

Review

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Review

Phytovirus Vectors, Detection Techniques, and Future Directions

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Abstract: The majority of the well-known genera of plant viruses, such as Caulimovirus, Reovirus, Tospovirus, Crinivirus, Luteovirus, Geminiviridae, and Tenuivirus, are vectored, spread, and transmitted by phytophagous insects. Mostly, they are vectored by the orders of Hemiptera and Thysanoptera, and by some species of Coleoptera, Orthoptera, and Dermaptera. The occurrence of a single species of these phytophagous insect orders resulted in one or more plant viruses in general, and the Hemipteran order in particular vectored a lot of plant virus species. This review manuscript is focused on vectors of plant viruses, techniques for their detection, and future directions. It will play a vital role in exploring scientific information concerning the association between plant viruses with their vector insects, host plants, techniques of plant virus detection, and some important points to be considered in the future sustainably.

Keywords: insect vector; host plant; plant virus; virus detection; virus transmission

1. Introduction

Insects provide food for birds, chickens, and humans, as well as natural enemies (predators, parasitoids, and parasites) of other insects (Garca-Lara and Saldivar, 2016; FAO, 2013), and pollination (Samways, 2018). In contrast to these benefits, many insect species are harmful to our plants by causing disease, injuring, spoiling, damaging, and reducing their yield and marketability (Hill, 1997). They also damage construction materials, buildings, and timber. In addition,

Insect pests vector phytoviruses on healthy plants. For instance, aphids and whiteflies vector many plant virus species, which cause vulnerability after being infested by those insect pests and their associated viruses. This is why the occurrence of a single phytophagous insect vector is one or more species of plant viruses. The insects that vectored plant viruses varied based on the diverse resources of their feeding habits and ecological factors (Janz *et al.*, 2006).

The well-known plant virus vector insects belong to the genera of Caulimovirus, Crinivirus, Luteovirus, Geminiviridae, Reovirus, Tospovirus, and Tenuivirus (Singh *et al.*, 2020). Most of them are vectored by the Hemiptera, Thysanoptera, and by some species of Coleoptera, Orthoptera, and Dermaptera orders. Among them, the Hemipteran order alone vectored 70% of all known insect-borne plant viruses. Hemipteran aphids and whiteflies can vector more than 500 plant virus species (Fereres and Raccah, 2015).

Generally, aphids, leafhoppers, whiteflies, thrips, psyllids, some beetle species, and mealy bugs are the most vectoring plant pathogens (Chandi *et al.*, 2018). Aphids, whiteflies, and psyllids are Hemipteran orders that have piercing and sucking mouthpart modifications. These insect groups are vectors of pathogens such as viruses, such as those in other groups (Garzo *et al.*, 2020; Heck, 2018). Irrespective of the type of transmission, a virus-vector relationship is highly specific and depends upon the potential of vectors to spread the plant disease. Naturally, they were traveling a short distance by themselves. But they used insects as vectors to travel a long way from infected to healthy host plants. Hence, this association makes them difficult to manage. A consistent feature between these interactions requires specific molecular interactions between the virus and the host, commonly *via* proteins (Dietzgen *et al.*, 2016).

Usually, insect-based vector transmission is recycled between the insect vectors that feed on plants and from the mother vector to her offspring (Purcell and Almeida, 2005). Most of these viruses are entered into host plants during chewing and sapsucking of the host plant parts. Hence, the objective of this paper is to review the vectors of plant viruses, their detection techniques, and future directions.

2. Vectors of Plant Viruses

2.1. Interactions of Plant Viruses and Host Insects

Plants in nature interact with multiple plant viruses, specifically with phytophagous insect hosts in the environment. Thus, phytophagous insects serve as plant virus reservoirs in ecological systems (Wielkopolan et al., 2021; Wu et al., 2020). Wu et al. (2020) reported that more than 1,213 RNA viruses in 40 families were identified from 32 orders, which included more than 600 insect species from different ecological habitats. Moya et al. (2004); Bull et al. (2007); Pybus and Rambaut (2005). However, host-insect and virus interactions are complex and have evolved (Jeger, 2020; Gandon, 2018; Gutiérrez et al., 2013). Insects are transmitting plant viruses through vectors comprehensively with biting and chewing types of mouth parts (Butter, 2021).

The host plants are important in mediating plant viruses and their vectors (Biere and Tack, 2013; Gutiérrez et al., 2013). In this case, the vector insect is feeding on plant parts to continue their lifecycle and generation and shares a wide range of symbiotic relationships, which can be beneficial or harmful. It is a fact that the relationships between plant viruses and vector insects are interspecific and vary with their host plant species, persistence, and ability to circulate within the bodies of their hosts or vectors (Chandi et al., 2018; Dietzgen et al., 2016; Harris, 1977; Kennedy et al., 1962). These interactions can be persistent, semi-persistent, or non-persistent transmissions. The interaction of plant viruses with insect hosts requires a specific molecular interaction for recognizing proteins between them (Dietzgen et al., 2016).

The host plants respond to insect pests by being injured or wounded and making suitable conditions for the growth and development of plant viruses after being injured. In short, insects are pests, vectors, and reservoirs of plant pathogens such as viruses (Wielkopolan et al., 2021; Wu et al., 2020; Gadhave et al., 2019).

Interactions between herbivores, insects, and pathogens can be mutualistic or antagonistic, with possible joint effects on the host depending on the species (Kluth et al., 2002). Mutually, the virus-induced changes in host plants might benefit the insect vector (Casteel and Jander, 2013). Insect vectors also benefit from transmitting plant viruses through host expansions and get good hosts. In line with this, Zhang et al. (2012) indicated that the whitefly performance is greatly enhanced on tobacco (*Nicotiana tabacum*) infected by begomovirus-infected tobacco (*Nicotiana tabacum*) by selecting and feeding on the virus-infected tissue. Martinière et al. (2013) reported that the *Cauliflower mosaic virus* rearranged itself within the cell when aphids punctured infected cells and promoted attachment to the aphid's stylets during feeding. These symbiotic interactions might occur due to viral recognition of aphid effectors or aphid-induced plant responses, and the aphid is actively manipulated by the alteration of the host plant-virus interactions. Therefore, understanding the functions of effectors and elicitors in complex interactions is critical for deciphering how plant viruses and insects colonize host organisms and how plant immunity is orchestrated (Ray and Casteel, 2022). The relationship between the insect vector, the virus, and their effectors may be dependent on insect vectors or the host. In other cases, even the interactions that occur naturally between insects and microbes can indirectly harm or help the other plant challenger through changes in plant chemistry and immunity. But these interactions can also be beneficial to the other individual as a certain entity (West et al., 2007). The pathogen could also alter behavior, altering phenotypic traits for transmission (Lefevre and Thomas, 2008). et al. (2012) report also agreed with this report in that plant viruses alter the insect behavior to enhance their spread. These interactions could be facilitated by proteins within plant viruses, and insect vectors. For instance, proteomic proteins are used to interact with plant viruses and insect vectors for transmission (Mittapelly and Rajarapu, 2020). The proteins found in the

host plant cells also respond to efficient plant virus transmission. Plant viruses are endocellular and can move inside their host cells for multiplication (Uzest *et al.*, 2011). Thus, understanding the mechanisms of these interactions is used to underpin the management strategies of plant viruses' infection by interfering with suitable host cells, nutrient uptake, and mechanisms of their transmission (Dietzgen *et al.*, 2016).

The vector-based transmission of plant viruses is categorized into virus helper component *proteins* and *capsid proteins* (Agranovsky, 2021). The viral helper protein components serve as an adaptor between the plant virus (capsid protein) and the receptor in the vectors. The receptors are used to assemble their interactions (Agranovsky, 2021). The capsid protein components are the infectious virions' way of protecting their genomes during entry and exit from the host cells. Plant viruses belonging to disparate groups developed unusual capsid proteins that are used to provide interactions with their vector. For example, the cauliflower mosaic virus is transmitted by aphids, which have major capsid, protein, and helper components.

Plant viruses are transmitted after being probed with their vector during feeding up the nutrient contents of the host plants (Cunniffe *et al.*, 2021). After herbivores, the insect's vector viruses infect the life cycle, population genetics, and evolution (Gutierrez *et al.*, 2013). Most of the plant viruses were visible following the infestations with a diversity of insect vectors. And they could affect their natural enemies' yield, quality, quantity, and marketability. For example, semi-persistent beet yellow virus occurred on *Beta vulgaris* and increased sugars by decreasing the total amino acid content after being infected and the quality of the parasitoid, *Lysiphlebus fabarum*, attracted towards the *Aphis fabae* by it (Albittar *et al.*, 2019).

Many host insects carry plant viruses but cannot transmit them to their host plants, so they are not vectors. Usually, insect-based vector transmission occurs by feeding (Purcell and Almeida, 2005). The infection of several exogenous and intestinal tract viruses threatens insect pests by entering into their bodies through natural openings (e.g., by orally/mouthparts during feeding and sap-sucking of plant parts including foliage). Insects are never given up easily to viral infections. But they fight against viral invaders from their intestinal tract by forming physical and immunological barriers to defend against their invasion. Cell-intrinsic antiviral immunity, peritrophic matrix, mucin layer, and local symbiotic microorganisms (Ma *et al.*, 2021).

Exploring plant viruses is not new to science. It accounts for more than one century (nearly 120 years ago). For example, studying the tobacco mosaic virus is the most studied plant virus. This indicated that the association between plants, vectors, and viruses has a long history. But the previous study's inefficiency in the study of plant viruses that are associated with undomesticated plants is evident. However, in undomesticated plants, viruses are common and sometimes considered mutually exclusive rather than pathogens. Moreover, the virulence of the plant virus is probably not beneficial for most plant interactions, so their relationship might be commensally and mutually (Roossinck, 2015).

Understanding the physiological and ecological interrelationship between insect vectors and plant viruses is important to know the viruses that invade and injure plants after being infested and infected (Purcell, 2009). Generally, plant pathogens are transmitted to susceptible host plants by insect vectors (Heck, 2018). Shi *et al.* (2021) indicated that plant viruses were transmitted if there were three participants or factors: 1) virus, 2) vector, and 3) host plant susceptibility. These factors achieved their goals by altering the host selection behavior of the vector insect to enhance and promote plant virus transmission (Ingwell *et al.*, 2012). The plant infected by the virus is changing organic compound volatile profiles for elicitation to settle their vectors (Jiménez-Martínez *et al.*, 2004; Eigenbrode *et al.*, 2002).

Naturally, plants infected by virus strains attract more insect vectors than healthy ones. This is also supported by the work of Adhab *et al.* (2019), who found that the turnip infected with the W260 strain of cauliflower mosaic virus attracted more aphids than healthy. After being infected, plant viruses encounter defense barriers at every step of their replication cycle; i.e., spread in agro-ecosystems the agro-ecosystems and transmission, plant cell infections, and systemic invasion. However, the host plant resists viruses by various passive or active mechanisms, including the RNA-

silencing machinery and the innate immune system, which are mediated by physical barriers (e.g., by forming thick waxy cuticle and its cell walls), blocking or lacking a component required for the virus to complete its life cycle, triggering immunity and its effectors, and silencing the function of the RNA system (Leonetti *et al.*, 2021).

The specific protein characteristics that encoded the surface structure of the plant virion were essential for its transmission by insect vectors. The plant virus particles were required to retain the specific binding sites when attached to specific sites in insect vectors until they were transmitted to host plants. Some plant viruses also have nonstructural protein helpers that act as a bridge for binding virions to vectors (Singh *et al.*, 2020).

Based on the duration of the plant viruses' persisting in the bodies of their insect vectors, they were categorized into non-persistent, semipersistent, and persistent (Sylvester, 1962).

Those transmitted within certain minutes after contacting their host body are known as non-persistent. They are formed into capsid-like structures and transmitted quickly after being contaminated by the mouthparts of the insect hosts and by using their stylet to puncture their intracellular mechanically. But they do not persist longer in the epidermis and mesophyll of the host plant cells (Powell *et al.*, 2005; 1995; Martin *et al.*, 1997; Powell, 1995) and are retained in the stylets for a while (Shi *et al.*, 2021). For instance, cucumber and cauliflower mosaic virus particles are transmitted by the aphid (*Myzus persicae*) (Moreno *et al.*, 2012). The semi persistent, on the other hand, will transmit for up to an hour after acquiring the host. They were also residing in chitin-lined areas without internalization of the host gut (James and Falk, 2006) and without spreading to the salivary glands (Shi *et al.*, 2021). But they are bound to the internal body of the insect body via the chitin lining of their gut (James and Zhou, 2015). The Tomato chlorosis virus in the genus of Crinivirus that is transmitted by whitefly (*Bemisia tabaci*) is a typical example of this virus. Unless their economic importance is not well known in the world, as the report from more than 20 countries, including China, indicated (Shi *et al.*, 2018). Even though serving as mediators of plant viruses to the host plants during transmission by retaining them in the insect vectors' bodies, for example, yellow crinivirus is infectious in the white fly foregut (*Bemisia tabaci*) (vector). It is transmitted when they regurgitate it (Chen *et al.*, 2011; Stewart *et al.*, 2010). In addition, several citrus aphid species, such as *Toxoptera citricida* transmitted the *Citrus tristeza* virus to citrus plants (Herron *et al.*, 2006). Unfortunately, mostly, they did not appear when they were entered into the host tissues. Their range of transmission also increased as the climate changed (Feres, 2015).

After contacting the bodies of their hosts, persistent plant viruses were transmitted within hours to days and were even inherited by insect progeny (Bragard *et al.*, 2013). They were retained in the insect vector guts and tissues. Unlike semi persistent, they were able to spread and invade the salivary glands (Shi *et al.*, 2021; Hogenhout *et al.*, 2008). This type of virus is divided into two parts: circulative (non-propagative) and propagative. The circulative viruses circulate through the alimentary canal to reach the hemocoel and accessory salivary glands; they do not replicate in vector tissues. But traverse the insect gut, hemolymph, and salivary tissue to reach the salivary glands for transmission to the host plants (Pinheiro *et al.*, 2015; Bragard *et al.*, 2013). Or they were spread to neighboring organs to reach the salivary glands for transmission and replication mechanisms in their vector tissues (Bragard *et al.*, 2013; Hogenhout *et al.*, 2008). In contrast, propagative viruses replicate and invade the salivary glands of their vector insect hosts before being transmitted (Bragard *et al.*, 2013; Ammar *et al.*, 2009).

The host plant cells have pectin and cellulose barriers that are used to limit the success of plant viruses' exiting, entering, and transferring from one host plant to another after being vectored by the host insect. But to overcome these barriers, plant viruses can also influence the physiology and behavior of the vector to increase their chances of transmission (Adhab, 2021; Kersch-Becker and Thaler, 2014). Understanding the behavior, physiology, and population dynamics of host insects is used to learn about their effects on insect vector feeding habits, evolutionary relationships with plant viruses, virus behavior in host plants, and transmission efficiency (Gutiérrez *et al.*, 2013). This might be due to having a lipid-based phytohormone such as jasmonate, which is more or less similar in structure to animal prostaglandins. They are used to confer plant defenses against various biotic and

abiotic challenges (Ali and Baek, 2020; Wu and Ye, 2020; Larrieu and Vernoux, 2016; Green and Ryan, 1972). Phytohormones jasmonate act on gene expression to slow growth, repair the damaged body, and order the metabolism to produce defensive molecules against the virus (Larrieu and Vernoux, 2016; Green and Ryan, 1972), which can be used to interfere with the preference and performance of insect pests (Walling, 2000). Furthermore, jasmonates stimulate defense by altering the qualitative and quantitative composition of plant volatile compounds, causing them to attract natural enemies and repel herbivorous insects (Kraus and Stout, 2019; Okada *et al.*, 2015; Lou *et al.*, 2005). Indirectly, chewing insects can promote and induce jasmonic acid in plants. This might be used to inhibit the expression of defenses associated with salicylic acid (Chisholm *et al.*, 2018; Thaler *et al.*, 2012; Koornneef and Pieterse, 2008).

Generally, non-persistent and semipersistent ants persist for a short time and cannot enter the hemolymph of insect vectors. But the persistent plant viruses are retained in the hemolymph of their vectors for a long time (Shi *et al.*, 2021).

2.2. Insects Mediated Plant Virus Transmission

Naturally, plant virus transmission has occurred following the injury of plant parts by aphids, leafhoppers, planthoppers, whiteflies, mites, nematodes, and beetles (Shi *et al.*, 2021; Singh *et al.*, 2020; Whitfield *et al.*, 2015; Ambethgar *et al.*, 2019; Bragard *et al.*, 2013; Hunter, 2008), through sap inoculation/mechanical, wounded sap, graft transmission, fruit viruses, mammals, and parasitic weeds, e.g. dodder, contaminated soils and agricultural operations, other herbivores, and physical contact with virus diseased plant parts. Plant viruses are vectored and transmitted by phytophagous insects as they move from infected to healthy plants for feeding (Gutiérrez *et al.*, 2013) and wound above and belowground plant organs (Labandeiraa and Prevec, 2014). Geminiviridae is the largest family of plant viruses, characterized by a circular, single-stranded DNA genome, devastating plants, and a prominent reason for global crop yield losses (Gupta *et al.*, 2021). It is replicated by rolling circularly and recombining dependently (Jeske *et al.*, 2001). They are primarily transmitted by hemipterous insect vectors as they move across host plants in search of nourishment. The best-known plant viruses alter the host gene expression profile to regulate the host cell across signaling pathways and induce severe diseases in plants. For example, geminiviruses are manifested in leaf curling, vein swelling, chlorosis, growth stunting, bending of stems, and reducing leaf size (Bhattacharyya *et al.*, 2015; Mansoor *et al.*, 2006).

Human beings are also playing a great role in the movement of plant viruses across continents, countries, states, villages, and farmlands by moving infected plant materials and other plant propagules to exchange crop or plant materials across the world (Rubio *et al.*, 2020). In addition, the increase in the diversity of virus vector insects owing to numerous factors, including climate change, can increase virus spread (Feres, 2015). Regularly, potential plant virus emergences result from human beings' contact with infected plants and genetically uniform hosts during agricultural practices. Viruses cause nearly 50% of emerging plant diseases (Bernardo *et al.*, 2018). Plants affected by drought stress are highly susceptible to viruses due to changes in their physiological functions. Therefore, they are highly susceptible to plant-vector interactions with plant viruses (van Munster *et al.*, 2017).

The diversity of plant viruses in natural ecosystems is still not well known. But, understanding their diversity of them is used to know the mechanisms and consequences of their movements and evolution to predict their status in the future. It is also used to manage them strategically through immunization (genetic resistance by plant breeding, plant transformation, and cross-protection) and prophylaxis to restrain them by using quarantine, certification, removing infected plants, and controlling natural vectors after they have been accurately identified (Rubio *et al.*, 2020).

It is true that the majority of plant viruses, estimated to be around 80%, were vectored by a phytophagous insect (Hohn, 2007). Mostly, it is vectored by the Hemiptera (whiteflies and aphids) and Thysanoptera (thrips) orders. Both orders have common features like small size, many generations per year, large populations, and cosmopolitan distribution (Tooker and Giron, 2020). The Hemiptera insect orders feed on the vascular tissue of the plant phloem (Buchholz and Trapp, 2016),

while Thysanoptera rasp and suck up mostly on young leaves, sprouts, and floral content (Wu *et al.*, 2020). Coleopterans (beetles) are also vectors of a lot of plant viruses (Wielkopolan *et al.*, 2021). In recent decades, the begomoviruses in America might have been transmitted by the vector of whiteflies (*Bemisia tabaci*). Rice yellow mottle virus is also disseminated by beetles, grasshoppers, and leafhoppers (Koudamilo *et al.*, 2015). Zest *et al.* (2007) reported that cauliflower mosaic virus is vectored by aphids. Bean common mosaic virus is also transmitted by insect vectors after contacting the infected plants' leaves as inoculums. Thus, this indicates that insects are the most important factor in plant virus transmission. The majority of plant viruses are transmitted by piercing-sucking phytophagous insects in particular, and some of them are indicated in Table 1. Insect vector-transmitted viruses have direct effects on host plants' ability to bite rates, feeding amounts, and gene immunity alterations to defend against other related pathogens (Eigenbrode *et al.*, 2018; Shrestha *et al.*, 2012; McKenzie, 2002; Czosnek *et al.*, 1997). The most well-known plant viruses, such as *Tobacco mosaic virus*, *Tomato spotted wilt virus*, *Tomato yellow leaf curl virus*, *Cucumber mosaic virus*, *Potato virus Y*, *Cauliflower mosaic virus*, *African cassava mosaic virus*, *Plum pox virus*, *Brome mosaic virus*, *Potato Virus X*, *Citrus tristeza virus*, *Barley yellow dwarf virus*, *Potato leaf roll virus*, and *Tomato bushy stunt virus* (Scholthof *et al.*, 2011), were vectored and transmitted by aphids, thrips, and whiteflies (Table 1).

Table 1. Insect-Mediated Plant Virus Transmission.

Insect Vectors	Host Crops	Target Viruses	References
Aphids	Cauliflower	Cauliflower mosaic virus	Blanc <i>et al.</i> (2014); Hoh <i>et al.</i> (2010); Zest <i>et al.</i> (2007); Plisson <i>et al.</i> (2005)
	Cowpea	Cowpea mosaic virus	James <i>et al.</i> (2013)
	Cucumber	Cucumber mosaic virus	Pirone and Megahed (1966)
	Bean	Bean common mosaic Virus	https://www.daf.qld.gov.au/__data/assets
	Brassicas	Turnip mosaic virus	https://www.daf.qld.gov.au/__data/assets
	Capsicum	Cucumber mosaic virus, potato virus y	https://www.daf.qld.gov.au/__data/assets
	Carrot	Carrot virus y	https://www.daf.qld.gov.au/__data/assets
	Celery	Celery mosaic virus	https://www.daf.qld.gov.au/__data/assets
	Cucurbitae family	Papaya ringspot virus (w strain), watermelon Mosaic virus, zucchini Yellow mosaic virus	https://www.daf.qld.gov.au/__data/assets

	Lettuce	Lettuce mosaic virus	https://www.daf.qld.gov.au/__data/assets
	Plum	Plum pox virus	Rimbaud <i>et al.</i> (2015)
	<i>Solanaceae family</i>	<i>Potato virus</i>	MacKenzie <i>et al.</i> (2013)
	Sweet corn	Johnsongrass mosaic Virus	https://www.daf.qld.gov.au/__data/assets
	Sweet potato	Sweet potato feathery Mottle virus	https://www.daf.qld.gov.au/__data/assets
	Tobacco	Tobacco rattle virus	Mulot <i>et al.</i> (2016)
	Potato	Potato virus y	Yang <i>et al.</i> (2019)
	Banana	Wolbachia	De Clerck <i>et al.</i> (2015); Leonard <i>et al.</i> (2015); Kollenberg <i>et al.</i> (2014); Xue <i>et al.</i> (2012); Augustinos <i>et al.</i> (2011)
Beetles Grasshoppers, rs,	Rice	Rice yellow mottle virus	Koudamilo <i>et al.</i> (2015)
Leafhopper	Maize	Maize chlorotic dwarf virus	Cassone <i>et al.</i> (2014)
	Rice	Rice yellow mottle virus	Koudamilo <i>et al.</i> (2015)
Leafhopper	Rice	Rice dwarf virus	Chen <i>et al.</i> (2004)
Plant Hoppers and Leafhoppers	Family Poaceae (such as rice)	Tenuiviruses. E.g. Rice stripe virus	Zhao <i>et al.</i> (2019); Zheng <i>et al.</i> (2014); Nault and Ammar (1989)
Thrips	Tomato	<i>Tomato spotted wilt virus</i>	Lu <i>et al.</i> (2020)
	Tomato	Tomato spotted wilt virus	Montero-Astua <i>et al.</i> (2016); Whitfield <i>et al.</i> (2015); Moritz <i>et al.</i> (2004)

	Chrysanthemum, groundnut, pelargonium flower break virus, and maize	Eight species in the genus: 1). Orthotospovirus (Tospoviridae); alstroemeria necrotic streak orthotospovirus-hosts include many ornamentals and vegetable crops; 2). chrysanthemum stem necrosis orthotospovirus host plants include chrysanthemums; 3). groundnut, ringspot orthotospovirus- host plants are many vegetable crops; 4). impatiens necrotic spot orthotospovirus 5). Tomato chlorotic spot or orthotospovirus 6. Tomato zonate spot, orthotospovirus and tomato yellow ring virus 7. Pelargonium flower break virus of the genus Alphacarmovirus, maize chlorotic mottle virus of the genus Machlomovirus (both in Tombusviridae), and yellow leaf curl virus of tomatoes.	He <i>et al.</i> (2020); Liu <i>et al.</i> (2017); Achon <i>et al.</i> (2017); Chen <i>et al.</i> (2017); Kusia <i>et al.</i> (2015); Wei <i>et al.</i> (2015); Batuman <i>et al.</i> (2014); Reitz <i>et al.</i> (2011); Hassani-Mehraban <i>et al.</i> (2010); Nagata <i>et al.</i> (2004)
Whiteflies	Tomato	Tomato chlorosis virus and Tomato severe rugose virus	Fereres <i>et al.</i> (2016); Liu <i>et al.</i> (2013); Gottlieb <i>et al.</i> (2010)
	Banana	Wolbachia	De Clerck <i>et al.</i> (2015); Leonard <i>et al.</i> (2015); Kollenberg <i>et al.</i> (2014); Xue <i>et al.</i> (2012); Augustinos <i>et al.</i> (2011)
	Cotton and Tomato	Cotton leaf curl Multan virus and Tomato yellow leaf curl	Zhao <i>et al.</i> (2019); Pan <i>et al.</i> (2018)

Wide range>420 species	Host plant	Family Geminiviridae begomoviruses	e.g. Nigam (2021); Rosen <i>et al.</i> (2015); Ghanim, (2014)
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2.3. Other Insect-Based Plant Pathogen Vectors

The insect-borne plant bacteria, phytoplasmas, nematodes, Oomycota, and fungi are vectored by insect vectors to continue their life cycle and are responsible for developing plant diseases (Wielkopolan *et al.*, 2021; Eigenbrode *et al.*, 2018). They also alter the behavior and performance of the plant growth stage. Regardless of pathogenicity, they spread, transmit, and maintain plant pathogens (Jeger and Bragard, 2019). Perhaps insects are not easily infected by viruses. They protect themselves by forming physical and immunological barriers (Ma *et al.*, 2021). But insect vectors are hazardous since they spread a lot of plant pathogen within a short period of time. On the other hand, insects can participate in fungal spore dispersion over long distances (Franco *et al.*, 2021) and enter host plants (Phoku *et al.*, 2016; El-Hamalawi and Stanghellini, 2005). For instance, an Ambrosia beetle assists the entry of fungal spores through feeding, injuring, and damaging (Zhao *et al.*, 2019; Hatcher, 1995). This type of insect vector transmission can occur horizontally (environmental source), vertically (maternal inheritance), or, rarely, inheritance from both parents, or *via* a mixture of horizontal and vertical transfer (Bright and Bulgheresi, 2010). Instead, the sooty mold fungus grows on the honeydew excreted by several Homoptera insect orders. Their management is also difficult with a single management method (Chandi *et al.*, 2018). Unfortunately, the transmission of the virus is not limited to insect vectors but can be vectored by other biotic factors (Bragard *et al.*, 2013).

2.4. Techniques of Plant Virus Detection

Historically, little attention has been given to undomesticated or wild plant viruses. But they served as an alternative host. However, the recent efforts of virologists have expanded to explore the true diversity of both domesticated and undomesticated plant viruses. They were detected by both parallel and non-parallel platforms of sequencing methods. Next-generation sequencing (NGS) (Villamor *et al.*, 2019; Maree *et al.*, 2018) and contemporary clustered regularly interspaced short palindromic repeats (CRISPR-Cas) are non-parallel methods (Shahid *et al.*, 2021). This has occurred after massively parallel sequencing or next-generation sequencing microbial detection methods. NGS technologies have impacted plant virology by offering scientists the ability to detect plant viruses that were previously undetected in quarantine and archeological plant samples and have helped to track the evolutionary footprints of viral pathogens. This new technology has become the gold standard for metagenomics and has improved our ability to fully sequence whole genome and genetic information from a given environment. Furthermore, next-generation sequencing is used for discovering, identifying, diagnosing, and exploring the population diversity of individual plant virus strains (Stobbe and Roossinck, 2016; Massart *et al.*, 2014; Stobbe *et al.*, 2013). It is also used for deep sequencing to determine even the minor variants found in a given infection (Simmons *et al.*, 2012).

The next-generation sequencing technology method has also improved the ability of researchers to fully sequence the whole genome in metagenomics. This makes the utilization of next-generation sequencing standardized to identify the RNA of novel species of plant viruses (Massart *et al.*, 2014; Stobbe *et al.*, 2013) by employing various techniques to enrich viral nucleic acids, such as isolating specific forms of RNA (dsRNA, siRNA, ssRNA) or virus particle isolation (Stobbe and Roossinck, 2014; Roossinck *et al.*, 2015). Whereas CRISPR-Cas-based genome editing and detection techniques are producing virus-resistant strains. It enabled us to generate genetically engineered plants by genetics, repair, DNA substitution of base pairs, editing, primes, small molecule detection, and biosensing in plant virology (Shahid *et al.*, 2021). In the former period, the plant virus was detected by protein-based immunological tests with the help of the technique of serology (ELISA), which is based on the specific binding of viral proteins with antibodies and molecular techniques (molecular

hybridization and DNA amplification)) through the binding of viral nucleic acids with specific sequencing of DNA or RNA probes, due to their sequence complementarity. They could be visualized by fluorescent dyes, enzymatic producing colorimetric, and radioactivity reactions by attaching to markers (Rubio *et al.*, 2020; Hull and Al-Hakim, 1988).

The molecular-based techniques for detection also included molecular hybridization and DNA amplification. This might be classified into polymerase chain reaction and isothermal amplification. The PCR product is used as a template for genomic DNA, which is obtained by reversing the transcription of viral RNA. It helps by being multiplied or copied into millions of viral genomes (DNA). A copy of a specific region in this method is usually visualized under electrophoresis or hybridization by using fluorescent probes (Hong and Lee, 2018). Amplification has occurred in three steps in this method: 1. denaturation and separation of the double-stranded DNA template into single strands at 90-95°C; 2. annealing at 40-60°C to allow the primers to bind the start and end of the target DNA; and 3. extension at 70-75°C, in which a thermostable DNA polymerase synthesizes new DNA strands beginning with the primers. But they are limited in utilization due to the fact that they are not enough to detect the novel low titers of virus sensitivity in an undomesticated plant.

3. Future Directions

Most plant viruses are vectored by insect pests. Therefore, developing the management of plant viruses should begin with managing their host insects. Because managing insect pests alone could have played a great role in alleviating the insect-based vector of plant viruses. This activity could reduce the cost of plant virus management at producer levels. But it needs further research on ecological influences on their distribution, species identification records (surveys), information on economic importance, resistance, variety identification, and crop systems to implement research-based recommendations. Therefore, research recommendations for insect vectors of plant virus management should be developed in the future by diagnosing and identifying the plant virus. It is essential to develop different management technologies to suppress plant viruses and vector insect pests simultaneously. To implement effective management options, farmers should be made aware of the importance of cooperation among themselves in a region with the local support of adequate extension services to minimize the damage caused by a plant virus. Thus, the sustainable management of plant viruses that vector and transmit them requires the efforts of both virologists and entomologists to overcome these devastating pests. because they are paradoxically causing hunger, malnutrition, and high food and production costs. Understanding theoretical pest management methods is insufficient unless accompanied by training, skills, knowledge, and experience sharing. These activities have required the understanding of biology, ecology, taxonomy, and their associated pests for further diagnosis and identification to solve the problems practically at the right time with the right tools at the right place by experts.

4. Conclusion

Phytophagous insects cause vector disease, injuring, spoiling, damaging, parasitizing, and reducing plants' yield and marketability. The phytophagous insect is contacted by diverse microbial communities in the environment. Among the insect orders, Hemiptera, Thysanoptera, Coleoptera, Orthoptera, and Dermaptera were vectored and transmitted plant viruses from infected to non-infected. Of these, hemipterans are ranked first in vectoring, spreading, and dispersing plant viruses. Aphids, whiteflies, leafhoppers, thrips, psyllids, beetles, and mealybugs were also among the insects mentioned in the vectoring and reserving of plant viruses. These were detected by parallel and nonparallel methods such as next-generation sequencing and CRISPR-Cas. CRISPR-Cas has occurred after the massively parallel sequencing (MPS) or next-generation sequencing microbial detection method. It is used for genome editing to develop effective plant virus resistance varieties. In the former period, it was detected by protein-based immunological tests with the help of ELISA and nucleotide-specific PCR assays. But they are limited in utilization due to the fact that they are not enough to detect the novel low titers of virus sensitivity in an undomesticated plant virus. In the future, the development of management methods for plant viruses should be begun with the

management of their host insects. Because managing insect pests alone could have played a great role in alleviating the insect-based vectored plant viruses. Thus, their sustainable management has required the integration of virology and entomology disciplines for understanding biology, ecology, taxonomy, and their associated pests.

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References

- Achon, M.A., Serrano, L., Clemente-Orta, G. and Sossai, S. 2017. First report of maize chlorotic mottle virus on a perennial host, Sorghum halepense, and maize in Spain. *Plant Disease*, 101, 393.
- Adhab, M. 2021. Be smart to survive: virus-host relationships in nature. *J Microbiol Biotech Food Sci.*, 10 (6) e3422.
- Adhab, M., Angel, C., Leisner, S., Schoelz, J.E. 2018. The P1 gene of the Cauliflower mosaic virus is responsible for breaking resistance in Arabidopsis thaliana ecotype Enkheim (En-2). *Virology*, 523: 15-21, doi: 10.1016/j.virol.2018.07.016.
- Adhab, M., Finke, D., Schoelz, J. 2019. Turnip aphids (*Lipaphis erysimi*) discriminate host plants based on the strain of Cauliflower mosaic virus infection. *Emir J Food Agric*, 31: 69-75. <https://doi.org/10.9755/ejfa.2019.v31.i1.1903>.
- Agranovsky, A. 2021. Proteins Capacity in Plant Virus-Vector Interactions and Virus Transmission. *Cells*, 10, 90. <https://doi.org/10.3390/cells10010090>.
- Albittar, L., Ismail, M., Lohaus, G., Ameline, A., Visser, B., Bragard, C., Hance, T. 2019. Bottom-up regulation of a tri-trophic system by beet yellow virus infection: consequences for aphid-parasitoid foraging behavior and development. *Oecologia*, 191(1). doi. 10.1007/s00442-019-04467-0.
- Ali, M. and Baek, K.-H. 2020. Jasmonic acid signaling pathway in response to abiotic stresses in plants. *Int. J. Mol. Sci.* 21:621. doi: 10.3390/ijms21020621.
- Ambethgar, V., Kollam, M., Chinnadurai, C., Ramsubhag, R., and Jayaraman, J. 2019. Ecology of emerging vector-borne plant viruses and integrated management approaches in vegetable production systems. *Tropical Agriculture*, 95 (2): 81-94.
- Ammar, E.D., Tsai, C.W., Whitfield, A.E., Redinbaugh, M.G., Hogenhout, S.A. 2009. Cellular and molecular aspects of rhabdovirus interactions with insect and plant hosts. *Annu. Rev. Entomol.*, 54:447-468.
- Augustinos, A.A., Santos-Garcia, D., Dionyssopoulou, E., Moreira, M., Papapanagiotou, A., Scarvelakis, M., Doudoumis, V., Ramos, S., Aguiar, A.F., Borges, P.A.V., Khadem, M., Latorre, A., Tsiamis, G., Bourtzis, K. 2011. Detection and characterization of *Wolbachia* infections in natural populations of aphids: Is the hidden diversity fully unraveled? *PLoS ONE*, 6(12), e28695. doi: 10.1371/journal.pone.0028695.
- Batuman, O., Rojas, M., Almanzar, A. and Gilbertson, R. 2014. First report of Tomato chlorotic spot virus in processing tomatoes in the Dominican Republic. *Plant Disease*, 98, 286.
- Bernardo, P., Charles-Dominique, T., Barakat, M., Ortet, P., Fernandez, E., Filloux, D., Hartnady, P., Rebelo, T.A., Cousins, S.R., Mesleard, F., Cohez, D., Yavercovski, N., Varsani, A., Harkins, G.W., Peterschmitt, M., Malmstrom, C.M., Martin, D.P., Roumagnac, P. 2018. Geometagenomics illuminates the impact of agriculture on the distribution and prevalence of plant viruses at the ecosystem scale. *The ISME Journal*, 12:173-184.
- Bhattacharyya, D., Gnanasekaran, P., Kumar, R.K., Kushwaha, N.K., Sharma, V.K., Yusuf, M.A., Chakraborty, S. 2015. A geminivirus beta satellite damages the structural and functional integrity of chloroplasts, leading to symptom formation and inhibition of photosynthesis. *J Exp Bot.*, 66(19):5881-95.
- Biere, A. and Tack, A.J.M., 2013. Evolutionary adaptation in three-way interactions between plants, microbes, and arthropods. *Funct Ecol*, 27: 646-660.
- Blanc, S., Drucker, M., Uzest, M. 2014. Localizing viruses in their insect vectors. 52:403-425, *Annual Review of Phytopathol.* doi: 10.1146/annurev-phyto-102313-045920.
- Bragard, C., Caciagli, P., Lemaire, O., Lopez-Moya, J.J., MacFarlane, S., Peters, D., Susi, P., Torrance, L. 2013. Status and prospects of plant virus control through interference with vector transmission. *Annu. Rev. Phytopathol.*, 51:177-201. <https://doi.org/10.1146/annurev-phyto-082712-102346>.
- Brault, V., Uzest, M., Monsion, B., Jacquot, E., Blanc, S. 2010. Aphids as transport devices for plant viruses. *Comptes Rendus – Biologies*, 333(6-7):524-538. [pmid:20541164](https://pubmed.ncbi.nlm.nih.gov/20541164/)
- Bright, M. and Bulgheresi, S. 2010. A complex journey: the transmission of microbial symbionts. *Nat Rev Microbiol.*, 8:218-30.
- Buchholz, A. and Trapp, S., 2016. How active ingredient localization in plant tissues determines the targeted pest spectrum of different chemistries *Pest Manage Sci*, 72: 929-939.
- Bull, J.J., Sanjuán, R., Wilke, C.O. 2007. Theory of Lethal Mutagenesis for Viruses. <https://doi.org/10.1128/JVI.01624-06>. *Journal of Virology*, 81(6): 2930-2939.
- Butter, N.S. 2021. *Insect Vectors and Plant Pathogens*. 1st Edition, CRC Press, 496 pages. ISBN 9780367780845.

- Cassone, B.J., S. Wijeratne, A.P. Michel, L.R. Stewart, Y.T. Chen, P. Yan, and M.G. Redinbaugh. 2014. Virus-independent and common transcriptome responses of leafhopper vectors feeding on maize infected with semi-persistently and persistent propagative transmitted viruses. *BMC Genom.*, 15:133. doi: 10.1186/1471-2164-15-133.
- Casteel, C.L., Jander, G. 2013. New synthesis: Investigating mutualisms in virus-vector interactions. *J Chem Ecol.* 39: 809.
- Chandi, R.S. 2020. Integrated Management of Insect Vectors of Plant Pathogens. *Agricultural Reviews*, doi: 10.18805/ag. r-1982.
- Chandi, R.S., Kataria, S.K., Kaur, J. 2018. Arthropods as Vectors of Plant Pathogens viz-a-viz their Management. *International Journal of Current Microbiology and Applied Science*, 7(8): 4006-4023: Review Article. <https://doi.org/10.20546/ijcmas.2018.708.415>.
- Chen, H.Y., Chen, Q., Omura, T., Uehara-Ichiki, T., Wei, T. Y. 2011. Sequential infection of rice dwarf virus in the internal organs of its insect vector after ingestion of virus. *Virus Research*, 160, 389-394. doi: 10.1016/j.virusres.2011.04.028.
- Chen, L., Jiao, Z., Liu, D., Liu, X., Xia, Z., Deng, C. et al. 2017. One-step reverse transcription loop-mediated isothermal amplification for the detection of maize chlorotic mottle virus in maize. *Journal of Virological Methods*, 240, 49-53.
- Chisholm, P.J., Sertsuvalkul, N., Casteel, C.L., Crowder, D.W. 2018. Reciprocal plant-mediated interactions between a virus and a non-vector herbivore. *Ecology*, 99, 2139-2144. doi:10.1002/ecy.2449.
- Cunniffe, N.J., Taylor, N.P., Hamelin, F.M., Jeger, M.J. 2021. Epidemiological and ecological consequences of virus manipulation of host and vector in plant virus transmission. *PLoS Comput Biol* 17(12): e1009759. <https://doi.org/10.1371/journal.pcbi.1009759>.
- Czosnek, H. and Rubinstein, G. 1997. Long-term association of tomato yellow leaf curl virus with its whitefly vector, *Bemisia tabaci*: Effect on the insect's transmission capacity, longevity, and fecundity. *J. Gen. Virol.*, 78:2683-2689.
- De Clerck, C., Fujiwara, A., Joncour, P., Leonard, S., Felix, M.L., Francis, F., Jijakli, M.H., Tsuchida, T., Massart, S. 2015. A metagenomic approach from an aphid's hemolymph sheds light on the potential roles of co-existing endosymbionts. *Microbiome*, 3:63. doi: 10.1186/s40168-015-0130-5.
- Dietzgen, R.G., Mann, K.S., Johnson, K.N. 2016. Plant Virus-Insect Vector Interactions: Current and Potential Future Research Directions. *Viruses*, 8:303-322.
- Eigenbrode, S.D., Bosque-Pérez, N., Davis, T.S. 2018. Insect-Borne Plant Pathogens and Their Vectors: Ecology, Evolution, and Complex Interactions. *Annu. Rev. Entomol.*, 63:169-191. <https://doi.org/10.1146/annurev-ento-020117-043119>.
- El-Hamalawi, Z.A. and Stanghellini, M.E. 2005. Disease development on lisianthus following aerial transmission of *Fusarium avenaceum* by adult shore flies, fungus gnats, and moth flies. *Plant Dis.*, 89:619-23.
- Fereres, A. 2015. Insect vectors as drivers of plant virus emergence. *Curr Opin Virol.*, 10:42-46. doi: 10.1016/j.coviro.2014.12.008.
- Fereres, A. and Raccach, B. 2015. *Plant Virus Transmission by Insects*; eLS John Wiley and Sons Ltd.: Chichester, UK.
- Fereres, A.; Peñafior, M.F.G.V.; Favaro, C.F.; Azevedo, K.E.X.; Landi, C.H.; Maluta, N.K.P.; Bento, J.M.S.; Lopes, J.R.S. 2016. Tomato Infection by Whitefly-Transmitted Circulative and Non-Circulative Viruses Induce Contrasting Changes in Plant Volatiles and Vector Behavior. *Viruses*, 8:225. <https://doi.org/10.3390/v8080225>.
- Franco, F.P., Túler, A.C., Gallan, D.Z., Gonçalves, F.G., Favaris, A.P., Peñafior, M.F.G.V., Leal, W.S., Moura, D.S., Bento, J.M.S., Silva-Filho, M.C. 2021. Fungal phytopathogen modulates plant and insect responses to promote its dissemination. *ISME J.* <https://doi.org/10.1038/s41396-021-01010-z>.
- Gadhve, K.R., Dutta, B., Coolong, Sribivasan, R. 2019. A non-persistent aphid-transmitted *potyvirus* differentially alters the vector and non-vector biology through host plant quality manipulation. *Science Advances* 9, 2503. <https://doi.org/10.1038/s41598-019-39256-5>
- Gandon, S. 2018. Evolution and Manipulation of Vector Host Choice. *The American Naturalist*, 192(1):24-34.
- Garzo, E., Moreno, A., Plaza, M., Fereres, A. 2020. Feeding Behavior and Virus-transmission Ability of Insect Vectors Exposed to Systemic Insecticides. *Plants*, 9:895-910. doi: 10.3390/plants9070895. <http://www.mdpi.com/journal/plants>
- Ghanim, M. 2014. A review of the mechanisms and components that determine the transmission efficiency of the *Tomato Yellow Leaf Curl virus* (*Geminiviridae*, *Begomovirus*) by its whitefly vector. *Virus Research*, 186:47-54. doi: 10.1016/j.virusres.2014.01.022.
- Gottlieb, Y., Zchori-Fein, E., Mozes-Daube, N., Kontsedalov, S., Skaljac, M., Brumin, M., Sobol, I., Czosnek, H., Vavre, F., Fleury, F., Ghanim, M. 2010. The transmission efficiency of tomato yellow leaf curl virus by the whitefly *Bemisia tabaci* is correlated with the presence of a specific symbiotic bacterium species. *Virology*, 84: 9310-9317. doi: 10.1128/JVI.00423-10.

- Gray, S.M. and Banerjee, N. 1999. Mechanisms of arthropod transmission of plant and animal viruses. *Microbiology and molecular biology reviews*, 63(1):128–148. *pmid*:10066833
- Green, T.R. and Ryan, C.A. 1972. Wound-induced proteinase inhibitor in plants leaves a possible defense mechanism against insects. *Science*, 175:776–7.
- Gupta, N., Reddy, K., Bhattacharyya, D., Chakraborty, S. 2021. Plant responses to geminiviruses infection: guardians of plant immunity. *Viol J.*, 18:143 (2021). <https://doi.org/10.1186/s12985-021-01612-1>.
- Gutierrez, S., Michalakakis, Y., Van Munster, M., Blanc, S. 2013. Plant-microbe–insect interactions: plant feeding by insect vectors can affect the life cycle, population genetics, and evolution of plant viruses. *Functional Ecology*, 27: 610–622. doi: 10.1111/1365-2435.12070
- Harris, K.F. 1977. Ingestion–egestion hypothesis of non-circulative virus transmission. Aphids as Virus Vectors, edited by K.F. Harris and K. Maramorosch, Academic Press, New York, NY, USA, pp. 165-220.
- Hassani-Mehraban, A., Botermans, M., Verhoeven, J.T.J., Meekes, E., Saaijer, J., Peters, D. et al. 2010. A distinct tospovirus causing necrotic streak on *Alstroemeria* sp. in Colombia. *Archives of Virology*, 155, 423–428.
- Hatcher, P.E. 1995. 3-way interactions between plant-pathogenic fungi, herbivorous insects, and their host plants. *Biol Rev.*, 70:639–94.
- He, Z., Guo, J-F., Reitz, S.R., Lei, Z-R., Wu, S-Y. 2020. Review: a global invasion by the thrip, *frankliniella occidentalis*: current virus vector status and its management. *Insect Science* 27, 626–645. doi: 10.1111/1744-7917.12721.
- Heck, M. 2018. Insect Transmission of Plant Pathogens: A Systems Biology Perspective. *M Systems*, 3(2), e00168-17. <https://doi.org/10.1128/mSystems.00168-17>.
- Herron, C.M., Mirkov, T.E., da Graça, J.V., Lee, R.F. 2006. Citrus *Tristeza virus* transmission by the *Toxoptera citricida* vector: in vitro acquisition and transmission and infectivity immune neutralization experiments. *J. Virol. Methods*, 134(1-2):205-11. doi: 10.1016/j.jviromet.01.006.
- Hogenhout, S.A., Ammar, E.D., Whitfield, A.E., Redinbaugh, M.G. 2008. Insect vector interactions with persistently transmitted viruses. *Annu. Rev. Phytopathol.*, 46:327–359.
- Hoh, F., Uzest, M., Drucker, M., Plisson-Chastang, C., Bron, P., Blanc, S., Dumas, C. 2010. Structural insights into the molecular mechanisms of cauliflower mosaic virus transmission by its insect vector. *J. Virol.*, 84:4706–4713. doi: 10.1128/JVI.02662-09.
- Hohn, T. 2007. Plant virus transmission from the insect point of view. *Proc Natl Acad Sci U S A*, 104: 17905–17906.
- Hong, S. and Lee, C. 2018. The Current Status and Future Outlook of Quantum Dot-Based Biosensors for Plant Virus Detection. *Plant Pathol J.*, 34(2): 85–92. doi: 10.5423/PPJ.RW.08.2017.0184. https://www.daf.qld.gov.au/data/assets/pdf_file/0005/68090/Management-of-aphid.pdf. Aphid-transmitted viruses in vegetable crops Integrated virus disease management (accessed on December 9, 2021).
- Hull, R. and Al-Hakim, A. 1988. Nucleic acid hybridization in plant virus diagnosis and characterization. *Trends Biotechnol.* 6, 213–218. doi: 10.1016/0167-7799(88)90076-5.
- Hunter, W.B. 2008. Plant Viruses and Insects. In: Capinera, J.L. (eds) *Encyclopedia of Entomology*. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-6359-6_2991.
- Ingwell, L., Eigenbrode, S., Bosque-Pérez, N. 2012. Plant viruses alter insect behavior to enhance their spread. *Sci. Rep.* 2:578. <https://doi.org/10.1038/srep00578>
- James, C. K. N., and Falk, B.W. 2006. Virus-vector interactions mediate nonpersistent and semi-persistent transmission of plant viruses. *Annu. Rev. Phytopathol.*, 44, 183–212.
- James, C.K.N., and Zhou, J.S. 2015. Insect vector-plant virus interactions associated with non-circulative, semi-persistent transmission: Current perspectives and future challenges. *Curr. Opin. Virol.*, 15:48–55.
- James, Neya, B, Elisabeth, Zida P. Oumar, and Traore. 2013. Effect of insecticide treatments and seed quality on the control of cowpea aphid-borne mosaic disease. *European Journal of Experimental Biology*, 3(6):370-381.
- Janz, N., Nylin, S., Wahlberg, N. 2006. Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC Evolutionary Biology*, 6(1):4. doi: 10.1186/1471-2148-6-4.
- Jeger, M. and Bragard, C. 2019. The epidemiology of *Xylella fastidiosa*; a perspective on current knowledge and a framework to investigate plant host-vector–pathogen interactions. *Phytopathology*, doi: 10.1094/PHYTO-07-18-0239-FI.
- Jeger, M.J. 2020. The Epidemiology of Plant Virus Disease: Towards a New Synthesis. *Plants*, 9: 1768. <https://doi.org/10.3390/plants9121768>.
- Jeske, H., Lütgemeier, M., Preiss, W. 2001. DNA forms indicate rolling circle and recombination-dependent replication of Abutilon mosaic virus. *Embo J.*, 20(21):6158–67.
- Jones, R.A.C. and Rayapati A. Naidu, R.A. 2019. Global Dimensions of Plant Virus Diseases: Current Status and Future Perspectives, *Annurev. of Virology*, 6:387–409.
- Kennedy, J.S. Day, M.F., Eastop, V.F. 1962. *A Conspectus of Aphids as Vectors of Plant Viruses*; Commonwealth Institute of Entomology: London, UK.
- Kersch-Becker, M.F. and Thaler, J.S. 2014. Virus strains differentially induce plant susceptibility to aphid vectors and chewing herbivores. *Oecologia*, 174: 883-892. <https://doi.org/10.1007/s00442-013-2812-7>.

- Kluth, S., Kruess, A., Tschardtke, T. 2002. Insects as vectors of plant pathogens: mutualistic and antagonistic interactions. *Oecologia* 133:193–199. doi: 10.1007/s00442-002-1016-3.
- Kollenberg, M., Winter, S., Gotz, M. 2014. Quantification and localization of Watermelon chlorotic stunt virus and tomato yellow leaf curl virus (*Geminiviridae*) in populations of *Bemisia tabaci* (Hemiptera, Aleyrodidae) with differential virus transmission characteristics. *PLoS ONE*, 9: e111968. doi: 10.1371/journal.pone.0111968.
- Koornneef, A., Pieterse, C.M. 2008. Cross talk in defense signaling. *Plant Physiology*, 146, 839–844, doi:10.1104/pp.107.112029.
- Koudamilaro, A., Nwilene, F.E., Togola, A., Akogbeto, M. 2015. Review Article: Insect Vectors of Rice Yellow Mottle Virus.
- Kraus, E.C., and Stout, M.J. 2019. Seed treatment using methyl jasmonate induces resistance to rice water weevil but reduces plant growth in rice. *PLoS ONE*, 14(9): e0222800. [HTTPS:// doi.org/10.1371/journal.pone.0222800](https://doi.org/10.1371/journal.pone.0222800).
- Kusia, E.S., Subramanian, S., Nyasani, J.O., Khamis, F., Villinger, J., Ateka, E.M. et al. 2015. First report of lethal necrosis disease associated with co-infection of finger millet with Maize chlorotic mottle virus and sugarcane mosaic virus in Kenya. *Plant Disease*, 99, 899.
- Labandeira, C.C. and Rose Prevec, R. 2014. Plant paleopathology and the roles of pathogens and insects. *International J. of Paleopathology*, 4:1–16. <http://www.elsevier.com/locate/ijpp>.
- Larrieu, A., Vernoux, T. 2016. How does jasmonate signaling enable plants to adapt and survive? *BMC Biol* 14: 79. <https://doi.org/10.1186/s12915-016-0308-8>
- Lefevre, T. and Thomas, F. 2008. Behind the scene, something else is pulling the strings: emphasizing parasitic manipulation in vector-borne diseases. *Infection, genetics and evolution*, 8(4): 504–519.
- Leonetti, P., Stuttmann, J., Pantaleo, V. 2021. Regulation of plant antiviral defense genes via host RNA-silencing mechanisms. *Virology*, 18:194. [https:// doi.org/10.1186/s12985-021-01664-3](https://doi.org/10.1186/s12985-021-01664-3).
- Liu, B.M., Preisser E.L., Chu D., Pan H.P., Xie W., Wang S.L., Wu Q.J., Zhou X.G., Zhang Y.J. 2013. Multiple forms of vector manipulation by a plant-infecting virus: *Bemisia tabaci* and *Tomato yellow leaf curl virus*. *J. Virology*, 87:4929–4937. doi: 10.1128/JVI.03571-12.
- Liu, L.Y., Ye, H.Y., Chen, T.H. and Chen, T.C. 2017. Development of a microarray for simultaneous detection and differentiation of different tospoviruses that are serologically related to tomato spotted wilt virus. *Journal of Virology*, 14, 1.
- Lou, Y. G., Du, M. H., Turlings, T. C. J., Cheng, J. A., and Shan, W. F. 2005. Exogenous application of jasmonic acid induces volatile emissions in rice and enhances parasitism of *Nilaparvata lugens* eggs by the parasitoid, *Anagrus nilaparvatae*. *J. Chem. Ecol.* 31, 1985–2002. doi: 10.1007/s10886-005-6072-9.
- Ma, E., Zhu, Y., Liu, Z., Wei, T., Wang, P., Cheng, G. 2021. Interaction of Viruses with the Insect Intestine. *Annu. Rev. Virol.*, 8:115–131. <https://doi.org/10.1146/annurev-virology-091919-100543>
- MacKenzie, T.D.B., Fageria, M.S., Nie, X., Singh, M. 2013. Effects of crop management practices on the current-season spread of *Potato Virus Y*. *Plant Disease*, 98(2):213–222.
- Mansoor, S., Zafar, Y., Briddon, R.W. 2006. Geminivirus disease complexes: the threat is spreading. *Trends Plant Sci.*, 11(5):209–212.
- Maree, H. J., Fox, A., Al Rwahnih, M., Boonham, N., Candresse, T. 2018. Application of HTS for routine plant virus diagnostics: state of the art and challenges. *Front. Plant Sci.* 9, 1082. doi: 10.3389/fpls.2018.01082.
- Martin, B., Collar, J.L., Tjallingii, W.F., Fereres, A. 1997. Intracellular ingestion and salivation by aphids may cause the acquisition and inoculation of non-persistently transmitted plant viruses. *J. Gen. Virol.* 1997, 78, 2701–2705.
- Martinière, A., Bak, A., Macia, J.L., Lautredou, N., Gargani, D., Doumayrou, J., Garzo, E., Moreno, A., Fereres, A., Blanc, S. and Drucker, M., 2013. A virus responds instantly to the presence of the vector on the host and forms transmission morphs. *Elife*, 2, p. e00183.
- Massart, S., Olmos, A., Jijakli, H., Candresse, T. 2014. Current impact and future directions of high throughput sequencing in plant virus diagnostics. *Virus Res.*, 188:90–96. doi: 10.1016/j.virusres.2014.03.029.
- Maule, A.J., Caranta, C., Boulton. M.I. 2007. Review: Sources of natural resistance to plant viruses: status and prospects. *Molecular Plant Pathology*, 8(2), 223–231. doi: 10.1111/J.1364-3703.2007.00386.
- McKenzie, C.L. 2002. Effect of Tomato Mottle Virus (ToMoV) on *Bemisia tabaci* Biotype B (Homoptera: Aleyrodidae) Oviposition and Adult Survivorship on Healthy Tomato. *Florida Entomologist*, 85:367–368. doi: 10.1653/0015-4040(2002)085[0367: EOTMVT]2.0.CO;2.
- Mittapelly, P. and Rajarapu, S.P. 2020. Applications of Proteomic Tools to Study Insect Vector–Plant Virus Interactions. *Life*, 10(8):143. [https:// doi.org/10.3390/life10080143](https://doi.org/10.3390/life10080143).
- Montero-Astua, M., Ullman, D.E., Whitfield, A.E. 2016. Salivary gland morphology, tissue tropism, and the progression of tospovirus infection in *Frankliniella occidentalis*. *Virology*, 493:39–51. doi: 10.1016/j.virology.2016.03.003.
- Moreno, A., Tjallingii, W.F., Fernandez-Mata, G.F., Fereres, A. 2012. Differences in the mechanism of inoculation between a semi-persistent and a non-persistent aphid-transmitted plant virus. *Journal of General Virology*, 93:662–667. doi: 10.1099/vir.0.037887-0.

- Moritz, G., Kumm, S., Mound, L. 2004. Tospovirus transmission depends on thrips ontogeny. *Virus Res.*, 100:143–149. doi: 10.1016/j.virusres.2003.12.022.
- Moya, A., Holmes, E., González-Candelas, F. 2004. The population genetics and evolutionary epidemiology of RNA viruses. *Nat Rev Microbiol* 2:279–288. <https://doi.org/10.1038/nrmicro863>.
- Mulot, M., Boissinot, S., Monsion, B., Rastegar, M., Clavijo, G., Halter, D., Bochet, N., Erdinger, M., Brault, V. 2016. A Comparative Analysis of RNAi-Based Methods to Down-Regulate Expression of Two Genes Expressed at Different Levels in *Myzus persicae*. *Viruses*, 8(11):316; <https://doi.org/10.3390/v8110316>.
- Nagata, T., Almeida, A.C.L., Resende, R.O. and de Avila, A.C. 2004. The competence of four thrips species to transmit and replicate four tospoviruses. *Plant Pathology*, 53, 136–140.
- Nalam, V., Louis, J., Shah, J. 2019. Plant defense against aphids, the pest extraordinaire. *Plant Science*, 279:96–107. <https://doi.org/10.1016/j.plantsci.2018.04.027>.
- Nault, L.R. 1997. Arthropod transmission of plant viruses: a new synthesis. *Annals of the Entomological Society of America*. 1997;90(5):521–541.
- Nault, L.R., and Ammar E. 1989. Leafhopper and planthopper transmission of plant viruses. *Annu. Rev. Entomol.*, 34:503–529. doi: 10.1146/annual.rev.en.34.010189.002443.
- Ng, J.C.K. and Falk, B.W. 2006. Virus-Vector Interactions Mediating Nonpersistent and Semi Persistent Transmission of Plant Viruses. *Annual Review of Phytopathology*, 44(1):183–212. [pmid:16602948](https://pubmed.ncbi.nlm.nih.gov/16602948/).
- Nigam, D. 2021. Genomic Variation and Diversification in Begomovirus Genomes: Implications for Host and Vector Adaptation. *Plants*, 10 (1706). <https://doi.org/10.3390/plants10081706>.
- Okada, K., Abe, H., and Arimura, G. 2015. Jasmonates induce both defense responses and communication in monocotyledonous and dicotyledonous plants. *Plant Cell Physiol*. 56, 16–27. doi: 10.1093/PCP/pcu158.
- Pan, L.-L., Cui, X.-Y., Chen, Q.-F., Wang, X.-W., Liu, S.-S. 2018. Cotton Leaf Curl Disease: Which Whitefly Is the Vector? *Phytopathology*, 108: 1172–1183. <https://doi.org/10.1094/PHYTO-01-18-0015-R>.
- Perilla-Henao, L.M., and Casteel, C.L. 2016. Vector-borne bacterial plant pathogens: interactions with hemipteran insects and plants. *Plant Science*, 7, 1163, doi: :10.3389/fpls.2016.01163.
- Phoku, J.Z., Barnard, T.G., Potgieter, N., Dutton, M.F. 2016. Fungal dissemination by housefly (*Musca domestica* L.) and contamination of food commodities in rural areas of South Africa. *International Journal of Food Microbiology*, 217:177–81.
- Pinheiro, P.V., Kliot, A., Ghanim, M., Cilia, M. 2015. Is there a role for symbiotic bacteria in plant virus transmission by insects? *Curr. Opin. Insect Sci.*, 8:69–78. doi: 10.1016/j.cois.2015.01.010.
- Pirone, T.P. and Megahed, E. 1996. Aphid transmissibility of some purified viruses and viral RNAs. *Virology*, 30:631–637. doi: 10.1016/0042-6822(66) 90168-1.
- Plisson, C., Uzest, M., Drucker, M., Froissart, M., Dumas, C., Conway, J., Thomas, D., Blanc, S., Bron, P. 2005. Structure of the mature P3-virus particle complex of cauliflower mosaic virus revealed by cryo-electron microscopy. *J. Mol. Biol.*, 346:267–277. doi: 10.1016/j.jmb.2004.11.052.
- Powell, G. 2005. Intracellular salivation is the aphid activity associated with the inoculation of non-persistently transmitted viruses. *J. Gen. Virol.*, 86, 469–472.
- Powell, G., Pirone, T., Hardie, J. 1995. Aphid stylet activities during potyvirus acquisition from plants and an in vitro system that correlates with the subsequent transmission. *Eur. J. Plant Pathol.*, 101:411–420.
- Purcell, A.H. 2009. Chapter 203: Plant Diseases and Insects. *Encyclopedia of Insects (Second Edition)*, Pages 802–806. <https://doi.org/10.1016/B978-0-12-374144-8.00212-5>
- Purcell, A.H. and Almeida, R.P.P. 2005. Insects as Vectors of Disease Agents.
- Pybus, O. and Rambaut, A. Evolutionary analysis of the dynamics of viral infectious disease. *Nature Reviews Genetics*, 10, 540–550 (2009). <https://doi.org/10.1038/nrg2583>.
- Ray, S. and Casteel, C.L. 2022. Effector-mediated plant–virus–vector interactions, *The Plant Cell*, 34 (5): 1514–1531. <https://doi.org/10.1093/plcell/koac058>.
- Reitz, S.R., Gao, Y.L. and Lei, Z.R. 2011. Thrips: Pests of concern to China and the United States. *Journal of Integrative Agriculture*, 10, 867–892.
- Rimbaud, L., Dallot, S., Borron, S., Soubeyrand, S., Jacquot, E. 2015. Assessing the Mismatch Between Incubation and Latent Periods for Vector-Borne Diseases: The Case of Sharka. *Phytopathology*, 105(11): 1408–1416. [pmid: 26512749](https://pubmed.ncbi.nlm.nih.gov/26512749/).
- Roossinck, M.J. 2015. Plants, viruses and the environment: ecology and mutualism. *Virology*, 479–480: 271–277. <https://doi.org/10.1016/j.virol.2015.03.041>.
- Roossinck, M.J., Martin, D.P., Roumagnac, P. 2015. Plant virus metagenomics: advances in virus discovery *Phytopathology*, 105:716–727. doi: 10.1094/PHYTO-12-14-0356-RVW.
- Rosen, R., Kanakala S., Kliot A., Pakkianathan B.C., Abu Farich B., Santana-Magal N., Elimelech M., Kontsedalov S., Lebedev G., Cilia M., Ghanim, M. 2015. Persistent, circulative transmission of begomoviruses by whitefly vectors. *Curr. Opin. Virol.*, 15:1–8. doi: 10.1016/j.coviro.2015.06.008.
- Rubio, L., Galipienso, L., Ferriol, I. 2020. Detection of Plant Viruses and Disease Management: Relevance of Genetic Diversity and Evolution. *Frontiers in plant science*, 11, 1092. <https://doi.org/10.3389/fpls.2020.01092>.

- Scholthof, K-B.G., Adkins, S., Czosnek, H., Palukaitis, P., Jacquot, E., Hohn, T., Hohn, B., Saunders, K., Candresse, T., Ahlquist, P., Hemenway, C., Foster, G.D. 2011. Top 10 Plant Viruses. *Mol. Plant Pathol.* 12(9):938–954 doi:10.1111/j.1364-3703.2011.00752. X.
- Shahid, M.S., Sattar, M.N., Iqbal, Z., Raza, A., Al-Sadi, A.M. 2021. Next-Generation Sequencing and the CRISPR-Cas Nexus: A Molecular Plant Virology Perspective. *Front. Microbiol.* 11:609376. doi: 10.3389/fmicb.2020.609376.
- Shi, X., Tang, X., Zhang, X., Zhang, D., Li, F., Yan, F., Zhang, Y., Zhou, X., Liu, Y. 2018. Transmission efficiency, preference, and behavior of *Bemisia tabaci* MEAM1 and MED under the influence of tomato chlorosis virus. *Frontiers in Plant Science*, 8. doi:10.3389/fpls.2017.02271
- Shi, X., Zhang, Z., Zhang, C., Zhou, X., Zhang, D., Liu, Y. 2021. The molecular mechanism of efficient transmission of plant viruses in variable virus–vector–plant interactions. *Horticultural Plant Journal*, 7 (6): 501–508. <https://doi.org/10.1016/j.hpj.2021.04.006>.
- Shrestha, A., Srinivasan, R., Riley, D.G., Culreath, A. 2012. Direct and indirect effects of a thrips-transmitted Tospovirus on the preference and fitness of its vector, *Frankliniella fusca*. *Entomol. Exp. Appl.*, 145:260–271.
- Simmons, H.E., Dunham, J.P., Stack, J.C., Dickins, B.J.A., Pagán, I., Holmes, E.C., Stephenson, A.G. 2012. Deep sequencing reveals the persistence of intra- and inter-host genetic diversity in natural and greenhouse populations of zucchini yellow mosaic virus. *J Gen Virol.*, 93:1831–1840. doi: 10.1099/vir.0.042622-0.
- Singh, S., Awasthi, L.P., Jangre, A. 2020. Transmission of plant viruses in fields through various vectors. *Applied Plant Virology*, Academic Press, pages 313–334. <https://doi.org/10.1016/B978-0-12-818654-1.00024-4>.
- Stewart, L.R., Medina, V., Tian, T.Y., Turina, M., Falk, B.W., Ng, J.C.K. 2010. A mutation in the Lettuce infectious yellow virus minor coat protein disrupts whitefly transmission but not in plant systemic movement. *J. Virol.*, 84, 12165–12173.
- Stobbe, A. and Roossinck, M. J. 2016. Plant Virus Diversity and Evolution. *Current Research Topics in Plant Virology*, pp.197–215. https://doi.org/10.1007/978-3-319-32919-2_8
- Stobbe, A.H., Daniels, J., Espindola, A.S., Verma, R., Melcher, U., Ochoa-Corona, F., Garzon, C., Fletcher, J., Schneider, W. 2013. E-probe diagnostic nucleic acid analysis (EDNA): a theoretical approach for handling next-generation sequencing data for diagnostics. *J Microbiol. Methods*, 94:356–366. doi: 10.1016/j.mimet.2013.07.002.
- Stobbe, A.H., Roossinck, M.J. 2014. Plant virus metagenomics: what we know and why we need to know more. *Front Plant Sci.*, 5:150. doi: 10.3389/fpls.2014.00150.
- Strange, R.N., and Scott, P.R. 2005. Plant disease: a threat to global food security. *Annu. Rev. Phytopathol.* 43, 83–116. doi: 10.1146/annurev.phyto.43.113004.133839.
- Sylvester, E.S. 1962. Aphid transmission of non-persistent plant viruses with special reference to the *Brassica nigra* virus. *Hilgardia*, 23:53–98.
- Thaler, J.S., Humphrey, P.T., Whiteman, N.K. 2012. Evolution of jasmonate and salicylate signal crosstalk. *Trends Plant Sci.* 17, 260-270. doi: 10.1016/j.tplants.2012.02.010.
- Tooker, J.F. and Giron, D. 2020. The evolution of endophagy in herbivorous insects. *Front Plant Sci*, 11, 581816.
- Uzest, M., Drucker, M., Blanc, S. 2011. La transmission d'un complexe: pas si simple. Cas du virus de la mosaïque du choufleur. *Virology*, 15(3): 192–204.
- Uzest, M., Gargani, D., Drucker, M., Hebrard, E., Garzo, E., Candresse, T., Fereres, A., Blanc, S. 2007. Proc Natl Acad Sci USA, 104:17959–17964.
- van Munster, M., Yvon, M., Vile, D., Dader, B., Fereres, A., Blanc, S. 2017. Water deficits enhance the transmission of plant viruses by insect vectors. *PLoS ONE*, 12(5), e0174398, doi: 10.1371/journal.pone.0174398.
- Villamor, D. E. V., Ho, T., Al Rwahnih, M., Martin, R. R., Tzanetakis, I. E. 2019. High throughput sequencing for plant virus detection and discovery. *Phytopathology* 109, 716–725. doi: 10.1094/PHYTO-07-18-0257-RVW.
- Walling, L. L. 2000. The myriad plant responses to herbivores. *J. Plant Growth Regul.* 19, 195–216. doi: 10.1007/s003440000026.
- Wamwiri, F.N. and Changasi, R.E. 2016. Tsetse flies (*Glossina*) as Vectors of Human African Trypanosomosis: A Review "BioMed Research International, vol. 2016, Article ID 6201350, 8 pages. <https://doi.org/10.1155/2016/6201350>.
- Wei, M.S., Li, G.F., Ma, J. and Kong, J. 2015. First report of Pelargonium flower break virus infecting Pelargonium plants in China. *Plant Disease*, 99, 735.
- West, S.A., Griffin, A.S. and Gardner, A., 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of evolutionary biology*, 20(2), pp.415–432.
- Whitfield, A.E., Falk, B.W., Rotenberg, D. 2015. Insect vector-mediated transmission of plant viruses. *Virology*, 479:278–289. doi: 10.1016/j.virol.2015.03.026.
- Wielkopolan, B., Jakubowska, M., Obrepalska-Stepłowska, A. 2021. Beetles as Plant Pathogen Vectors. *Front. Plant Sci.*, 11 <https://doi.org/10.3389/fpls.2021.748093>
- Wu, H., Pang, R., Cheng, T., Xue, L., Zeng, H., Lei, T., Chen, M., Wu, S., Ding, Y., Zhang, J., Shi, M., Wu, Q. 2020. Abundant and diverse RNA viruses in insects revealed by RNA-Seq analysis: ecological and evolutionary implications. *mSystems*, 5: e00039-20. <https://doi.org/10.1128/mSystems.00039-20>.

- Wu, S.Y., Xing, Z.L., Ma, T.T., Xu, D.W., Li, Y.Y., Lei, Z.R., Gao, Y.L., 2020. Competitive interaction between *Frankliniella occidentalis* and locally present thrips species: a global review. *J Pest Sci*, 94: 5–16.
- Wu, W, Shan, H-W, Li, J-M, Zhang, C-X, Chen, J-P, Mao, Q. 2022. Bacterial Symbionts in the Transmission of Plant Viruses by Hemipteran Vectors. *Front. Microbiol.* 13:805352. doi: 10.3389/fmicb.2022.805352.
- Wu, X. and Ye, J. 2020. Manipulation of Jasmonate Signaling by Plant Viruses and Their Insect Vectors. *Viruses*, 12:148-164. doi: 10.3390/v12020148, www.mdpi.com/journal/viruses.
- Xue, X., Li, S.J., Ahmed, M.Z., De Barro, P.J., Ren, S.X., Qiu, B.L. 2012. Inactivation of *Wolbachia* reveals its biological roles in whitefly hosts. *PLoS ONE*, 7: e48148. doi: 10.1371/journal.pone.0048148.
- Yang, Q., Arthurs, S., Lud, Z., Liang, Z., Mao, R. 2019. Use of horticultural mineral oils to control potato virus Y (PVY) and other non-persistent aphid-vectorable viruses. *Crop Protection*, 118:97-103, <https://doi.org/10.1016/j.cropro.2019.01.003>.
- Zaffaroni, M., Rimbaud, L., Mailleret, L., Cunniffe, N.J., Bevacqua, D. 2021. Modeling interference between vectors of non-persistently transmitted plant viruses to identify effective control strategies. *PLoS Comput Biol.*, 17(12): e1009727. <https://doi.org/10.1371/journal.pcbi.1009727>.
- Zhang, T., Luan, J.B, Qi, J.F., Huang, C.J., Li, M., Zhou, X.P., Liu, S.S. 2012. Begomovirus-whitefly mutualism is achieved through repression of plant defences by a virus pathogenicity factor. *Mol Ecol.* 21: 1294-1304.
- Zhao, P., Yao, X., Cai, C., Li, R., Du, J., Sun, Y., Wang, M., Zou, Z., Wang, Q., Kliebenstein, D.J. 2019. Viruses mobilize plant immunity to deter nonvector insect herbivores. *Science Advances*, 5, eaav9801.
- Zhao, T., Ganji, S., Schiebe, C., Bohman, B., Weinstein, P., Krokene, P., Borg-Karlson, A.K., Unelius, C.R. 2019. Convergent evolution of semiochemicals across kingdoms: bark beetles and their fungal symbionts. *ISME J.*, 13:1535-45.
- Zhao, W., Wang, Q., Xu, Z., Liu, R., Cui, F. 2019. Distinct replication and gene expression strategies of the Rice Stripe virus in vector insects and host plants. *J Gen Virol.*, 100(5):877-888. doi: 10.1099/jgv.0.001255.
- Zheng, L.M., Mao, Q.Z., Xie, L.H., Wei, T.Y. 2014. Infection route of rice grassy stunt virus, a Tenuiviruses, in the body of its brown plant hopper vector, *Nilaparvata lugens* (Hemiptera: Delphacidae) after ingestion of virus. *Virus Res.*, 188:170–173. doi: 10.1016/j.virusres.2014.04.008.

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