the transmission of plant viruses. Much progress has been made in understanding the role of viruses in transmission aspects but a review was combining the morphological and behavioural adaptation of the aphid in virus transmission was missing. The biology and behavioural mechanisms within the aphid have helped them to become efficient plant-virus vectors, and in return they have benefitted (at least in some cases) by the improved nutritional characteristics of their host plants. It has been evident that both circulative and non-circulative viruses have specific binding sites in the aphid body. The host selection behaviour is one of the key elements which has made aphids an efficient plant-virus vector. The EPG technique has directed into new insights in the behavioural aspects of aphid host selection. Better understanding of the vector will provide innovative strategies to control plant viruses.

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Table 1: Indirect effects on aphid biology mediated by the plant viruses through modifications in the host plant

Pathosystem			Effects on aphid	Reference
Vector sp.	Host plant	Virus		
Myzus persicae	*Solanum tuberosum*	PLRV	Preferential settling on infected plants due to changes in VOCs	[64,102–107]
			Mean relative growth rate and r_m rate were significantly enhanced in infected plants	[108]
		PVY	Preferential settling on infected plants due to changes in VOCs	[109]
	Solanum sarrachoides	PLRV	Infected plants attract and arrest aphid by changing VOCs	[110]
			Nymphal survival, fecundity, reproductive periods, adult longevity, and r_m were significantly higher in infected plants	[111]
	Capsicum annuum	CMV	Populations growth was significantly higher infected plants	[112]
			Preferential settling on infected plants due to changes in VOCs	[113]
	Cucurbita pepo	CMV	Aphids were attracted by infected plants but the performed poorly due to reduced nutritional quality resulting rapid emigration	[114]
	Nicotiana benthamiana	TuMV	Preferential settling on infected plants and enhanced reproduction	[115]
		PLRV	Greater number of aphids settled on infected and increase fecundity	[116]
		CMV	Aphid reproduction and survival were significantly enhanced	[101]
	Ipomoea batatas	SPFMV, SPVG and SPV	The r_m and the net reproductive rate were significantly greater on mixed virus-infected plants	[117]

	Beta vulgaris	BYV	Rapid and significant increase in aphid performance on infected plants	[118,119]
	Capsicum annuum	PCV-1	Significant increase in reproduction on infected plants	[113]
	Nicotiana tabacum	CMV	Negatively affects on growth rate and longevity and increased alate production on infected plants	[120]
			Virus mediate H2O2 production reduced the host preference and encouraged migration	[121]
		PVY	Infected plants attracted more aphids and influenced probing behaviour	[122]
	Arabidopsis thaliana	TuMV	Infected plants attract and arrest aphid by changing VOCs	[109,123]
		CMV	Infected plants increased both individual growth rate and colony growth	[124]
	Camelina sativa	TuYV	The pre-reproductive period was significantly shorter and r_m were significantly higher	[125]
Brevicoryne brassicae	*Camelina sativa*	TuYV	Pre-reproductive period was significantly longer and reduced daily fecundity and r_m	[125]
		CaMV	Reduced daily fecundity r_m	[125]
Macrosiphum euphorbiae	*Solanum sarrachoides*	PLRV	Nymphal survival, fecundity, reproductive periods, adult longevity, and r_m rate was higher in infected plants	[111]
Acyrthosiphon pisum	*Vicia faba*	BYMV	Preferential settling on infected plants and reduction in aphid survival	[126]
	Pisum sativum	PEMV	Preferential settling on infected plants due to changes in visual cues and/or by changing host chemicals	[127,128]
		BLRV	Fecundity was significantly enhanced in infected plants	[129]
Rhopalosiphum padi	*Triticum aestivum*	BYDV	Preferential settling on infected plants due to changes in VOCs	[130,131]
			Significantly increased fecundity and development time under increase temperature and CO2 levels	[132]
	Avena sativa	BYDV	Increased alate production	[133]

	Avena strigose	BYDV	Increase food consumption and fecundity on infected plants by altering nutrition quality of the host plant	[134]
Rhopalosiphum maidis	*Avena strigose*	BYDV	Increase food consumption and fecundity on infected plants by altering nutrition quality of the host plant	[134]
Schizaphis graminum	*Avena sativa*	BYDV	Increase the rate of population growth	[133]
Macrosiphum granariiun	*Avena sativa*	BYDV	Increase the rate of population growth	[135]
Sitobion avenae	*Avena sativa*	BYDV	Lower efficiency of phloem sap utilisation on infected plants and reduction in r_m	[136]
Micromyzus kalimpongensis	*Ammomum subulatum*	CBDV	Preferential settling on infected plants, shortened nymphal period, increased longevity and fecundity	[137]
Aphis gossypii	*Cucumis sativus*	CMV	Alates attracted to infected plants but preferred to settle and reproduce on un-infected plats	[138]
	Cucurbita pepo	CMV	Increase emigration from infected plants by changing VOCs	[112]
		CMV	Preferential settling on infected plants due to changes in VOCs and rapid emigration from infected plants due to reduces host-plant quality	[114]
		ZYMV	Reduced colonization and feeding in infected plants	[139]
		PRSV	Increase longevity, fecundity and r_m in infected plants	[140]
Aphis glycines	*Glycine max*	AMV, SMV and BPMV	Increase mortality on infected plants	[141]
Aphis fabae	*Phaseolus vulgaris*	CMV	Probing behaviour was altered in infected plants	[142]

PLRV *Potato leafroll virus*, PVY *Potato Virus Y*, CMV *Cucumber mosaic virus*, TuMV *Turnip mosaic virus*, SPFMV *Sweet potato feathery mottle virus*, SPVG *Sweet potato virus G*, SPV *Sweet potato virus*, BYV *Beet yellows virus*, PCV-1 *Pepper cryptic virus 1*,TuYV *Turnip yellows virus*, CaMV *Cauliflower mosaic virus*, BYMV *Bean yellow mosaic virus*, PEMV *Pea enation mosaic virus*, BLRV *Bean leaf roll virus*, BYDV *Barley yellow dwarf virus*, CBDV *Cardamom bushy dwarf virus*, ZYMV *Zucchini yellow mosaic virus*, PRSV *Papaya ringspot virus*, AMV *alfalfa mosaic virus*, SMV *Soybean mosaic virus*, BPMV *Bean pod mottle virus.*

Table 2 Direct effects of the virus on their aphid vector

Aphid species	Virus	Direct or dynamic effect to the aphid vector	Reference
Rhopalosiphum padi	BYDV	Viruliferous aphids changed preference to healthy plants	[143]
		Viruliferous aphids gained enhanced thermal tolerance	[144]
		Viruliferous aphids increased weight at ambient CO_2 levels	[145]
Myzus persicae	PLRV	Viruliferous aphids changed preference to healthy plants	[146]
	SMV	Viruliferous aphids performed well under water stress	[147]
Aphis gossypii	CMV	Viruliferous aphids prefers noninfected plants and changed the probing behaviour	[138]
	CABYV	Viruliferous aphids prefers noninfected plants over infected plants	[148]

BYDV *Barley yellow dwarf virus*, PLRV *Potato leaf roll virus*, SMV *Soybean mosaic virus*, CMV *Cucumber mosaic virus*, CABYV *Cucurbit aphid-borne yellows virus.*

Box 1. Plant virus categorization based on time taken for acquisition, retention and inoculation and ability to replicate inside the insect body. Based on above characters plant viruses transmitted by insects can be classified to two main categories, namely circulative and noncirculative plant viruses. Circulative also known as persistent viruses can be further classified in to circulative propagative and circulative non-propagative viruses. For noncirculative plant viruses, two distinct classification modes have proposed i.e., 1. based on the virus acquisition and retention time and 2. based on molecular interaction with the virus particles and stylet receptors. Both classifies non-circulative viruses into another two groups.

Figure 1. Simplified model of non-calculative and circulative virus transmission mode in aphids. Aphid stylet is the acquisition apparatus of plant viruses and retention site of nonpersistent viruses. (**a**) the cross section of an aphid stylet exposes the two main canals, the food canal and the salivary canal formed by interlocking two maxillary stylets which are enclosed in a pair of mandibular stylets. Each mandibular stylet is supplied with two nerve dendrites. (**b**) In noncirculative virus transmission virus particles can either bind directly to the stylet receptors (capsid strategy) or via a helper component (helper strategy) produced by the virus. The virus retention site at the stylet is known as the acrostyle (AS) which is located in the common canal resulting from fusion between the food canal (FC) and the salivary canal (SC). (**c**) Illustration of an aphid feeding on a plant tissue. The aphid is penetrating the plant tissue using its stylet. Upon penetration aphid secrets saliva and a sheath is formed upon hardening of the saliva encasing the stylet. The stylet path, mainly take an intercellular route to the phloem. (d)The virus moves to the gut of the aphid and passes the gut epithelium to enter the haemolymph of the insect. The gut of the insect act as the internalization site for the circulative plant viruses. During the transcytosis of the virus it may or may not replicate (propagative and non-propagative types). (b) Virus particles released in to the hemolymph entered in to accessary salivary glands (ASG) by first crossing the basal lamina (BL) surrounding the gland, then the basal plasmalemma (BPL). Finally, the virus particles are released in the salivary duct (SD).

Supp. Figure 1. Typical lifecycle of *Myzus persicae*. *M. persicae* is a well-studied polyphagous aphid which can transmit around 50 plant viruses. The aphid consists both alate and apterous forms in its life cycle. It is mainly reproduced non sexually through parthenogenesis. Both alate and apterous forms are produced through parthenogenesis as demanded by the environment. The aphid also can go through sexual reproduction.

Supp. Figure 2. Monitoring of aphid feeding behaviour by the electrical penetration graph (EPG) method. (**a**) Simplified illustrates the EPG set up. The circuit connecting the aphid via a gold wire and to the plant via a copper electrode placed in the soil is completed when aphid start probing and thus the wave forms can be observed. Each wave form corresponds to a different stage in aphid feeding on plant tissue. (**b**) A simplified example of different wave forms generated during aphid feeding. NP; Non-penetration, A; Cuticle penetration, B; salivation in mesophyll, C; stylet pathway, pd; stylet puncture, F; penetration difficulties. (**c**) The stylet puncture is demarcated by the potential drop(pd) which has three distinct phases. The phase II is further divided in to three, i.e., II-1 and II-2 is important in nonpersistent virus inoculation while sage II-3 is involved in acquisition of nonpersistent viruses. (**d**) Wave form E1 and E2 represents sustained feeding in phloem tissue. The waveforms represent the inoculation and acquisition of phloem-limited viruses which occurs at phloem-pd (^{Ph}pd). E1, salivation into phloem sieve elements and the inoculation step of phloem-limited viruses; E2, passive phloem sap uptake from sieve elements and acquisition step of phloem-limited viruses. Persistent virus acquisition occurs during this stage.

[1] Based on International Committee on Taxonomy of Viruses (ICTV) [149] and ViralZone root [150].

[2] Only one virus species from this family has been identified to be aphid transmitted [Geminiviridae [38,151], Reoviridae [151], Alphaflexiviridae [152]]

[3] Not all viruses belonging to this genus are transmitted by aphid

[4] Transmitted at a low efficiency by aphid [153]

[5] Requires a helper virus for aphid transmission