TRENDS IN AGRICULTURE SCIENCE
ISSN:2583-7850

Popular Article
Domain: Agriculture Science
Vol 5 Issue 5, May 2026, 714-721

Non-insect and insect-mediated transmission of plant viruses in crop systems

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doi.org/10.5281/TrendsinAgriculture.20590473

Abstract

Plant viruses are disseminated through both non-insect and insect-mediated mechanisms. Non-insect transmission includes mechanical inoculation, seed transmission, fungi, nematodes, vegetative propagation, and parasitic plants such as dodder. Insect transmission is the most significant mode and includes aphids, whiteflies, leafhoppers, mites, thrips, and beetles, operating through non-persistent, semi-persistent, circulative non-propagative, and circulative propagative pathways. These mechanisms determine virus retention, acquisition time, and spread efficiency. Together, these transmission routes contribute to virus survival, epidemiology, and large-scale crop losses, highlighting the importance of integrated disease management and vector control.

Introduction

Plant viruses are obligate parasites; they need to move from infected to healthy plants in order to survive and for continuity of their life cycle. They cannot move themselves, as they are nonmotile and also cannot penetrate the cuticle and the cell wall of plants. Penetration of the cuticle and the cell wall of host plants is not required for some plant viruses, specifically, those transmitted through seeds or by vegetative propagation. Some methods of transmission involve entering by penetration through a wound in the surface layers, such as in mechanical inoculation and transmission by insects. Movement of plant viruses are achieved either mechanically or by external agent, such as through vegetative propagation, seeds, fungi, nematodes, insects, and phanerogamic plant parasites (Van Regenmortel *et al.,* 2000). Most of the plant viruses are transmitted by insect vectors; only a few viruses are transmitted by human activities during operational practices such as vegetative plant propagation, interculture operations, transfer of infected material from one place to another, and introduction of new crops or varieties in existing or new geographical areas.

Plant-virus transmission is a very important factor in identifying a virus as a cause of disease. Once established within a host, plant viruses can survive until the plant dies, which depends on the type of plant. A plant virus can survive for hundreds of years in a perennial such as an individual tree, but it can survive on annual plants only for the crop season. Viruses usually depend for survival on the frequency of movement from susceptible plant to another plant belonging to the same or a different family. Knowledge of transmission of plant viruses is important for several reasons:

- Reorganization of cause: It helps to detect and identify causal agents of disease by transmission from infected to healthy plant.
- Know the mode of spread in the field: Study of transmission helps in identification of mode of spread of plant viruses in field.
- Development of disease: Virus transmission plays an important role in the development of disease. If transmission can occur rapidly from plant to plant in commercial crop developed the epiphytotic in particular area.
- Development of management strategies: It helps in the study of the establishment of a biological relationship between host and virus and interaction between virus and its vector. It is usually essential for the development of satisfactory control measures.
- Study of the virus properties: Some methods of transmission, particularly mechanical transmission, are very important for the study of virus properties in the laboratory.

A) Pathway of plant-virus transmission

Most of the plant viruses causing diseases in crops are transmitted from infected plants to healthy ones by various means, such as vegetative propagation, seeds, sap inoculations through mechanical injury, sap-sucking insects, and other organisms such as fungi and nematodes. Transmission of plant viruses can occur either horizontally or vertically, or both. Horizontal transmission is support to increase demonstratively disease prevalence and infection under highly favorable conditions such as high susceptible host population density, high inoculum levels, and high virus replication rates. Vertical transmission results in long-term virus persistence in the vector. Vertical transmission supports the evolution of benign infection. According to (Chen *et al.,* 2006) any plant-virus infection can follow two transmission processes. Plant virus transmission can be occur through the following two pathways in the nature.

Horizontal transmission:

Horizontal transmission is carried by external agents such as insect vectors, human activities, pruning, agriculture tools, and other direct or external contamination. In this pathway of transmission, viruses are directly or indirectly transmitted among individuals of the same generation. In direct horizontal transmission plant viruses are transmitted by a direct route such as airborne infection and foodborne infection, whereas in indirect transmission, plant viruses are transmitted through intermediate biological vectors such as aphids, whiteflies, and leafhoppers, which acquire and transmit virus from diseased plant to healthy plants.

Vertical transmission

Vertical transmission occurs when a virus's goes in to the progeny from the infected parent's plant either through asexual propagation such as cuttings, grafting, and budding etc. or in sexual reproduction via infected seeds. In this pathway, viruses are passed vertically from mother to offspring via egg, either on the surface of the egg, called "transovum transmission," or within the egg, called "transovarian transmission" (Clayton and Tompkins, 1994).

B) Methods of transmission

Plant viruses do not have the ability to penetrate the cuticle and cell wall of plant cells; therefore, these act as a barrier to infection. Plant viruses, except those transmitted by seed or by vegetative propagation, can penetrate the outer surface of the plant. To break down the natural barrier present in the plants, viruses are required to penetrate the cuticle and cell wall of the plant tissues by various methods, such as mechanical injury or invasion by vectors. These methods play an important role in the transmission of plant viruses. For the most part, plant viruses enter plants through a wound developed on the plant surface either mechanically or by insects. The majority of plant viruses are transmitted from plant to plant by insect vectors, especially those that feed on living green plant parts. Fewer plant viruses are transmitted by other methods, such as seeds, vegetative propagation, saps, fungi, nematodes, and phanerogamic plant parasites. Transmission of plant viruses can be categorized into types of transmission: Non-insect transmission and insect- transmission.

1. **Non-insect transmission**

a. Transmission by sap inoculation/mechanical: Transmission may occur naturally by rubbing of plant parts, contact between infected and healthy plants, movement of animals, or human activities. Infective virus particles or viral RNA enter plant cells through wounds, establish infection, and spread within the plant. Viruses such as Tobacco Mosaic Virus, cucumber green mottle mosaic virus, carnation mottle virus, tobacco necrosis virus, tomato bushy stunt virus, and potato virus X are commonly transmitted mechanically because they occur in high concentrations in infected plants. TMV can also spread through contaminated hands, clothing, implements, and even processed tobacco leaves.

Mechanical transmission is an important method for studying plant viruses. It is commonly used for virus identification, purification, multiplication, and determining host range through the formation of local lesions on inoculated leaves. In this method, viruses are transmitted through wounds or abrasions on the plant surface without any biological interaction or specificity. Artificial mechanical inoculation is usually done by grinding infected leaves in phosphate buffer and gently rubbing the extract onto healthy leaves dusted with carborundum powder to create small wounds. Infected plants may develop local lesions, mosaic, mottling, leaf deformation, or necrosis as symptoms of viral infection.

b. Transmission through seed: Seed transmission is the transfer of viruses from infected seeds to seedlings and mature plants. It is an important means of survival and spread of many plant viral diseases, especially in commercial crops. However, not all plant viruses are seed transmitted. More than 200 plant-virus diseases are known to spread through seeds, particularly in leguminous crops. Viruses may be present on the seed coat or inside the cotyledon and embryo. For successful seed transmission, the virus must remain viable during seed storage and infect the seedling after germination. About 15–20% of plant viruses are seed transmitted. Transmission rates vary depending on the host plant, virus type, environmental conditions, and stage of infection of the mother plant. Early infection usually results in higher transmission rates. Seed transmission is economically important because it introduces viruses into crops at an early stage, leading to rapid disease spread, often with the help of insect vectors. Infected seeds can also carry viruses over long distances, contributing to the worldwide distribution of plant viral diseases.

c. Transmission by fungi: Transmission of plant viruses by fungi was first demonstrated with the association of chytrid fungus, *Olpidium brassicae,* and big vein disease of lettuce by Fry (1958) and Grogan *et al.* (1958). Thirty viruses or virus like agents are transmitted by five species of fungal vectors. Among these, two species of Chytridiomycetes (*O. brassicae* and *O. bornovanus)* and three species of Plasmodiophoromycetes (*Polymyxa graminis, P. betae,* and *Spongospora subterranea*) are recognized as vectors of plant viruses. *O. brassicae, O. bornovanus,* P. *graminis, P. betae*, and *S. subterranea* are root parasitic fungi. The latter germinates and produces the zoospores, which function as infective agents and penetrate lettuce roots.

d. Transmission through vegetative propagation: Vegetative propagation is an important method of plant virus transmission in many crops. In this process, viruses are transferred from infected parent plants to new plants through vegetative parts such as tubers, bulbs, rhizomes, cuttings, grafts, runners, and suckers. Since the propagated material is derived directly from infected plants, the virus remains present in the newly developed plants. This mode of transmission is common in crops like potato, sugarcane, banana, cassava, and several ornamental plants. Vegetative transmission plays a major role in the survival and spread of plant viruses because infected planting materials can carry viruses over long distances and across growing seasons. The use of infected propagative material often results in reduced plant vigor, poor yield, and decline in crop quality. Therefore, the use of virus-free planting material and certification programs is essential for managing viral diseases transmitted through vegetative propagation.

e. Transmission by nematodes: Many plant viruses are transmitted by ectoparasitic nematodes belonging to the families Longidoridae and Trichodoridae. During feeding, virus particles attach to the cuticular lining of the nematode esophagus and are later released into healthy plants through saliva. Both adults and larvae can transmit viruses, but larvae lose infectivity after molting. Two major groups of plant viruses are transmitted by nematodes: Nepoviruses and Tobraviruses. Nepoviruses are polyhedral, single-stranded RNA viruses belonging to the family Comoviridae. They are mainly transmitted by species of Xiphinema and Longidorus. Their particles are about 30 nm in diameter and contain bipartite ssRNA genomes. Tobraviruses possess straight tubular particles and include important viruses such as tobacco rattle virus and pea early-browning virus. They are transmitted by species of *Trichodorus* and *Paratrichodorus*. Trichodorid nematodes can retain viruses for long periods, sometimes up to a year, aiding in disease spread and survival.

f. Transmission by dodder: Dodder (*Cuscuta* spp.), especially *C. campestris* and *C. subinclusa*, transmits many economically important plant viruses by forming a bridge between infected and healthy plants through haustorial connections. These connections allow close association between dodder and host phloem without complete cell fusion. Viruses are taken up from the infected host along with phloem sap and move into dodder tissues, often accumulating near growing regions. They can then be transferred to healthy plants mainly through phloem connections or via plasmodesmata. Movement is largely driven by nutrient flow between host and parasite. Dodder transmission has been reported for several plant viruses, including cucumber mosaic virus, tobacco mosaic virus, potato stem mottle virus, beet curly top virus, and cucumber mosaic virus in cucurbits.

2. Insect transmission

The transmission of plant virus to a new host plant may occur after feeding on an infected plant by the vector within seconds to minutes, hours to days, or days to weeks and sometime it may occur in the next generation. The different modes of viral transmission by vectors are described here:

a) Non-persistent Transmission: In non-persistent transmission, viruses are retained briefly in the stylet of insect vectors and can be transmitted to healthy plants within seconds or minutes. Aphids commonly transmit these viruses after feeding for less than a minute on infected plants. The viruses are usually present in epidermal or parenchyma cells and are retained only for a short time. Examples include papaya ringspot virus and cucumber mosaic virus. Transmission occurs either through direct interaction of the viral coat protein with the vector or with the help of viral helper proteins.

b) Semi-persistent Transmission: Semipersistent viruses require longer feeding periods (12–24 hours) for acquisition and are retained in the insect foregut for several hours or days. These viruses do not circulate within insect tissues but accumulate in the anterior gut. Aphids, whiteflies, and leafhoppers commonly transmit such viruses, for example beet pseudo yellows virus.

c) Circulative, Nonpropagative Transmission: In circulative, nonpropagative transmission, viruses pass through the insect gut into the hemolymph and finally reach the salivary glands without replicating inside the vector. Transmission requires long feeding periods and is common in aphids, whiteflies, beetles, and leafhoppers. Viruses such as luteoviruses, geminiviruses, and nanoviruses are transmitted in this manner.

d) Circulative, Propagative Transmission: Circulative, propagative viruses not only circulate within the insect body but also replicate inside vector tissues before transmission through saliva. These viruses include members of Rhabdoviridae, Reoviridae, and Tospoviridae. Leafhoppers and planthoppers are important vectors. Viral replication and movement within insect tissues enhance efficient transmission and disease spread.

Insect vectors of plant viruses

a) Transmission through aphids: Aphids are the most common vector of plant viruses. Mechanisms of transmission are best understood by considering the routes of virus movement in the aphid (circulative vs noncirculative) and the sites of retention or target tissues (e.g., stylets, salivary glands). Capsid proteins are a primary, but not necessarily sole, viral determinant of transmission. A summary of the taxonomic affiliations of the aphid-transmitted viruses, including 8 families, 18 genera, and taxonomically unassigned viruses (Ng and Perry, 2014) is presented.

b) Whiteflies include over 1300 species, but only a few are important vectors of plant viruses. Most whitefly-transmitted viruses belong to the genus Begomovirus (family Geminiviridae), though criniviruses, ipomoviruses, torradoviruses, and some carlaviruses are also transmitted. Major vector species occur in the genera *Bemisia* and *Trialeurodes*. Among them, *Bemisia tabaci* is the most significant vector, while *Trialeurodes vaporariorum*, *T. abutilonea*, and *T. ricini* also transmit viruses. Whiteflies acquire viruses while feeding on phloem sap using their piercing-sucking mouthparts and spread them to new plants during subsequent feeding. Thus, whiteflies play a major role in the transmission and dissemination of several economically important plant viruses.

c) Transmission through leaf hopper/ plant hopper: Most leaf hopper and plant hopper vectors transmit plant viruses in a circulative manner. The majority of leaf hoppers and plant hoppers transmit plant viruses multiply with the vector body. These viruses have a defined latent period during which leaf hoppers cannot transmit virus after an acquisition feed. This is the main characteristic of these viruses. The acquisition feeding period of these viruses is at least 30 minutes. The latent period of these viruses may be relatively short (hours) or long (at least a week). Most of the leafhopper and planthopper species transmit plant viruses in acirculative/propagative manner in which vectors remain viruliferous for most of their lives after a single acquisition feeding on a virus source (Harris, 1979).

d) Transmission by mite: The plant viruses are transmitted by mites belonging to different families, such as Siteroptidae, Acaridae, Tenuipalpidae, Tetranychidae, Tarsonemidae, and Eriophyidae. Many worm mites (Eriophyidae), false spider mites (Tenuipalpidae), and spider mites (Tetranychidae) are known vectors of virus diseases infecting cereals, fruit trees, pulse crops, and coffee plants. Wheat streak mosaic virus (WSMV), wheat spot mosaic virus (WSPMV), ryegrass mosaic virus (RgMV), fig mosaic virus, cherry mottle leaf virus, currant reversion disease, pigeon pea sterility mosaic disease, and rose rosette diseases are transmitted by the different species of eriophyid mites.

e) Transmission by thrips: Thrips are placed under the order Thysanoptera and are known to be vectors of plant viruses. Different species of thrips belonging to genera *Frankliniella, Scirtothrips, Microcephalothrips,* and *Ceratothripoides* transmit plant viruses. Thrips transmit plant viruses belonging to genera Tospovirus, Ilarvirus, Carmovirus, Sobemovirus, and Machlomovirus (Jones, 2003). Plant viruses are acquired during the first and early second larval instars, when there is a temporary association between midgut, visceral muscles and salivary glands (Moritz *et al.,* 2004). They are reintroduced into a plant with the saliva of a feeding adult. Between acquisition and inoculation, there is a latent period before the virus can be transmitted, during which time virus multiplies. An adult may remain viruliferous for life, which may be 20-40 days. However, nonviruliferous adult thrips seem not to acquire the virus when feeding on infected plants (Assis Filho *et al.,* 2004).

f) Transmission by beetle: Plant-feeding beetles transmit more than 40 plant viruses belonging to genera such as Machlomovirus, Bromovirus, Carmovirus, Comovirus, Sobemovirus, and Tymovirus. These viruses are specifically adapted to beetle transmission and are generally not transmitted by insects with sucking mouthparts. During feeding, infected beetles release virus particles in regurgitant onto wounded plant tissues.The viruses enter through chewing damage and may spread internally through plant tissues, including movement via the xylem to distant cells. This allows infection beyond the initial feeding site. Thus, beetle transmission represents a specialized and efficient mode of virus spread associated with mechanical injury during feeding.

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