Review

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Phytovirus Vectors, Detection Techniques, and Future Directions

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Phytovirus Vectors, Detection Techniques, and Future Directions

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Abstract: The phytophagous insect pests were vectors and could transmit the majority of the phytoviruses to their host plants. The orders of Hemiptera and Thysanoptera were the most common vectors of phytoviruses. The orders Orthoptera, Dermaptera, Coleoptera, Lepidoptera, Diptera, Thysanoptera, and Hemiptera were also the vectors of phytoviruses. Furthermore, aphids, whiteflies, cicadas, spittlebugs, leafhoppers, planthoppers, assassin bugs, plant bugs, stink bugs, lygaeid bugs, and thrips were among the most phytophagous insects that vector and transmit phytoviruses to healthy plants. The occurrence of a single species of these phytophagous insects resulted in one or more phytoviruses in general, and the Hemipteran order, in particular, vectored a lot of phytoviruses species. This review manuscript is focused on vectors of phytoviruses, techniques for their detection, and future directions. It will play a vital role in exploring scientific information concerning the interactions of phytoviruses and vector insects, the effect of phytoviruses on host behavior, mediators of phytoviruses transmission, persistent phytoviruses, some other insect vectors of the phytopathogen, mechanisms of host plant resistance against phytoviruses, and techniques of phytoviruses detection, as well as some important points to be considered in the future sustainably.

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

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1. Introduction

Phytoviruses cause nearly 50% of emerging plant diseases (Bernardo *et al.*, 2018). Dutta *et al.* (2022) reported that phytoviruses cause 47% of the total agricultural production when compared with the overall crop losses caused by plant pathogens. It was estimated that more than 50% of the emerging plant diseases were phytoviruses, which are inevitable or unmanageable. The intensity and interactions were also high for stressed plants due to plant stress (e.g., drought occurrence) and changes in their physiological functions (van Munster *et al.*, 2017).

Phytophagous insect vectors transmit the most phytoviruses from infected to healthy plants (Cunniffe *et al.*, 2021; Whitfield *et al.*, 2015). For instance, aphids and whiteflies are the vectors of many phytoviruses species, which cause vulnerability after being infested by them. Their occurrence resulted in the transmission of phytoviruses across many plants, which could be varied based on the diversified resources of their feeding, habits, and ecological factors (Janz *et al.*, 2006) and genera (Singh *et al.*, 2020).

Singh et al. (2020) reported that the phytophagous insects spread Caulimovirus, Reovirus, Tospovirus, Crinivirus, Luteovirus, Geminiviridae, and Tenuivirus from infected plants to healthy plants. Majorly, cicadas, spittlebugs, leafhoppers, planthoppers, aphids, white flies, assassin bugs, plant bugs, stink bugs, lygaeid bugs, and thrips (Fereres and Raccah, 2015; Terra and Ferreira, 2012), psyllids, some beetle species, and mealy bugs played a great role in vectoring the phytovirus (Chandi *et al.*, 2018). Mostly, the Hemiptera (whiteflies and aphids) and Thysanoptera (thrips) orders vectored the majority of phytoviruses. Both orders have common features like small size, many generations per year, large populations, and cosmopolitan distributions (Tooker and Giron, 2020). The Hemiptera insect orders feed on the vascular tissue of the plant phloem (Buchholz and Trapp, 2016), while the Thysanoptera rasp and suck up mostly on the young leaves, sprouts, and floral contents (Wu et al., 2020). Aphids, whiteflies, and psyllids are more likely to vector viruses to plants than other insect groups (Garzo *et al*., 2020; Heck, 2018).

The beetles, grasshoppers, and leafhoppers also vectored the rice yellow mottle virus (Koudamiloro *et al*., 2015). Thus, these indicate that insects are the most important factor in phytovirus transmission.

In addition, the families of colepterans (beetles), such as Chrysomelidae, Coccinellidae, Curculionidae, and Meloidae, are vectors of phytoviruses (Wielkopolan et al., 2021; Fereres and Raccah, 2015; Gergerich, 2001). It was also estimated that beetles transmitted around 11% of insect-borne viruses (Bhat and Rao, 2020; Smith *et al*., 2017). Both the othopteran and coleopteran orders were vectors of the rice yellow mottle virus (Koudamiloro *et al*., 2015). Further, eight orders of insects, such as Orthoptera, Dermaptera, Coleoptera, Lepidoptera, Diptera, Thysanoptera, Hemiptera, and Homoptera, were vectors of phytoviruses (Sarwar, 2020). However, most of the phytovirus vectors and their interactions with the insect vector, effects on the host's behaviour, mediators of transmission, persistence of another phytopathogen based on their occurrence, mechanisms of host plant resistance against phytoviruses, and detection techniques were not well known. Therefore, the objective of this paper is to review phytoviruses, their detection techniques, and future directions. Understanding these issues will be used to manage both pests, i.e., insects, and phytoviruses on the host plants.

2. Phytovirus Vectors

2.1. Phytoviruses Insect Vector Interactions

Exploring phytoviruses is not new to science. It accounted for more than one century (nearly 120 years ago). For example, the tobacco mosaic virus is the most studied phytovirus. These indicated that the association between plants, vectors, and viruses has a long history. This is why, in nature, plants interact with multiple phytoviruses, specifically phytophagous insects. Many insect species were acting as phytovirus reservoirs in ecological systems (Wielkopolan *et al*., 2021; Wu *et al*., 2020). In line with this, Wu *et al*. (2020) reported that there were more than 600 insect species that vectored more than 1,213 RNA viruses. The ways they interact with hosts are complex and have evolved over time (Jeger, 2020; Gandon, 2018; Gutiérrez *et al*., 2013). In this case, the vector insect is feeding on plant parts to continue their lifecycles and generations. These situations made them share a wide range of symbiotic relationships, which could be beneficial or harmful to ecological systems. It is a fact that the relationships between phytoviruses and vector insects are interspecific. This means they varied with the 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).

The interaction of phytoviruses with insect hosts requires specific molecular interactions for recognising proteins between them (Deshoux *et al*., 2018; Dietzgen *et al*., 2016). They also recycled the insects between the insect vectors that feed on plants and from the mother vector to her offspring for transmission (Purcell and Almeida, 2005).

Most of the phytoviruses were entered into the host plants during chewing and sap-sucking by the host plants. These leave the host plants injured or wounded. The phytoviruses found favourable conditions for growth and development by following the injured parts of the host plant. 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). Therefore, understanding the functions of effectors and elicitors in complex interactions is critical for deciphering how phytoviruses and insects colonise host organisms and how plant immunity is orchestrated (Ray and Casteel, 2022).

The vector-based transmission of phytoviruses is categorised into helper component proteins and capsid proteins/coat proteins (Agranovsky, 2021). The viral helper protein components were serving as an adaptor between the phytovirus (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 that are used to protect their genomes during entry and exit from the host cells and provide interactions with their vector. Phytoviruses were among the various groups that produced the unusual capsid proteins. For example, the cauliflower mosaic virus that was transmitted by aphids had major capsid proteins and helper components. Most of the time, the phytoviruses also possess RNA as their genome along with the capsid proteins, while a few viruses contain DNA (Prasad *et al*., 2019).

Usually, insect-based vector transmission occurs through feeding (Purcell and Almeida, 2005). Many host insects carry phytoviruses but are unable to transmit them to their host plants. The insect vectors of viruses were threatened by them since the phytoviruses attacked several exogenous and intestinal tracts after entering their bodies through natural openings (e.g., orally or through mouthparts during feeding and sap-sucking of plant parts, including foliage). On the contrary, insect vectors never give up their bodies easily to viral infections. But they fight against viral invaders by forming physical and immunological barriers to defend against their invasions. For example, they used cell-intrinsic antiviral immunity, the peritrophic matrix, the mucin layer, and local symbiotic microorganisms (Ma *et al*., 2021).

Understanding the physiological and ecological interactions between insect vectors and phytoviruses is critical for understanding how they invade and injure plants after they have been infested and infected (Purcell, 2009). Generally, plant pathogens are transmitted to susceptible host plants by insect vectors (Heck, 2018). These goals are achieved by altering the host selection behavior of the vector insect to enhance and promote phytovirus transmission (Ingwell *et al*., 2012). A phytoviruses was used to manipulate the host plant phenotypes to increase the suitable behaviours for vectors to transmit (Chesnais *et al*., 2020; Mauck *et al*., 2012). Furthermore, the post-acquired nature of vectors with viruses makes them stronger and more conducive than those that are purely pre-acquired. It was also reported that the effects of a circulative, non-propagative virus (Turnip Yellows Virus) on a behaviour suite increased the velocity of movement, fecundity, and activity levels of virulent aphids (*Myzus persicae*) towards the host plants (*Montia perfoliata*). Because they highly exploit the resources in a short period of time, even reaching the phloem to ingest more sap, regardless of plant infection status, whereas non-viruliferous aphids exhibit fecundity and biomass after the host plant is infected with the Turnip Yellows virus. But they had the lowest rates of dispersal and locomotor activity (Chesnais et al., 2020). Thus, the acquisition of either virus particles or plant material is altered by viral infection without replication in the vector. The behaviour of aphids *(M. persica*) after virus acquisition showed that locomotion behaviour was affected by feeding the turnip yellow virus-infected plant when compared with that feeding on the artificial medium containing purified virus particles (Marmonier *et al*., 2022). Vectors can prefer to settle on and feed on infected and noninfected host plants. Persistent transmission and vector preference depended on the vector's infection status, the viruses that could have altered the quality of the host plant to feed, and population dynamics (Cunniffe *et al*., 2021). Ingwell *et al*. (2012) also reported that the phytoviruses altered the behaviour of insects to enhance their spread and host selection behaviour by their insect vector. This study also found that after acquiring the Barley yellow dwarf virus in vitro, the aphid (*Rhopalosiphum padi*) prefers to feed on non-infected wheat plants, whereas noninfective aphids prefer to feed on BYDV-infected plants. This behavioural change should promote the spread of a virus since noninfective vectors prefer to feed on the infected plants for transmission. Javed *et al*. (2021) also reported that the behaviour of vectors, such as host fitness, seeking, and feeding, is determined by the vectorial capacity, pathogen transmission, and epidemiology of the vector-borne disease, and that these factors alter the behavioural traits of the arthropod vector.

The best-known phytoviruses alter the host gene expression profile to regulate the host cell across signalling pathways and induce severe diseases in plants. For example, the geminiviruses manifest in leaf curling, vein swelling, chlorosis, growth stunting, bending of stems, and reducing leaf size (Bhattacharyya *et al*., 2015; Mansoor *et al*., 2006). The plant infected by the viruses also changed its organic compounds and volatile profiles for elicitation to settle their vectors (Jiménez-Martnez *et al*., 2004; Eigenbrode *et al*., 2002). Thus, 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 the cauliflower mosaic virus attracted more aphids than healthy Arabidopsis thaliana. After being infected, the phytoviruses encountered defense barriers at every step of their replication cycles, i.e., spread in the agro-ecosystems and transmissions, plant cell infections, and systemic invasions. The host plant, on the other hand, resists viruses through a variety of passive and active mechanisms. These included the RNA-silencing machinery and the innate immune system, which are mediated by physical barriers (e.g., by forming thick waxy cuticles and cell walls), blocking or lacking a component required for the virus to complete its life cycle, activating immunity and its effectors, and leading to the silencing of RNA system functions (Leonetti *et al*., 2021).

In another turn, there were also specific protein characteristics that encoded the surface structure of the plant virion and were essential for its transmission by insect vectors. The phytoviruses particles were required to retain the specific binding sites when attaching to the specific sites in insect vectors until they were transmitted to host plants. Some phytoviruses also have nonstructural protein helpers that act as bridges for binding virions to vectors (Singh *et al*., 2020).

2.2. Effect of Phytoviruses on the Host Behavior

Insects transmit phytoviruses after being probed comprehensively with their vectors. These transmissions occur during biting and chewing by their mouth parts to get good nutrient contents and through host range expansions (Butter, 2021; Cunniffe *et al*., 2021). After herbivores, the insect`s vector viruses could affect the life cycle, population genetics, and evolution (Gutierrez et al., 2013). Most of the phytoviruses were visible following the infestations with a diversity of insect vectors.

An interaction between herbivore insects and pathogens could be mutualism, commensalism, or antagonism (Roossinck, 2015; Kluth *et al*., 2002). Mutually, the virus-induced changes in host plants might benefit the insect vector (Casteel and Jander, 2013). Moreover, insect vectors also benefit from transmitting phytoviruses. In line with this, Zhang *et al*. (2012) found that begomovirus performance is greatly enhanced on tobacco (*Nicotiana tabacum*) that is infested with whiteflies. Martinière *et al*. (2013) also 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 altering the host plant-virus interactions.

The relationship between the insect vector, the virus, and their effectors may be dependent on insect vectors or the host range. In other cases, interactions between insects and viruses may have to occur naturally. In turn, they indirectly harmed or helped the other plant by altering its chemistry and immunity. But interactions could also be beneficial to the other individual as a certain entity (West *et al*., 2007). The pathogen could also alter behaviour and phenotypic traits for transmission and spread (Lefevre and Thomas, 2008).

The proteins of the host plants facilitate interactions between phytoviruses and insect vectors. For instance, proteomic proteins are used as mediators of interactions between phytoviruses and insect vectors for transmission (Mittapelly and Rajarapu, 2020). The proteins found in the host plant cells also responded efficiently to phytovirus transmission. Phytoviruses are endocellular and move inside their host cells for multiplication (Uzest *et al*., 2011). On the other hand, the host plants are serving as a mediator for phytoviruses and their vectors (Biere and Tack, 2013; Gutiérrez *et al*., 2013). Thus, understanding the mechanisms of these interactions is used to underpin the management strategies of the phytoviruses. It is used for interfering with their suitable host cells, nutrient uptakes, and mechanisms of their transmission (Dietzgen *et al*., 2016). And they could also minimise their effects on their natural enemies' yield, quality, quantity, and marketability. For example, semi-persistent beet yellow viruses that infected Beta vulgaris increased sugars by decreasing total amino acid content and the quality of the aphid parasitoid Lysiphlebus fabarum's attraction to Aphis fabae (Albittar *et al*., 2019).

2.3. Transmission Mediators for Phytoviruses

Naturally, phytovirus 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; Ambethgar *et al*., 2019; Whitfield *et al*., 2015; Bragard *et al*., 2013; Hunter, 2008). Phytophagous insects vectored and transmitted phytoviruses from infected to healthy plants (Gutiérrez *et al*., 2013). They vectored it during feeding and wounding above- and below-ground plant organs (Labandeiraa and Prevec, 2014). Specifically, piercing-sucking phytophagous insects were highly active in these activities, and some of them are indicated in Table 1. The insect vector virus transmission has direct effects on the host plant's ability to bite rates, feed amounts, and make 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 phytoviruses, such as tobacco mosaic virus, tomato spotted wilt virus, tomato yellow leaf curl virus, cucumber mosaic virus, cucumber mosaic virus, 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). Aphids spread more than half of the known phytovirus species (Fingu-Mabola and Francis, 2021). The first and early second larval stages of thrips species such as *Frankliniella gemina, F. occidentalis, F. schultzei, F. zucchini, Scirtothrips dorsalis, Thrips palmi*, and *T. tabaci* were transmitted to host plants through their circulatory systems (Lima *et al*., 2022; Jeske *et al*., 2001).

Geminiviridae is the largest phytovirus family that has a circular single-stranded DNA genome. It destroys plants and is a major cause of global crop yield losses (Gupta *et al*., 2021) that were replicated after rolling circles for recombining dependently.

Naturally, phytoviruses travelled a short distance. Hence, they used phytophagous insects as vectors to travel long distances. In addition to vector insects, human beings also play a great role in the movement of phytoviruses across continents, countries, states, villages, and farmlands by moving infected plant materials and other plant propagules to exchange crops 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 the spread of the virus (Farooq *et al*., 2021; Fereres, 2015). Regularly, potential phytoviruses emergences result from human contact with the infected plants carrying the uniform gene during agricultural practices. After physical contact with virus-infected plant parts, it spread to the wounded plant, fruit viruses, mammals, parasitic weeds, such as dodder-contaminated soils and agricultural operations, and other herbivores.

Table 1. Insect-Mediated Phytovirus Transmission.

Insect Vectors	**Host Crops**	**Target Viruses**	**References**
Aphids	Cauliflower	Cauliflower mosaic virus	Blanc *et al*. (2014); Hoh *et al*. (2010); Zest *et al*. (2007); Plisson *et al*. (2005)
	Cowpea	Cowpea mosaic virus	James *et al*.(2013); Scott and Fulton (1978)
	Cucumber	Cucumber mosaic virus	Pirone and Megahed (1966)
	Bean	Bean common mosaic Virus	https://www.daf.qld.gov.au/__data/assets; Scott and Fulton (1978)
	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 *et al*. (2015)
	Solanaceae family	*Potato virus*	MacKenzie *et al*. (2013)
	Sweet corn	Johnson grass mosaic	https://www.daf.qld.gov.au/__data/assets

		Virus	
	Sweet potato	Sweet potato feathery Mottle virus	https://www.daf.qld.gov.au/__data/assets
	Tobacco	Tobacco rattle virus	Mulot *et al.* (2016)
	Potato	Potato virus y	Yang *et al.* (2019)
	Banana	Wolbachia	De Clerck *et al.* (2015); Leonard et al. (2015); Kollenberg *et al.* (2014); Xue et al. (2012); Augustinos *et al.* (2011)
	Cauliflower	Cauliflower mosaic virus	Zest *et al.* (2007)
Beetles Grasshoppers,	Rice	Rice yellow mottle virus	Koudamiloro *et al.* (2015)
Leafhopper	Maize	Maize chlorotic dwarf virus	Cassone *et al.* (2014)
	Rice	Rice yellow mottle virus	Koudamiloro *et al.* (2015)
Leafhopper	Rice	Rice dwarf virus	Chen *et al.* (2004)
Plant Hoppers and Leafhoppers	Family Poaceae (such as rice)	Tenuiviruses. E.g. Rice stripe virus	Zhao *et al.* (2019); Zheng *et al.* (2014); Nault and Ammar (1989)
	Tomato	*Tomato spotted wilt virus*	Lu *et al.* (2020)
	Tomato	Tomato spotted wilt virus	Montero-Astua *et al.* (2016); Whitfield *et al.* (2015); Moritz *et al.* (2004)
Thrips (Thysanoptera: Thripidae)	Chrysanthemum, groundnut, pelargonium flower break virus, and maize	Important thirps species are found in the genus: 1). Orthotospovirus (Tospoviridae): alstroemeria necrotic streak orthotospovirus; 2). chrysanthemum stem necrosis orthotospovirus; 3). groundnut ringspot orthotospovirus; 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.	Lima *et al.* (2022); He *et al.* (2020); Liu *et al.* (2017); Achon *et al.* (2017); Chen *et al.* (2017); Kusia *et al.* (2015); Wei *et al.* (2015); Batuman *et al.* (2014); Reitz et *al.* (2011); Hassani-Mehraban *et al.* (2010); Nagata *et al.* (2004)

Whiteflies Gennadius (Hemiptera: Aleyrodidae	Tomato	Tomato chlorosis virus and Tomato severe rugose virus	N'cho *et al*. (2022); Sangeetha *et al*. (2018); Pakkianathan *et al*. (2015); Fereres *et al*. (2016); Wang *et al*. (2016); Liu et al. (2013); *Gottlieb et al*. (2010)
	Banana	Wolbachia	De Clerck *et al*. (2015); Leonard *et al*. (2015); Kollenberg *et al*. (2014); Xue *et al*. (2012); Augustinos *et al*. (2011)
	Cotton	Cotton leaf curl Multan virus and Tomato yellow leaf curl	Zhao *et al*. (2019); Pan *et al*. (2018)
	Wide Host range>420 plant species	Family Geminiviridae e.g. begomoviruses	Nigam (2021); Rosen *et al*. (2015); Ghanim, (2014)
	Cassava, Sweet Potatoes Tobacco	Tomato yellow leaf curl disease and Cassava mosaic disease	N'cho *et al*. (2022); Berlinger (1986); Legg *et al*. (2011)
Mexican bean beetles	Soybean	Bean pod mottle virus	Gedling *et al*. (2018); Smith *et al*. (2017)

2.4. Phytoviruses Persistent

Based on the duration of the phytoviruses' persistence in the bodies of their insect vectors, they were categorized into non-persistent, semi-persistent, and persistent (Sylvester, 1962). Non-persistent signals are those that are transmitted within a few minutes of contacting their host body. They are formed into capsid-like structures and transmitted quickly after being contaminated by using the mouthparts and stylets to puncture their intracellular membranes 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, the *cucumber and cauliflower mosaic virus* particles were transmitted by aphids (*Myzus persicae*) (Moreno *et al*., 2012).

The semi-persistent viruses, on the other hand, will transmit for up to an hour after acquiring the host. They were also residing in the 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 Crinivirus that is transmitted by the whitefly *(Bemisia ta*baci) is a typical example of this virus. Unless, as a report from more than 20 countries, including China, shows (Shi *et al*., 2018), their economic importance is not widely recognized around the world. Even though they are serving as mediators of phytoviruses, for example, the yellow crinivirus is infectious in the whitefly 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*, played great roles in transmitting the *Citrus tristeza* virus to the citrus plants (Herron *et al*., 2006). Unfortunately, they did not appear when they were entered into the host tissues. Their range of transmission also increased as the climate changed (Fereres, 2015).

The persistent phytoviruses were transmitted within hours to days after contact with the bodies of their hosts and were even inherited by the insect progeny (Bragard *et al*., 2013). They were retained in the insect vectors' 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, propagative viruses were circulated through the alimentary canal of the vector to reach the hemocoel and accessory salivary glands. Then, they could replicate and systemically invade vector insect tissues before being transmitted *via* salivary glands (Bragard *et al*., 2013; Ammar *et al*., 2009). But the circulative, non-propagative viruses do not replicate in vector tissues.

Nevertheless, they traverse the insect gut, hemolymph, and salivary tissue membranes to reach the salivary glands for transmission to the host plants (Pinheiro *et al*., 2015; Bragard *et al*., 2013). Or they were spread to the neighboring organs to reach the salivary glands for transmission and replication mechanisms in their vector tissues (Bragard *et al*., 2013; Hogenhout *et al*., 2008). Generally, non-persistent and semi-persistent viruses persist for a short time and cannot enter the hemolymph of insect vectors. But the persistent phytoviruses are retained in the hemolymph of their vectors for a long time (Shi *et al*., 2021).

2.5. Other Insect-Based Vectors of Phytopathogens

The insect-borne plant bacteria, phytoplasmas, nematodes, Oomycota, and fungi are vectored by insect vectors to continue their life cycles 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 spread a lot of plant-pathogen within a short period. 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 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 biotics (Bragard *et al*., 2013) and abiotic factors stresses (e.g., temperature, CO_2, O_3, water stress) can have a dramatic effect on viral transmission (van Munster, 2020).

2.6. Mechanisms of Host Plant Resistance against Phytoviruses

The host plant cells have pectin and cellulose barriers that are used to limit the success of phytoviruses' exiting, entering, and transferring from one host plant to another after being vectored by the host insect. According to Flor's (1971) concept of the gene-for-gene model, the host plants can recognize and actively defend themselves from virus infections in various ways. Many authors reported on how the host plant defends itself against phytoviruses. For instance, Marwal and Gaur's (2020) reviewed paper indicated that the host plant had a defense mechanism known as pathogenesis-related biochemicals. These were sourced from the metabolites and proteins of the host plants. The dominant resistance (R) genes (that confirm resistance) and corresponding avirulence protein (Avr) (pathogen Avr gene-encoded proteins [effector/elicitor proteins involved in pathogenicity]) are derived from plant proteins (Marwal and Gaur, 2020; De Ronde *et al*., 2014). A consistent feature of plant and phytovirus interactions requires specific molecular interactions, commonly *via* proteins (Dietzgen *et al*., 2016).

Negatively, this protein affects phytoviral replication and the expression of viral molecules. It also leads to a series of hypersensitive responses (HR) to minimize their effects on the host plant's immunity (pathogen-associated molecular pattern–triggered immunity and effector-triggered immunity), while the Avr protein renders the host plant`s RNA silencing mechanism and innate immunity (Bucher and Prins, 2006; Loebenstein and Carr, 2006; Bucher *et al*., 2003; Goldbach *et al*., 2003). According to Nez-Farfán *et al*. (2007), the plant fights phytoviruses through resistance (the plant completely immunizes itself from infection) and tolerance (the plant's production levels remain above the economic threshold despite infection). In conventional breeding methods, phytoviruses are managed to take advantage of the inherent resistance of plants (Akhter *et al*., 2021). But to overcome these barriers, phytoviruses 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 phytoviruses, virus behavior in host plants, and transmission efficiency (Gutiérrez *et al*., 2013). This might be due to having a lipid-based phytohormone, for example, 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). Jasmonate acts on gene expressions by slowing the rate of growth, repairing the damaged body, and ordering 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 and virus transmission (Walling, 2000). Furthermore, jasmonates stimulate the defensive mechanism 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, the chewing insects can promote and induce jasmonic acid in the 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).

3. Techniques of Phytoviruses Detection

Historically, little attention has been given to undomesticated or wild phytoviruses. 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 phytoviruses. 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), contemporary clustered regularly interspaced short palindromic repeats (CRISPR-Cas), and bioinformatics have drastically changed the research on viral pathogens (Massart *et al*., 2014). This has occurred after massively parallel sequencing or next-generation sequencing of microbial detection methods. NGS technologies have impacted plant virology by offering scientists the ability to detect phytoviruses that were previously undetected in quarantine and archaeological 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 the whole genomes and genetic information from a given environment. Furthermore, next-generation sequencing is used for discovering, identifying, diagnosing, and exploring the population diversity of individual phytovirus 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 researchers' ability to fully sequence entire genomes in metagenomics.This makes the utilization of next-generation sequencing standardized to identify the RNA of novel species of phytoviruses (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 (Roossinck *et al*., 2015; Stobbe and Roossinck, 2014). whereas CRISPR-Cas-based genome editing and detection techniques are producing virus-resistant strains. It enabled us to generate genetically engineered plants by genetics, DNA repair, substitution of base pairs, editing prime, small molecule detection, and biosensing in plant virology (Shahid *et al*., 2021). In the former period, the phytovirus was detected by protein-based immunological tests with the help of the techniques of serology (ELISA). This technique 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, enzymatically produced colorimetric markers, or radioactivity reactions by attaching markers (Rubio *et al*., 2020; Hull and Al-Hakim, 1988). The detection of phytoviruses in insects is also carried out by ELISA and PCR methods (Sobko *et al*., 2021).

The molecular-based techniques for detection also included molecular hybridization and DNA amplification. This might be classified into polymerase chain reactions 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). In this method, a copy of a specific region 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 because they are not sensitive enough to detect the novel low titers of virus sensitivity in an undomesticated plant. Nanophytovirology (nanoparticles) has a potential management approach against viral plant diseases. This is due to the nanoparticles having a special physiochemical property that allows them to interact with viruses, their vectors, and host plants in a variety of specific and useful ways (Farooq *et al*., 2021). For instance, nano-bio sensors can be used for the detection of vectors that act as carriers of viruses. For example, it was used to detect the plasmodiophoromycete, a fungal vector of beet necrotic Polymyxa betae (yellow vein virus), the causative agent of sugarcane rhizomania disease (Safarpour *et al*., 2012; Mouhanna *et al*., 2008).

4. Future Directions

Insect pests vector and transmit most phytoviruses. Therefore, developing the management of phytoviruses 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 phytoviruses, Hence, knowing the diversity of phytoviruses in natural ecosystems, which is still poorly known, is very important to know the mechanisms of their transmission and evolution and to predict their status in the future. It is also used to manage them strategically through plant breeding to obtain immunisation or genetic resistance, 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.

This activity could reduce the cost of phytovirus management at the producer level. But it needs further research on ecological influences on their distributions, 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 for phytovirus management should be developed in the future by diagnosing and identifying the phytovirus. It is very important to develop different management technologies to suppress phytoviruses 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 minimise the damage caused by phytovirus. Thus, the sustainable management of phytoviruses 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, food losses, 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.

5. Conclusions

Phytophagous insects cause disease by vectoring it, injuring, spoiling, damaging, parasitizing, and reducing the plants' yield and marketability. Diverse microbial communities in the environment contact the phytophagous insect. Hemiptera, Thysanoptera, Coleoptera, Orthoptera, and Dermaptera were among the insect orders that vectored and transmitted phytoviruses from infected to non-infected plants. From these, hemipterans are ranked first in vectoring, spreading, and dispersing phytoviruses. The aphids, whiteflies, leafhoppers, thrips, psyllids, beetles, and mealybugs were also among the insects mentioned in the vectoring and reserving of phytoviruses. These were detected by parallel and nonparallel methods such as next-generation sequencing and CRISPR-Cas. CRISPR-Cas was discovered following the microbial detection method of massively parallel sequencing (MPS) or next-generation sequencing (NGS). It is used for genome editing to develop effective phytovirus 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 because they are not enough to detect the novel low titers of virus sensitivity in an undomesticated phytovirus. In the future, the development of management methods for phytoviruses should begin with the management of their host insects. because managing insect pests alone could have played a great role in alleviating the insect-based vectored phytoviruses. Thus, their sustainable management has required the integration of virology and entomology disciplines by understanding biology, ecology, taxonomy, and their associated pests.

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