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Major vectors of the plant viruses: a review

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Abstract
The majority of plant viruses that cause diseases in agricultural crops rely on biotic vectors for transmission and survival. Viral diseases of plants cause enormous economic losses particularly in the tropics and semi-tropics which provide ideal conditions for the perpetuation of viruses and their vectors. Intensive agricultural practices necessitated by the ever-increasing demands of the rapidly growing population and the introduction of new genotypes, cropping patterns and crops have further aggravated the problem of viral diseases. The largest class of plant virus-transmitting vectors is insects but other vectors include mites, nematodes and chytrid fungi. The best-characterized plant viral insect vectors are aphids, thrips, leafhoppers, plant hoppers and whiteflies. The different modes of viral transmission by vectors include non-persistent, semi-persistent and persistent, whereby the transmission window to disseminate the virus to a new host plant after feeding on an infected plant by the vector lasts from seconds to minutes, hours to days, or days to weeks, respectively. Many diverse approaches have been tried to minimize the losses caused by these diseases. The mechanisms of arthropod-virus associations are many and complex, but common themes are beginning to emerge which may allow the development of novel strategies to ultimately control epidemics caused by arthropod-borne viruses.

Keywords: Aphids, plant hopper, transmission, whitefly, vector and virus

Introduction
The biological aspects of plant virus transmission are known to mankind from about hundred years [64]. First plant virus-vector interaction was observed during the late 19th century in rice fields involving leafhoppers as mentioned by Gibbs and Harrison [21]. Later with proper extraction and filtration techniques several affirmations to the insect transmission of plant viruses was given that involved leafhoppers and aphids as vector for beet curly top mosaic virus and cucumber mosaic virus [6, 17]. The role of thrips *Frankliniella occidentalis* (Pergande) in the spread of TSWV showed us the real degree of damage and associated danger in future which these interactions can cause in our agroecosystems [38]. The most notable plant viruses prevailing within agroecosystems worldwide includes geminiviruses, closteroviruses, and tospoviruses [23] which comprises of around 21 families and 8 unassigned genras which are economically vital as the severity of viral diseases are concerned [28]. Insects that involved in transmission are mainly hemipterans which constitute around 50 percent of the total transmission of viruses in the agroecosystem, thrips, beetles, nematodes and fungi are the rest whereas researches are still under progress for around 30 percent of other unassigned vectors [26]. Most plant viruses are the result of a coevolution of virus and vector.

Transmission is itself a biologically complex phenomenon involving three basic steps acquisition, retention and inoculation [24, 48]. The relative time involved depends upon the type of transmission adopted by the vector which can be illustrated as circulative or non circulative. Almost 50 percent of viruses are transmitted by aphids out of hemipterans and these involve cuticular binding of the virus particles to the distal portion of the stylet which remains adherent till the next moult or next insertion of the stylet to the host cell [9, 30]. Circulative transmission comprises of retention of viruses over longer period of time within the insect body which bypass the insect alimentary canal and through heamocoel reaches salivary glands. Vector transmissibility has been defined by conducting several comparative evaluations of vector-specific strains and vector-non transmissible variants. The capsid protein is mainly responsible in the lack/loss of transmissibility of both circulative and non-circulative transmitted viruses.

Virus diversity and distribution
International committee on taxonomy of viruses stated about a 1000 viruses that are known to cause viral diseases in plants [36].

These viruses mainly mark their presence in the tropics [60] to Antarctica [27] with infection incidence as high as 60 percent based on current and older technologies.

Most of our information about plant-virus interactions comes from viruses that infect a small subset of plant species, that are prevalent in low diversity plantings (crop monocultures), and that have strong phenotypes (symptoms; negative effects on yield) [73, 59]. Perennial plants interact differently with viruses due to their long-lived lifestyle, cycling between periods of dormancy and growth, and greater potential to acquire more than one virus (co-infections) over multiple seasons.

Major concern lies within the annuals and crop fields due to their less stress bearing ability and short duration which expose them for viruses under sub tropical and tropical areas. Out of all plant affecting viruses majority have small and single stranded (ss), RNA genome, but some viruses also poses double-stranded (ds) RNA, ssDNA or dsDNA genomes.

Types of transmission

Viruses being obligate parasites needs to be transmitted from one susceptible host to another for their continuity and survival along with that they require successful introduction within the host cell for replication of their genetic material. These transmissions are mediated in two ways if occurred with the help of vectors, human pruning shears and tools and other direct, external contamination then it is termed as a horizontal transmission. Whereas vertical transmissions occurs when a plant gets it from its parent plant. Either through asexual propagation (cuttings) or in sexual reproduction via infected seeds.

Mechanical transmission of plant viruses involves the introduction of infective virus or biologically active virus into a suitable site in the living cells through wounds or abrasions in the plant surface commonly called as sap inoculation and are used for experimental purposes under lab conditions.

Transmission is not just an interaction between a susceptible host and virulent virus particle it does involve various other factors like stage of plant growth its type and nutrition along with several environmental factors such as light, temperature and time of year or season.

Methods of transmission

Viruses involved in the plant diseases are evolved overtime alongside their vectors to develop the most suitable interaction which is potent to the plant and essential for the survivability of the plant viruses. Vectors of plants viruses involve a significant amount of molecular interactions that proves to be beneficial for the virus particle to overcome the hostile environmental conditions and successful transmission to a new host cell. On the basis of these interactions transmission of plant viruses is classified as circulative or non circulative involving the pattern of movement within the host body prior to transmission [48b, 44, 20]. Viruses that do not cross membranes within the vector are collectively known as non circulative viruses, and these can be classified as either non-persistent or semi-persistent viruses. In contrast, circulative viruses are described as persistent circulative or persistent propagative viruses. Circulative viruses are further classified as persistent and non persistent types. Persistent viruses soon after ingestion of by the insects, requires their transportation into the hemocoel and, subsequently, into the salivary glands, from there they are transmitted to new plants during feeding [23b]. Non-persistent viruses are acquired by insect vectors as they probe the host plant to determine if it is a suitable food source or during the feeding process itself. They remain associated with within the initial portion of alimentary canal and usually remain transmissible for only a few minutes to, at most, a few hours following acquisition [23c].

On the other hand are the persistent viruses, which, after acquisition by the vector, are retained in a transmissible form throughout the life of the vector. Efficient transmission of persistent viruses requires longer acquisition feeding periods that can vary from hours to days and, frequently, have lengthy latent periods during which the virus cannot be transmitted. The best-studied persistent viruses are those in the family *Geminiviridae*, particularly within the genus *Begomovirus*. Viruses are classified as semipersistent, such as those in *Closteroviridae*, encompass those with a wide range of transmission modes between the extremes of non-persistent and persistent transmission [50, 13, 22].

Transmitting agents

Transmission by aphids

Aphids are one of the most preferable types of transmitter of plant viruses among all homopterans mainly due to its unique feeding behaviour and fast multiplication rates due to parthenogenesis and shorter life cycles. They accounts for almost 50 percent of total transmitted plant viruses across the globe (275 different types approximately) [71].

Aphids also have good sense ability for the visual cues that enables them to locate their host as compared to other members of the homopteran family [37, 35, 18].

Aphid transmission is both of non-circulative and circulative type earlier group of viruses comprises of members from *Bromoviridae* [14, 52, 49], *Potyviridae* [3, 70, 7, 51] *and Caulimoviridae* [72, 46, 42] and the later circulative type comprises of *Poleroviridae* [12].

Aphid posses hollow, needle-like mouthparts that can be penetrated into the plant cell wall, either by mechanical force and/or with the assistance of salivary and gut enzymes. This rupturing of the cell wall makes the availability of plant cell contents to the aphid which is later sucked into the stylet. This feeding mechanism does not hinder the cell living in any way and is available for virus replication within the infected cell. Plant virus genomes encode movement proteins that enable them to move to the neighbouring cells [11].

Transmission by whiteflies

Transmission of viruses by whiteflies is associated with mainly five genus of viruses *Begomovirus,* Crinivirus, *Closterovirus,* and *Ipomovirus or Carlavirus*.

Out of these 90 percent are of *Begomovirus* genus. Out of the total reported whiteflies species *Bemisia* and *Trialeurodes* genera are virus vectors. In the genus *Bemisia*, only *B. tabaci* (Gennadius) has been shown to be a vector whereas in the *Trialeurodes* genus, *Trialeurodes vaporariorum* (Westwood), *T. abutiloneus* (Haldeman) and *T. ricini* (Misra) transmit viruses [32]. Begomoviruses are the most numerous of the *B. tabaci* (Gennadius)-transmitted viruses and cause crop yield losses of between 20 percent and 100 percent [8]. Symptoms include yellow veining, yellow mosaics, stunting vein thickening and leaf curling [2].

In the Americas, tomato is affected by a large number of *Begomovirus* species, which can also infect other crops [55], and these pose a risk to the agriculture of the European–Mediterranean region. New Begomovirus species on tomato are continually being discovered and some may be the result of genetic recombination between viruses present in multiple infections. After acquisition by whiteflies, begomoviruses are persistent and are retained for periods ranging from a few weeks to life [19]. The interaction between whiteflies and geminiviruses, especially *B. tabaci* (Gennadius) and Tomato yellow leaf curl virus (TYLCV), has been reviewed [15].

Whitefly instar nymphs and adults feed by inserting their proboscises into the leaf, penetrating the phloem and withdrawing sap. It is during this feeding process that plant viruses are acquired. Adult whiteflies may disperse and transmit the virus to new plants while feeding.

Transmission by leafhoppers and plant hoppers

Transmission in this class of insects is mainly of circulative nature which encompasses a wide group of viruses. The main abundance of hoppers is seen in areas with high temperature and relatively higher levels of humidity in mainly crops of south and south East Asia. They are believed to transmit mainly the yellow group of viruses and the most devastating example is of the tungro group of viruses Rice Tungro Bacilliform virus (RTBV) and Rice Tungro Spherical Virus (RTSV) which accounts for huge losses across the south east nations of Asia [4].

Transmission by nematodes

Nematodes belonging to the families Longidoridae (longidorids) and Trichodoridae (trichodorids) are generally known to transmit viruses, belonging to the genera Nepovirus and Tobravirus. These nematodes are basically ectoparasites that remain outside the roots that they feed on and use an extendable stylet to pierce cells located at, or just behind the root tip.

Nematodes acquire plant viruses during their feeding period on an infected plant and this acquired virus is then carried for infection on healthy plants in subsequent feedings. For a successful transmission to occur, the virus should be well introduced into a cell that survives the nematode feeding process, at least for a period long enough to allow some virus replication and movement into adjacent cells. This has been observed for *Paratrichodorus anemones* (Loof), the vector nematode of the tobravirus Tobacco rattle virus (TRV), where in the later stages of feeding a significant proportion of feeding episodes are abandoned before completion, leaving the cells alive [34]. There is a high degree of specificity in this association, in that particular virus isolates may be transmitted only by certain nematode species [53, 54] Tobraviruses and nepoviruses are both positive-sense, single stranded RNA viruses and have two genomic RNAs, the larger referred to as RNA1 and the smaller RNA2, that are packaged into separate virus particles [43, 25].

Transmission by mites

Mites share a very narrow spectrum but efficient vectors belonging to, Eriophyidae and Tetranychidae families [16]. They are very small in size (<250 μm) and hence easily dispersed by wind [31]. *Aceria tosichella* (Keifer) is one of the best studied mite vectors which transmit the wheat streak mosaic virus (WSMV) in wheat [63] and corn [62]. The second important mite transmitted plant virus, pigeonpea sterility mosaic virus (PPSMV) causes mosaic and sterility symptoms in pigeonpea [40, 39] and is transmitted by the eriophyid mite vector, *Aceria cajani* (Keifer), in semi-persistent manner [61, 57]. The transmission efficiency obtained from a single Eriyophid mite *A. cajani* is up to 53% but can be elevated to nearly 100% when >5 mites per plant are used [40b]. *A. cajani* can acquire PPSMV after a minimum acquisition access period (AAP) of 10–15 min and inoculate the virus after a minimum inoculation access period (IAP) of 60–90 min at 20–30°C [56]. The mite retains infectivity through the moults and remains infectious up to a period of 9 days. Though *A. cajani* possesses a short stylet of ~2 μm that allows penetration only into the epidermal tissues and, at most in the underlying mesophyll cells [58]

Transmission by chytrid fungi

Transmission of plant viruses by fungi is mainly associated with species of obligate soil inhabiting type fungi belonging to two major classes Chytridiales and Plasmodiophorales. Fungi are known to infect epidermal cells or root hairs near the root tips and produce zoosporangia containing many motile zoospores which add up viruses with viability [65, 45].

Virus transmission occurs by zoospores in two ways

1. **Non-persistent transmission:** viruses transmitted by *Olpidium radicale* (Schwartz) (cucumber leaf spot virus, cucumber necrosis virus and tobacco necrosis virus and its satellites are acquired from soil water on the outer membrane of zoospores). The virus particles though appear to enter the zoospore through infection canal, but they do not enter the resting spore during its formation.
2. **Persistent transmission:** Viruses transmitted by other fungi (*Olpidium brassicae* (Woronin), *Spongospora subterranean* (Wallr) and *Synchytrium endobioticum* (Schilb.)) are acquired from plant cells and enter the resting spores of vectors and are released with zoospores on germination [66, 65b].

There are nearly thirty soil-borne viruses which are known to be transmitted by five species of fungal vectors. Out of ten polyhedral viruses, nine belonging to family *Tombusviridae*, are acquired through in-vitro manner and do not occur within the resting spores of their vectors, *Olpidium brassicae* and *O. bornovanus* (Sahtiyanci). Eighteen rod-shaped viruses belonging to the furo- and bymovirus groups survives within the resting spores of their vector, *O. brassicae, Puccinia graminis* (Pers.), *Puccinia betae* and *S. subterranean* [10]. Some of the examples include lettuce big vein virus (*O. brassicae*), beet necrotic yellow vein virus (*P. betae*), barley mild mosaic virus (*P. graminis*), Indian peanut clump virus (*P. graminis*), wheat soil-borne mosaic virus (*P. graminis*), rice necrosis mosaic virus (*P. graminis*) and potato mop top virus (*S. Subterranean*) [58b].

Management of plant virsus

Plant virus diseases are known to cause significant economic losses, specifically in the tropical and subtropical regions throughout world [69]. Virus particles though have no direct control agent just like pesticides and at the same time farmers also have a very minute amount of knowledge regarding symptoms and transmitting agents' posses a very stiff challenge in their management. Symptoms such as leaf distortion, streaking and stunting, vein clearing, or mosaic when observed in the field are often mistaken for abiotic stresses or plant chimeras [68, 33]. Small scale farmers in developing countries often lack knowledge and believe that pesticides can control the diseases thus increasing their cost of cultivation.

In 2002 a survey conducted in southern areas of India to understand the farmers' perception and knowledge about tomato yellow leaf curl virus and its insect vector (Whitefly) which involved 174 tomato growing farmers from five Karnataka districts [47]. They found that majority of farmers were generally aware about the leaf curl symptom i.e. curly leaves with reduced size and stunted plants but alarmingly only 2 percent of the growers knew that the disease was transmitted by whiteflies.

If the farmer misses the right opportunity to counter the disease he may be under complete economic loss [29]. Chilli peppers (*Capsicum spp*. (Linn.)) are important crops across the tropics and subtropics grown for home consumption and also as an income source. As the pepper cultivation area is increasing, particularly in southern and eastern Asia so too is the pests and diseases incidence such as chilli leaf curl virus. In India, the epidemic break down of the particular virus resulted in huge economic losses thus completely prohibiting the farmers to grow chillies in future [41, 5]. Similarly, Mungbean (*Vigna radiate* (R. Wilczek)) is one of the favourite crop of the farmers in south Asia and south east Asia but the crop is under threat of *begomoviruses* continuously which can lead to a sudden disaster [1, 67].

Management of plant viruses is successful by control of their vectors right before reaching the ETL (economic threshold level) levels and at the same time manual observation of infected plants roughing out the deformed plants or those showing symptoms of a viral infection. A strict scheduling of plant protection measures with adequate resourcing of plant protection equipments.

Conclusion

Plant viruses are known to have a complex and diverse form of transmissibility patterns attributed to their unique pattern of interaction with their vectors.. Transmission pattern of plant viruses is either horizontal or vertical depending on the agent involved which further describes the mechanism of transmission in a circulative and non-circulative manner. Circulative transmission is again comes under as persistent and non persistent types. Circulative type of transmission is mainly opted in sap sucking pests such as leafhoppers and whiteflies. The majority of transmitters are from the sap sucking group of insects whereas others such as fungi, mites and nematodes have a very limited type of interaction restricted within a small group of families. What is most important by having deep knowledge in this regard is to develop several mechanisms that in one way or other affect these interactions. This leads in exploring ways in providing resistance to plants and effective and timely control of crop pests or the vectors of plant viruses. Ultimately the direct benefit should be utilised by the farmer by avoiding possible economic losses and in maintain the food security.

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