

Seed transmission of potyviruses: A threat to crop health

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Abstract

Plant introductions, including the movement of seeds across international borders, significantly contribute to the emergence of viral pathogens, which account for approximately half of all emerging plant diseases. Among plant virus families, the Potyviridae stand out as the largest and most economically impactful. The potyvirus genus with 201 species widespread across various crops, causes substantial crop losses globally. These viruses are primarily transmitted by aphids in a nonpersistent manner, with some also capable of transmission through seeds. Global food security is significantly impacted by the crucial part that seed transmission plays in the epidemiology and spread of different plant viruses. With transmission rates varying greatly between viruses and host plants, over 231 viruses were discovered to be capable of spreading through seeds, including 20 seed-transmitted potyviruses. The seed transmission efficiency of potyviruses such as maize dwarf mosaic virus (MDMV), cowpea aphid-borne mosaic virus (CABMV), and bean common mosaic virus (BCMV) ranges from 3% to 95%. Other notable viruses include soybean mosaic virus (SMV) (58% transmission) and pea seed-borne mosaic virus (PSbMV) (100% transmission). The diversity in seed transmission efficiency among viruses demonstrates the important role that seeds play in the propagation and dissemination of viral pathogens. In addition, seed transmission permits viruses to survive in unfavorable environments, promotes long-distance spread via international seed exchange, and acts as the main point of infection for viruses that have vertical transmission. The complex dynamics of seed transmission and the complex relationship between viruses and their host plants highlight the significance of strict phytosanitary measures in protecting global agriculture from the destructive effects of viruses transmitted through seeds. This review focuses on potyvirus seed transmission, with an emphasis on determining the significance of this mode and understanding the potential role of seed transmission in potyviruses.

Keywords: genus; potyvirus; seed transmission; transmission efficiency

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Introduction

Plants constantly face a barrage of pests and pathogens, causing substantial annual losses of about 40% in crop yields. Viruses, one of the primary threats to global food security, cause nearly half of plant diseases and cause economic losses in excess of \$30 billion per year (Jones and Naidu, 2019). Seed transmission serves as a highly effective strategy for pathogens, particularly viruses, to sustain their populations within host plants. In 1972, Baker emphasized the significance of seed transmission, highlighting its role in introducing pathogens to new areas, enabling survival during host absence, selecting and disseminating host-specific strains, and serving as foci for infection distribution (Bashir and Hampton, 1994). Many viruses struggle to survive outside host tissue, making long-term perpetuation challenges, especially for those infecting annual plants. Seed infection, however, proves to be a successful mechanism, ensuring the pathogen's long-term survival which is intricately linked to the host (Stace-Smith and Hamilton, 1988). This mechanism not only allows pathogen survival from one season to the next but also facilitates long-distance dissemination through infected seeds (Albrechtsen 2006). An example is wheat streak mosaic virus (WSMV), where phylogenetic studies indicate its introduction and distribution in Australia likely occurred through imported seeds (Dwyer *et al.*, 2007).

The phenomenon known as vertical transmission is the way in which viruses are transferred from infected plants to their offspring. This mode of transmission through seeds is present in about 18% of plant viruses with RNA genomes, including those from families like Potyviridae, Tobamoviridae, Comoviridae, Flexiviridae, Partitiviridae, and viroids. For DNA viruses, the seed-borne nature and seed transmission of cocoa swollen shoot virus were long speculated before being confirmed by Quainoo *et al.* (2008). Suspicions regarding the seed-borne and seed transmission capabilities of geminiviruses, such as Abutilon mosaic virus and Beet curly top virus (BCTV), trace back as far as 1868 (Keur, 1934) and documentation by Bennett in 1936 (Renukadevi *et al.*, 2022). Westerdijk (1910) first suspected the seed transmission of tobacco mosaic virus through tomato seeds, and Allaerd (1914) later confirmed. In 1915, the annual report of Connecticut Agricultural Experiment Station documented the soybean mosaic virus. In 1917, the seed transmission of Lima bean mosaic virus was reported by Mc Clintock (1917), whereas Stewart and Reddick (1918) reported seed transmission of bean common mosaic virus (BCMV) through bean seeds. Similarly, in 1919, the seed transmission of cucumber mosaic virus (CMV) in wild cucumber (*Echinocystis lobata*) was reported by Doolittle (1919). Newhall (1923) reported lettuce mosaic virus in lettuce; and Kendrick and Gardner (1924) reported soybean mosaic virus transmission in soybean.

Subsequently, BCMV transmission through seed was reported by various researchers (Burkholder and Muller, 1926; Merkel, 1929). Smith (1964) reported eight seed-transmitted viruses, and years later, Fulton recorded 36 seed-transmitted viruses in 63 plant species in 1964. Bennett (1969) reported 47 viruses. Agarwal and Sinclair (1988) listed 156 viruses transmitted through seed in several plant species. Neergaard (1977) and Agarwal and Sinclair (1988) compiled extensive information on seed-transmitted viruses.

Stace-Smith and Hamilton (1988) asserted that approximately 18% of known plant viruses have the potential for seed transmission in one or more hosts. Subsequently, Mink (1993) listed 108 viruses (excluding Partitiviridae) and 7 viroid diseases that can be transmitted through seeds. Hull (2002) reported that one seventh of all known plant viruses are transmitted through seeds. Albrechtsen (2006) from the Danish seed health center for developing countries listed 113 conventional viruses, 31 cryptoviruses, and 12 viroids as seed-transmitted. Power and Flecker (2003) reported 131 viruses transmitted through seeds. Since then, the number of seed-transmitted viruses has significantly increased each year, with current reports indicating that more than 231 viruses can be transmitted through seeds in various cultivated and weed hosts.

The family Potyviridae comprises twelve genera: *Brambyvirus*, *Bymovirus*, *Ipomovirus*, *Macluravirus*, *Poacevirus*, *Potyvirus*, *Rymovirus*, and *Tritimovirus*. Collectively, these genera encompass 244 species, with the potyvirus genus being the largest, containing 201 species (International Committee on Taxonomy of Viruses, 2022). Among them, 20 potyviruses are seed transmitted (Sastry, 2013). The distinction between genera and

species is based on factors such as sequence identity, host range, transmission mode, cytopathology, vector transmission, and antigenicity (King *et al.*, 2012; López-Moya *et al.*, 2001). This family of plant pathogens, particularly those transmitted by aphids, stands out as highly successful (Rybicki and Pietersen, 1999). In potyvirus genus, potato virus Y (PVY) causes yield losses ranging from 10% to 80%. Emerging viral pathogens are now responsible for 47% of plant diseases, and the figures are expected to rise further (Gibbs *et al.*, 2020) which needs establishment of stringent phytosanitary measures particularly seed transmission, becomes increasingly important. This review, which focuses on the transmission of plant viruses via seeds, aims to present compelling arguments that highlight the significance of this mode of transmission.

Methodology

This review was perceived through a comprehensive search of scientific literature to gather information on the seed transmission of potyviruses. The search strategy included the use of specific keywords such as “potyvirus,” “Plant virus transmission,” virus detection in seed parts “seed transmission,” “seed infection”. The search was performed using English- language sources in multiple scientific databases including PubMed, Google Scholar, Scopus and Web of Science.

Inclusion criteria were set to focus on studies that provided detailed insights into the mechanisms of seed transmission, the economic impact of potyviruses and strategies for managing seed – transmitted viruses. Articles published in peer- reviewed journals, conference papers and relevant books were considered. Studies without sufficient empirical data or those published in non- peer- reviewed sources were excluded to ensure the reliability and validity of the information presented.

Importance of seed transmission

Seed transmission of viruses enables their long-term survival within viable seeds, providing a means to persist when hosts or vectors are unavailable. It facilitates long-distance virus dissemination, potentially through bird dispersion and human trade of infected seeds, leading to cross-continental virus jumps. The most critical epidemiological impact of seed transmission lies in its role as a primary source of infection for viruses with vertical transmission, which subsequently spread via vectors and cause devastating epidemics. Particularly, this method becomes significant as many vectors, especially aphids, transmit viruses rapidly, rendering insecticides ineffective in controlling virus spread (Suzuki *et al.*, 2018).

In the context of ongoing climate change, virus seed transmission offers crucial advantages for plant viruses. It ensures virus survival during adverse conditions like prolonged droughts and aids geographic expansion when climate conditions become favourable in distant regions unreachable by viruliferous vectors. Elevated temperature and light intensity associated with global warming have been shown to increase the survival of infected seeds and the rate of seed transmission. Consequently, seed transmission remains of greater importance in plant virus epidemics and is a significant concern for food safety, leading to numerous regulations on seed phytosanitary measures at national and international levels (Garcia-Arenal *et al.*, 2010).

Seed transmission significantly influences virus fitness, driving extensive theoretical analysis aiming to predict conditions optimal for pathogen transmission. In the case of plant viruses, maximum seed transmission rates require optimal plant reproduction and, therefore, lower virulence (i.e., reduced effect of infection on seed production). Experimental analyses involving serial virus passages through strict vertical transmission support this notion, showing increased rates of infected seeds and reductions in virus accumulation and virulence. Notably, optimizing seed transmission also benefits the host plant by potentially evolving the virus towards a commensal relationship, thereby enhancing plant fitness. Limited evidence suggests that seed transmission plays a central role in both plant and virus evolution (Elena *et al.*, 2015).

Factors influencing seed transmission

Seed transmission rates vary depending on a variety of factors, including host cultivar characteristics, virus isolates, environmental interactions, infection timing, and potential viral synergism. The primary factors affecting seed transmission are host-virus interactions and infection timing, with environmental influences playing a secondary role (Mink, 1993). Furthermore, the relationship between the virus and its vector may influence seed transmission, with horizontally transmitted viruses rarely being seed-transmitted, whereas non-persistently transmitted viruses are more likely to transmit seeds (Bennett, 1969). Within a species, different cultivars can have different seed transmission rates. For example, with lettuce mosaic virus (LMV), seed transmission rates varied from 1% to 8% depending on lettuce variety (Grogan and Bardin, 1950). Similar variation was found in an examination of 38 pea cultivars for pea seedborne mosaic virus (PSbMV), with five cultivars showing no seed transmission at all (Stevenson and Hagedorn, 1973). This varietal diversity may have a genetic basis, as demonstrated by soybean seed transmission of soybean mosaic virus (SMV), in which multiple genes contribute to high transmission rates (Domier *et al.*, 2011).

Transmission rates can also vary among isolates of the same virus within a single host. For example, the seed transmission frequencies of peanut mottle mosaic virus (PeMoV) varied depending on the virus isolate (Adams and Kuhn, 1977). Similar isolate-specific differences were found in PSbMV, with some isolates being transmissible and others not (Roberts *et al.*, 2003). The interaction between host cultivar and virus isolates also influences seed transmission rates, as shown in a study of bean cultivars and bean common mosaic virus (BCMV) isolates (Morales and Castano, 1987).

Temperature and rainfall are two environmental factors that can affect seed transmission rates. Temperature influenced seed transmission in soybean mosaic virus (SMV), with optimal transmission occurring at 20 °C and decreasing at 15 °C and 25 °C (Tu, 1992). Reduced rainfall, which influences vector behaviour, was linked to lower PSbMV incidence in the field (Courtts *et al.*, 2009). Maule and Wang (1996) emphasise the complexity of factors influencing seed transmission rates by describing multifaceted interactions among host, virus, vector, and environment. Seed transmission rates are also influenced by the age of the host plant at the time of inoculation. In general, seed transmission rates appear to decrease with the age or developmental stage of the plant at the time of infection, as observed in SMV and BCMV (Morales and Castano, 1987). Several potyviridae, including PSbMV, BCMV, and PeMoV, show age-dependent effects on seed transmission rates (Wang and Maule, 1992; Kaiser and Mossaheb, 1974; Paguio and Kuhn, 1974).

Synergistic interactions can also affect seed transmission rates, though the direction of influence varies. For example, co-infection of PSbMV with pea early browning virus (PEBV) resulted in blocked seed transmission in PSbMV, but not in PEBV (Wang and Maule, 1997). In contrast, other viral families, such as turnip yellow mosaic virus (*Tymoviridae*) and southern bean mosaic virus (*Sobemovirus*), showed synergistic effects that increased seed transmission rates (de Assis Filho and Sherwood, 2000; Kuhn and Dawson, 1973).

Significance of location of virus in the seed parts

Many records of potyviruses are spread explained only by seed transmission. The viruses are spread from one part of the globe to another by international trade. Sowing of potyvirus infected seeds result in multiple infection foci, which distributed in the field randomly could very well serve as inoculum source for aphid vector. Thus, there is high potential of seed borne viruses to initiate epidemics. For the detection of the viruses in the seeds, either whole seed or seed parts separated into cotyledons, seed coat and embryonic axis are used. When the virus is detected in embryo, the seed to seedling transmission rate is decided by two factors: the first is the ability of the virus to survive in the embryo, and the second is its ability to be reactivated (Albrechtsen, 2006); But the seedling transmission was not so far reported, if the other parts such as seed coat or endosperm were detected with virus.

Using sensitive detection assays, it is clear that the direct invasion of the embryo results in high rate of seed to seedling transmission. Seed transmission as a result of the virus being carried on the seed surface is uncommon among Potyviruses. This mode of transmission through contaminated seed surface is met with tobamovirus group, where the management of the viruses is fairly easy by decontaminating the whole seed.

It is necessary that sensitive and specific detection protocols are developed, strict quarantine measures are imposed to prevent introduction of virus infected seed into new areas.

The hidden journey: how potyviruses travel within seeds

Though seed transmission is not uncommon among potyviruses, the exact mechanism by which the virus enters the germ line remains unknown. Two potential routes of embryonic infection have been suggested: direct invasion of embryonic tissue post-fertilization or infection of gametes before fertilization through ovules or pollen. The seed transmission rate is likely a result of both indirect and direct embryotic invasion (Wang and Maule, 1994). Embryotic invasion is considered the main route for potyvirus entry into the seed. Infected maternal plant tissues, particularly the ovules and integuments, can harbour the virus, which then moves toward the developing embryo via plasmodesmata (cytoplasmic connections) or the suspensor (a temporary structure connecting the embryo to the maternal seed coat). Studies on pea seed-borne mosaic virus (PSbMV) demonstrate direct invasion of the embryo through the micropylar region at early seed development. Unlike animal viruses, which utilize receptor-mediated mechanisms for cell entry in the extracellular environment, plant viruses, including potyviruses, are confined to intracellular compartments, and their cell-to-cell movement is regulated by plasmodesmata (Figure 4) (Heinlein *et al.*, 1995; Oparka *et al.*, 1997; Rojas *et al.*, 1997; Rodriguez-Cerezo *et al.*, 1997).

Several viral proteins, such as Coat Protein (CP), Helper Component Protein (HC-Pro), and CI, play roles in cell-to-cell movement within host plant tissues (Astier *et al.*, 2001). CP is essential for viral movement, while HC-Pro aids entry and exit from the host vascular system (Urcuqui-Inchima *et al.*, 2001). The movement of potyviruses through the plant aligns with carbon metabolites' transport from source leaves to immature leaves, following the path of photo assimilates (Maule and Wang, 1996). The genetic basis of viral seed transmission in pea seedborne mosaic virus (PSbMV) involves the 5' UTR, HC-Pro, and CP regions, as indicated by chimeras (Johansen *et al.*, 1996). Cylindrical inclusions during PSbMV infections suggest a role for CI in seed transmission (Roberts *et al.*, 2003). All implicated proteins, except the 5' UTR, are associated with viral movement. Virus movement within plants significantly affects vertical transmission, with phloem-limited viruses generally not seed-transmissible (Mink, 1993). In PSbMV studies, evidence supports direct embryo invasion via the suspensor, where the virus moves from maternal cells in the micropyle to the endospermic cytoplasm and embryonic suspensor, ultimately entering the embryo (Wang and Maule, 1994; Roberts *et al.*, 2003). Seed transmission relies partially on timing and chance due to the transient nature of embryo entry.

Seed infection through pollen is less common than through ovules in many instances. Various viral families, including Secoviridae, Vigraviridae, Bromoviridae, and Tymoviridae, provide extensive evidence for indirect embryo invasion via ovules (Carroll and Mayhew, 1976; Yang *et al.*, 1997; de Assis Filho and Sherwood, 2000). In the potyvirus genus, evidence for ovule-based seed transmission is inconclusive, with conflicting results in lettuce mosaic virus (LMV) studies (Ryder, 1964; Hunter and Bowyer, 1994). Nevertheless, certain potyviruses, like LMV, exhibit indirect invasion through pollen, as observed through electron microscopy. Sugarcane mosaic virus (SCMV) displays both direct embryo invasion and indirect invasion through infected pollen (Li *et al.*, 2007). Distinctions exist between viruses infecting the embryo and those in other seed tissues or on the seed surface, influencing seedling infection rates (Stace-Smith and

Hamilton, 1988). While seed transmission via the seed surface is uncommon in the potyvirus genus, the majority of seed-transmitted viruses are carried within the embryo (Johansen *et al.*, 1994; Albrechtsen, 2006).

Potyriviruses

Numerous hosts are susceptible to potyriviruses, including significant crops like beans, tomatoes, potatoes, and peppers. A total of 24 potyriviruses are gaining economic importance based on their yield losses (Table 1) and list of seed transmitted potyriviruses reported (Table 2).

Table 1. List of major potyriviruses

No	Virus Name	Genus	Primary Host(s)	References
1.	Bean common mosaic virus (BCMV)	Potyvirus	Beans, Legumes	Kumar <i>et al.</i> , 2011
2.	Bean yellow mosaic virus (BYMV)	Potyvirus	Beans, Legumes	Yadav <i>et al.</i> , 2020
3.	Blackeye cowpea mosaic virus (BCMNV)	Potyvirus	Cowpea, Bean	Odu <i>et al.</i> , 2021
4.	Clover yellow vein virus (CYVV)	Potyvirus	Clover, Alfalfa	Liu <i>et al.</i> , 2022
5.	Cowpea aphid-borne mosaic virus (CABMV)	Potyvirus	Cowpea, Mung bean, Soybean	Adebola <i>et al.</i> , 2023
6.	Dasheen mosaic virus (DasMV)	Potyvirus	Taro	Maia <i>et al.</i> , 2021
7.	Hippeastrum mosaic virus (HiMV)	Potyvirus	Amaryllis, Snowdrop, Daffodil	Lockhart <i>et al.</i> , 1994
8.	Johnsongrass mosaic virus (JGMV)	Potyvirus	Maize, sorghum	Oliveira <i>et al.</i> , 2022
9.	Leek yellow stripe virus (LYSV)	Potyvirus	Leek, Onion, Garlic, Chives	Randa-Zelyüt <i>et al.</i> , 2022
10.	Lettuce mosaic virus (LMV)	Potyvirus	Lettuce, Cucurbits, Spinach	Li <i>et al.</i> , 2022
11.	Maize dwarf mosaic virus	Potyvirus	Maize	Zheng <i>et al.</i> , 2023
12.	Papaya ringspot virus (PRSV)	Potyvirus	Papaya, Cucurbits	Ghosh <i>et al.</i> , 2020
13.	Pea seed-borne mosaic virus (PSbMV)	Potyvirus	Pea, Lentil, Chickpea, Faba bean	Farrag <i>et al.</i> , 2022
14.	Peanut mottle virus (PeMoV)	Potyvirus	Peanut, Cowpea, Soybean	Adejumo <i>et al.</i> , 2023
15.	Pepper veinal mottle virus (PVMV)	Potyvirus	Pepper	Chen <i>et al.</i> , 2023
16.	Plum pox virus (PPV)	Potyvirus	Stone fruits (Plum, Apricot, Peach)	Cambra <i>et al.</i> , 2022
17.	Potato virus Y (PVY)	Potyvirus	Potato, Tobacco, Pepper, Tomato	Sumiah <i>et al.</i> , 2021
18.	Soybean mosaic virus (SbMV)	Potyvirus	Soybean	Sun <i>et al.</i> , 2020
19.	Sugarcane mosaic virus (SCMV)	Potyvirus	Sugarcane, Maize, Sorghum	Khan <i>et al.</i> , 2021
20.	Tobacco etch virus (TEV)	Potyvirus	Tobacco, Pepper, Tomato, Cucurbits, Legumes	Yang <i>et al.</i> , 2020

21.	Turnip mosaic virus (TuMV)	Potyvirus	Brassicas, Crucifers (turnip, Cabbage, radish)	Babu <i>et al.</i> , 2013
22.	Watermelon mosaic virus (WMV)	Potyvirus	Cucurbits (watermelon, melon, pumpkin)	Verma <i>et al.</i> , 2020
23.	Yam mosaic virus (YMV)	Potyvirus	Yams	Adebola <i>et al.</i> , 2023
24.	Zucchini yellow mosaic virus (ZYMV)	Potyvirus	Cucurbits (zucchini, Squash, cucumber)	Singh <i>et al.</i> , 2023

Table 2. Seed transmitted potyviruses and their important hosts

No	Virus	Acronym	Seed Transmission	Host Plants	Percent seed transmission (%)	References
1.	Bean common mosaic virus	BCMV	High	Common bean, cowpea, lima bean	3 - 95	Kumar <i>et al.</i> , (2011)
2.	Bean yellow mosaic virus	BYMV	Low	Common bean, lima bean, green bean	2.4	Maina <i>et al.</i> (2020)
3.	Cowpea aphid-borne mosaic virus	CABMV	Moderate	Cowpea, soybean, lima bean	18.5 -37.1	Faquet <i>et al.</i> (2001)
4.	Hippeastrum mosaic virus	HiMV	Low	Amaryllis lily, hippeastrum, clivia	0.2	Hendrina Brants <i>et al.</i> (1965)
5.	Leek yellow stripe virus	LYSV	Low	Leek, garlic, shallot	20	Sasaki <i>et al.</i> (2022)
6.	Lettuce mosaic virus	LMV	Low	Lettuce, endive, escarole, celery	1 - 8	Krause-Sakate <i>et al.</i> (2002)
7.	Maize dwarf mosaic virus	MDMV	Yes	Maize, sorghum, teosinte	9 -72	Knoke and Louie, 1981
8.	Papaya ringspot virus	PRSV	Low	Papaya, watermelon, cantaloupe	0.15	Laney <i>et al.</i> (2012)
9.	Pea seed-borne mosaic virus	PSbMV	High	Pea, lentil, chickpea, faba bean	100	Amanda <i>et al.</i> (2022)
10.	Peanut mottle virus	PeMoV	Low	Peanut, groundnut	0.5 - 8.3	Soumya <i>et al.</i> (2014)
11.	Plum pox virus	PPV	Low	Plum, apricot, peach, almond	0.2- 3	Myrta <i>et al.</i> (1998)
12.	Potato virus Y	PVY	Moderate	Potato, tobacco, pepper, tomato	15	Halterman <i>et al.</i> (2012)
13.	Soybean mosaic virus	SMV	Yes	Soybean, common bean, cowpea, peanut	58	Widyasari <i>et al.</i> (2020)
14.	Sugarcane mosaic virus	SCMV	Yes	Sugarcane, sorghum, maize	3.9	Li <i>et al.</i> (2011)
15.	Sunflower mosaic virus	SuMV	Low	Sunflower, safflower, marigold	0.8- 2	Harveson, <i>et al.</i> (2017)
16.	Telfairia mosaic virus	TeMV	Yes	Fluted pumpkin	1.9 - 32.7	Adighe <i>et al.</i> (2014)
17.	Tobacco etch virus	TEV	Low (varies by strain)	Tobacco, tomato, pepper, lettuce	0.2- 3	Fajardo-Martinez <i>et al.</i> (2019)

18.	Turnip mosaic virus	TuMV	Moderate	Turnip, cabbage, radish, broccoli	20-50	Nooshin <i>et al.</i> (2019)
19.	Watermelon mosaic virus	WMV	Moderate (varies by strain)	Watermelon, cantaloupe, cucumber, squash	0.5	Singh <i>et al.</i> (2004)
20.	Zucchini yellow mosaic virus	ZYMV	Yes	Squash, pumpkin, zucchini, cucumber	1.6	Simmons <i>et al.</i> (2013)

Genome organization of Potyviruses

The taxonomic classification of potyvirus is as follows: it belongs to the realm *Riboviria*, the kingdom *Orthornavirae*, the phylum *Pisuviricota*, the class *Stelpaviricetes*, the order *Patatavirales*, the family *Potyviridae*, and the genus *Potyvirus* (ICTV, 2022). Potyviruses exhibit a flexible filamentous virion structure, approximately 680-900 nm long and 11-20 nm in diameter (Gibbs *et al.*, 2020) and have a monopartite genome consisting of a single linear molecule of positive single stranded RNA, approximately 10 Kb long (Revers and García, 2015). This RNA contains a single open reading frame (ORF) encoding a polyprotein, which is cleaved by three virally encoded proteases (P1, HC-Pro, and NIa) into ten smaller functional proteins (P1, HC-pro, P3, 6K1, CI, 6K2, VPg, NIa-pro, Nib, and CP), along with a small frameshift-derived peptide (PIPO). The 5' end of the genomic RNA is flanked by a non-coding region (NCR) of less than 200 base pairs, including a terminal protein (VPg) that enhances translation. At the 3' end, there is another 200-base pair NCR followed by a poly(A) tail. The polyprotein encoded by the central region of the potyvirus genome is processed into mature viral proteins P3-6K1-CI-6K2-VPg and NIaPro-Nib-CP by the NIaPro proteinase (Adams *et al.*, 2005). The functions of the individual proteins are explained in detail in Figure 1. They have distinctive pinwheel inclusion bodies of the Cylindrical Inclusion (CI) protein. Most important species of potyvirus include bean common mosaic virus (BCMV), maize dwarf mosaic virus, lettuce mosaic virus (LMV), plum pox virus (PPV), potato virus Y (PVY) and zucchini yellow mosaic virus (ZYMV) (Berger 2001).

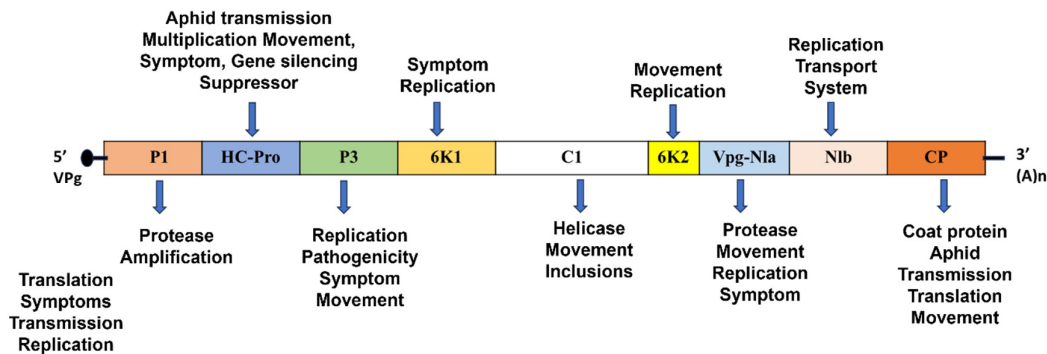


Figure 1. Genome organization of potyvirus

Symptomatology

Potyviruses can infect plants and cause a range of symptoms, such as yellowing, curling of the leaves, necrosis (death of plant tissues), mosaic patterns on the leaves, and growth stunting. The type of host plant and the particular potyvirus strain involved can affect these symptoms. Furthermore, some potyviruses have the ability to cause systemic infections, which impact various plant parts. To reduce the negative effects of potyvirus infections on crop yield and quality, early detection and management are essential.

Seed transmitted potyviruses

Seed transmission is a potential source of inoculum for further spread by aphids in cropping season, decides the severity and yield loss. The most important potyviruses which are highly seed transmissible and described below (Table 2, Figure 2).

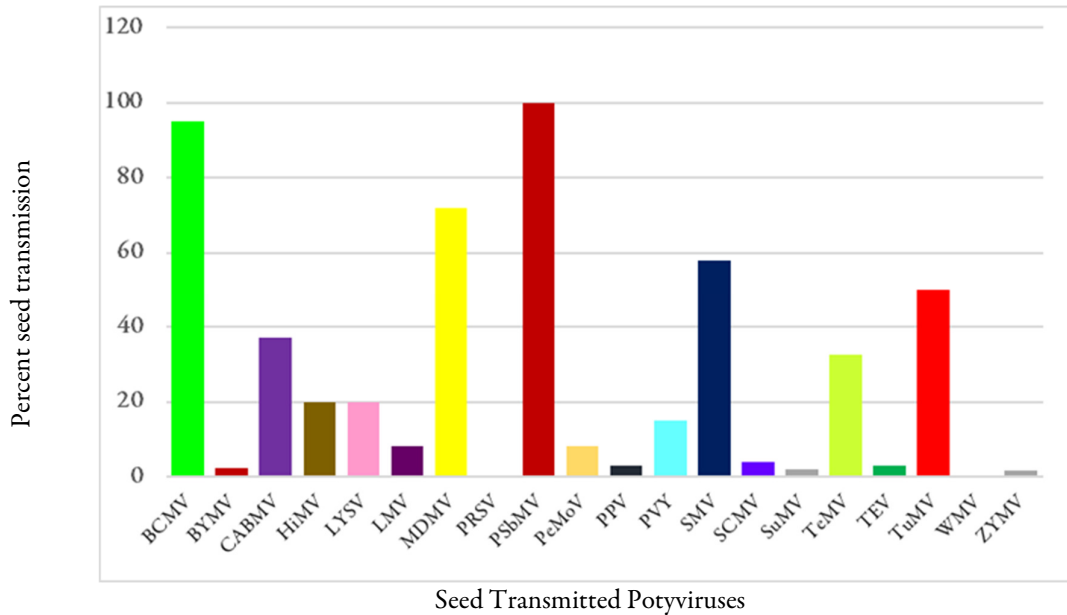


Figure 2. Percent seed transmission of potyviruses: PSbMV has the highest percent seed transmission at 100%. PRSV and WMV exhibit relatively low percent seed transmission at 0.15% and 0.50%, respectively. Additionally, viruses such as BYMV, HiMV, PeMoV, PPV, SuMV, TEV, and ZYMV fall within a moderate range of percentages

Pea seed borne mosaic virus (PSbMV)

Mink *et al.* (1969) reported the first case of pea seed-borne mosaic virus in the United States. Pea seeds infected with PSbMV serve as the primary reservoir of inoculum. Once the virus is transmitted through the seeds to germinating seedlings, it spreads to neighbouring healthy peas in the field through aphid vectors. Significant abnormalities in the appearance of seeds occur when pea plants contract PSbMV either before or during seed development. Common issues comprise necrotic rings and linear patterns on the seed coat, often described as 'tennis ball' symptoms, as well as malformation, splitting, and a decrease in seed size. These symptoms are particularly noticeable in white-seeded pea varieties. Typically, the number of seeds leading to infected seedlings is considerably less than the number of seeds displaying symptoms. Musil demonstrated PSbMV seed transmission in Czechoslovakia in 1966. In Japan, Inouye reported variable rates, ranging from 30% to 10% in different pea cultivars. Some pea introductions to the USA exhibited remarkably high seed transmission rates, reaching 100%. PSbMV was also found to be seed-transmitted in lentils at frequencies of 32-44%, and in a low percentage of seeds of *Vicia articulata*, *V. narbonensis*, and *V. pannonica* (Hampton and Muehlbauer, 1977; Hampton and Mink, 1975). Stevenson and Hagedorn (1973b) found PSbMV in all parts of infected plant inflorescence. Virus transmission occurred via the female parent and pollen, with pollen contributing less than 1% to a 6% seed transmission rate. All inflorescence components, including carpels, filaments, petals, pollen, and sepals, contained the virus. Mink *et al.* (1969) observed that certain growth conditions increased PSbMV seed transmission from 16-25% to 65-90%.

Amanda *et al.* (2022) explored the susceptibility of diverse pea cultivars to PSbMV through experimental trials. Each cultivar's susceptibility was investigated using progeny seeds obtained from five

infected pea plants, treated as biological replicates, which displayed successful infections. Subsequently, a seed transmission study was conducted, wherein both symptomatic and asymptomatic seeds (ten of each) from five chosen PSbMV-positive plants were grown under greenhouse conditions. After five weeks of planting, two leaves from the newest growth of each plant were collected and subjected to DAS-ELISA testing to identify PSbMV infection. The individual plants' PSbMV infection frequency was recorded. Cultivar classification into predefined categories—ranging from highly resistant (no infection) to highly susceptible (>40%)—was determined solely based on the PSbMV transmission rate to progeny plants. The investigation specifically emphasized the process of seed transmission in understanding the interaction between pea cultivars and PSbMV.

Bean common mosaic virus (BCMV)

Bean common mosaic virus was first identified by Pierce (1934). It was then investigated by Abdel-Salam *et al.* (1989) after being reported in Egypt in the 1960s. The epidemiology of BCMV disease is significantly influenced by seed transmission. According to Ekpo and Saettler (1974), BCMV may be able to directly invade the embryo by inducing the formation of new plasmodesmata or by using an as-yet-unidentified mechanism to traverse the cell wall between the testa and the suspensor. It is evident that in this system, embryo infection happened through both direct and indirect pathways. El-Sayed *et al.* (2023) conducted an experiment by using double antibody sandwich ELISA (DAS-ELISA) to determine the presence of BCMV-BICM in various parts of cowpea cv. 'Balady' seeds. 100 seeds from BCMV-BICM infected plants were individually soaked in water for two days to prevent cross-contamination. The seed coats were manually removed, and the embryos were aseptically dissected into cotyledons and embryo axis. These parts were then washed and triturated separately in seed antigen buffer. Each extract served as an antigen in DAS-ELISA. Results showed that BCMV-BICM infected the coat, cotyledons, and embryo axis of the tested cowpea cv. 'Balady'. The incidence of positive BCMV-BICM tests in these parts was recorded at 16%, 3%, and 3%, respectively. However, Sekar *et al.* (1988) reported contrasting results, mentioning that infectious BCMV-BICM was present in cotyledons and embryo axis but absent from the seed coats in mature seeds of infected cowpea cultivars. Aishwarya *et al.* (2020) conducted studies on bean common mosaic virus (BCMV), significant viral disease affecting legumes, especially cowpeas. The primary mode of virus dispersal, through seed transmission, poses challenges in containing its spread to new locations. The researchers conducted seed transmission studies on cowpea variety C-152 using a grow-out test at the two-leaf stage, revealing a variable seed transmission rate of 20-30% in pot culture experiments. Confirmation of the seed-borne nature of BCMV in cowpeas was achieved through DAS ELISA, with serological studies highlighting the presence of BCMV in the embryo and cotyledon, though not in the seed coat. The overall findings underscored the internal seed-borne nature of the virus, emphasizing its presence in the embryo and cotyledon but not the seed coat, across both cultivars.

Jossey *et al.* (2013) propose that the molecular aspects governing seed transmission of bean common mosaic virus (BCMV) or bean common mosaic necrosis virus (BCMNV) remain unknown. Research on soybean mosaic virus suggests the potential significance of CP/HC-Pro interactions, analogous to mechanisms for aphid-mediated transmission. Ekpo and Saettler (1974) established that BCMV in beans primarily transmits through internal seed infection in the embryo or cotyledons rather than testa contamination. Electron micrographs by Hoch and Provvidenti (1978) supported this, revealing BCMV particles throughout cells and tissues in both dormant and germinating bean seeds from experimentally infected plants. Remarkably, *Phaseolus vulgaris* seeds can retain infectious BCMV for at least 30 years (Pierce and Hungerford, 1929), contributing significantly to global spread through trade. Historical outbreaks in 1977 in Europe and America were likely initiated by contaminated seed stocks. Despite previous resistance, cultivars like 'Black Turtle', 'Columbia Pinto', and others succumbed to BCMV infection in 1977 and 1981 epidemics caused by seed contamination in the northwestern USA (Hampton *et al.*, 1983). Forster *et al.* (1991) and Klein *et al.* (1988) reported the origin of another bean common mosaic virus (BCMV) epidemic in the United States in 1988 was

identified as contaminated seed stock. A survey conducted in the same year revealed BCMV presence in 7% of tested plants, impacting various *Phaseolus* species. Subsequent to this, in 1989, seed lots were found to be contaminated, resulting in significant damage to bean crops in south-central and south-western Idaho. This contamination led to the rejection of 650 acres of bean crops, emphasizing the crucial role of seed transmission in the persistence and dissemination of BCMV.

Maize dwarf mosaic virus

Maize dwarf mosaic virus was initially identified in 1964 in corn and Johnsongrass in Illinois. MDMV has been found in maize seeds at approximately 0.5%, with newer strains possibly exhibiting higher transmission rates (Knoke and Louie, 1981). In sweetcorn, MDMV was observed in the pericarp but rarely in the endosperm and embryo, with mature seeds occasionally showing MDMV in the pericarp and endosperm but not in the embryo (Mikel *et al.*, 1984). Nemchinov *et al.* (1990) detected MDMV in all floral meristems during organogenesis stages, including mature pollen grains and all parts of mature seeds. Mikel *et al.* (1982) confirmed MDMV presence in silks but not in pollen grains. MDMV was also detected in glumes, anthers, and unfertilized or fertilized kernels (Mikel *et al.*, 1984b). MDMV transmission from infected maize seeds to seedlings has been demonstrated in sterilized soil (Shepherd and Holdeman, 1965; Williams *et al.*, 1968; Hill *et al.*, 1974; Mikel *et al.*, 1984b). Weed hosts, particularly Johnsongrass, and aphids are considered major sources of inoculum, with aphids transmitting the pathogen non-persistently (McDaniel and Gordon, 1985; Scott, 1985).

Soybean mosaic virus (SMV)

Soybean mosaic virus was first reported in the United States by Clinton in 1916, and transmitted by over 30 aphid species, particularly *Aphis glycines* (soybean aphid), with field occurrences correlating with soybean aphid flights (Hill *et al.*, 200). Bowers *et al.* (1978) found that soybean mosaic virus (SMV) in flowers, immature seeds, and green pods of mature Midwest seeds, but not in testas. Merit seeds had a lower incidence of viral antigen. The percentage of mature seeds containing SMV aligned with the percentage of infected seedlings. SMV transmission through seeds was minimally affected by storage at 14 °C for 6 months. Testas contained infectious SMV, with Merit seeds showing a lower incidence. Timing of SMV inoculation during the growing season influenced only seed transmission, averaging 16% before flowering and 3% after.

SMV can infect soybean seeds, with higher infection rates and yield losses observed in plants infected before flowering (Nakano *et al.*, 1988; Ren *et al.*, 1997b). SMV infected soybean seeds as potential source of inoculum (Figure 3). Seed infection rates, influenced by soybean cultivar and virus strain, can reach up to 75%, typically staying below 5% (Hill, 1999). SMV infection may result in smaller, less vigorous seeds with reduced oil content but increased protein and amino acid levels (El-Amrety *et al.*, 1999; Jossey *et al.*, 2013). Yield reduction due to SMV ranges from 8-25%, with potential losses reaching 66-86% when co-infected with bean pod mottle virus (Hill, 1999; Bowers *et al.*, 1978). SMV strains vary in symptom severity and cultivar infectivity, with at least eight resistance genes influencing varying resistance levels (Hill, 1999). Soybean mosaic virus (SMV) is transmitted through seeds and aphids, with aphids transmitting the virus non-persistently. The interaction between viral proteins HC-Pro and CP is crucial for successful transmission. The CP's DAG sequence is essential for transiently binding to HC-Pro, facilitating virus particle attachment to the aphid stylet. This interaction is key to promoting SMV transmission by aphids (Widyasari *et al.*, 2020).

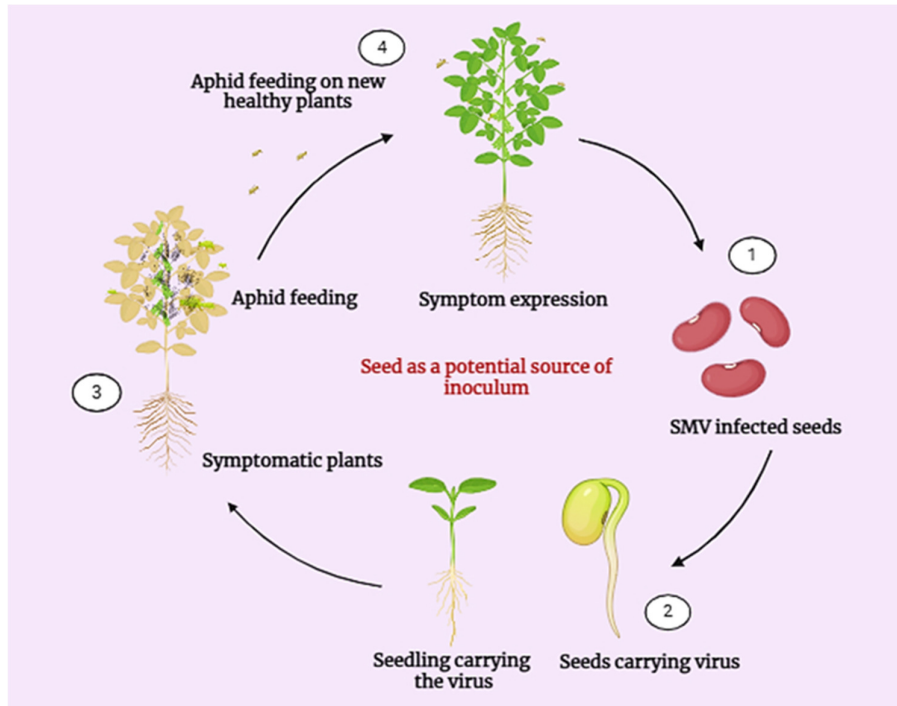


Figure 3. Seed transmission of potyviruses: (1) Plant virus can infect seeds directly through the suspensor, resulting in infected embryos after fertilization (2) seed carrying virus and germinating seedling is infected with virus (3) Infected seedlings (and adult plants) from infected seeds will be sources of primary inoculum, allowing virus to spread through vectors. (4) The cycle ends with viruses contaminating seeds from infected plants, resulting in a second round of transmission. Additionally, infected plants via vectors can produce contaminated seeds. (Figure created with Biorender.com)

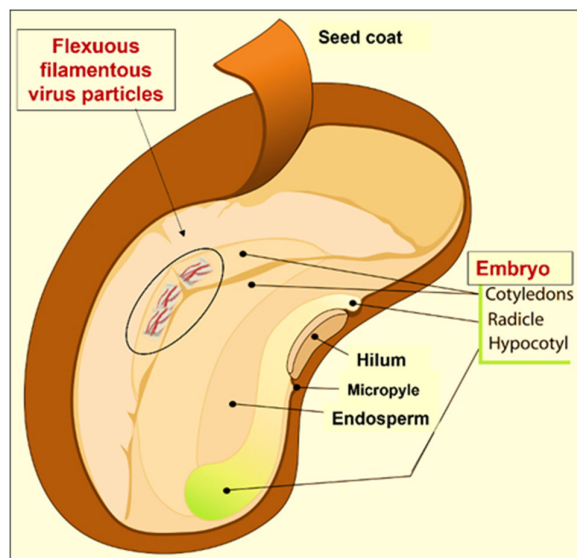


Figure 4. Soybean seed infected with Soybean mosaic virus (SMV) (Image by LadyHats (public domain))

Cowpea aphid-borne mosaic virus (CABMV)

The first reports of CABMV infecting cowpea (in Italy) came from Vidano and Conti in 1965, and Lovisolo and Conti in 1966 provided an overview of the characteristics of CABMV. The transmission of

cowpea aphid-borne mosaic virus (CABMV) through cowpea seeds is crucial for ensuring the virus's survival and facilitating long-distance dissemination through international seed exchange (Hampton *et al.*, 1992). The primary factor influencing seed transmission is the infection of gametes by the virus (Tsuchizaki *et al.*, 1970), playing a significant role in the epidemiology of CABMV (Bashir *et al.*, 2000). Phatak (1974) reported the detection of CABMV in the plumule of growing infected seeds, with some cases showing the presence of the virus in cotyledons. The virus was not detected in the seed coat. Tsuchizaki *et al.* (1970) identified the virus in pollens, anthers, and ovaries of CABMV-infected cowpea plants, with higher concentration in anthers than ovaries. They also found that seed transmission occurred when mother plants were inoculated at least 20 days before flowering, while virus recovery from pollen required inoculation at least 17 days before flowering. In the cowpea variety 'Zairai-Tsurunashi-Kintoki' infected with CABMV, virus particles and cytoplasmic inclusions were observed in meristematic tissues at 0.1 ± 0.2 mm from the apical end. Electron microscopy of individual pollen revealed virus particles in 6.8% and 18.6% of pollens from cowpea plants infected with CABMV-1 and CABMV-3 strains, respectively. Developing immature embryos are not susceptible to direct invasion by the virus in non-seed transmission virus-host combinations but are infected through direct invasion in seed-transmitted virus-host combinations (Tsuchizaki and Hibino, 1971). Twelve CABMV isolates were mechanically inoculated into three cowpea genotypes in a greenhouse setting, and Bashir and Hampton (1994) examined the rate of seed transmission. The combination of cowpea genotype and virus isolate determined the transmission rate. In genotype, isolate RN-27C showed the highest rate of CABMV transmission (55%). In every cowpea genotype, none of the three isolates (RN-27C, RN-28C, and PI-44C) were able to spread. Within the range of $1.1 \pm 13.3\%$ in cowpea, the transmission of naturally infected seeds has been documented. (Kaiser and Mosshebi, 1975; Mazyad *et al.*, 1981; Mali *et al.*, 1989; Hampton *et al.*, 1992). CABMV causes pod deformation, reduces seed size, causes seed discoloration, and decreases seed germination. However, there is no correlation between yield reduction and the percentage of seed transmission (Kaiser and Mosshebi, 1975). CABMV survives in infected seeds, volunteer host plants, or viruliferous aphids. Infected seeds serve as primary inoculum foci in the field, while aphids play a crucial role in the secondary spread of the disease (Thottappilly, 1992).

Knowledge gaps

While considerable progress has been made in understanding the seed transmission of potyviruses, significant gaps in knowledge remain. One critical area where information is lacking is the persistence of these viruses in seeds over time. Specifically, there is limited research on how long potyviruses can remain viable and infectious within seeds, which is crucial for assessing the risk of long-term virus transmission. Additionally, there is a dearth of effective strategies and methods to prevent the international spread of infected seeds. Current seed treatment techniques may not be sufficient to eliminate potyviruses and there is a need for innovative approaches to ensure seed health and safety in global trade.

Furthermore, the mechanisms by which these viruses are transmitted within different seed structures are not fully understood. This knowledge gap hampers the development of precise diagnostic tools and targeted interventions. Highlighting these gaps underscores the complexity of potyvirus interactions with seeds and emphasizes the urgent need for further research in these areas. Addressing these gaps will not only enhance our understanding of potyvirus biology but also contribute to the development of more effective control measures, thereby safeguarding crop health and improving agricultural sustainability.

Conclusions

A thorough examination of various plant viruses and their seed transmission reveals the complex interactions between viruses, host plants and environmental factors. Investigations into bean common mosaic virus (BCMV), cowpea aphid-borne mosaic virus (CABMV), maize dwarf mosaic virus (MDMV), pea seed borne mosaic virus (PSbMV), soybean mosaic virus (SMV), papaya ringspot virus (PRSV) provided invaluable insights into the mechanisms, rates and consequences of seed transmission across a range of crops. The critical role that seed transport plays in the persistence and global spread of these viruses, which have a major impact on crop health and productivity, is illustrated by its importance. The findings emphasise the importance of understanding host-virus interactions, which include factors such as resistance levels in various cultivars, virus isolates, and environmental nuances. The concealed journey of potyviruses within seeds complicates our understanding of seed transmission. While the exact mechanisms of embryonic infection are unknown, the presence of viral proteins, cell-to-cell movement, and genetic factors all contribute to the observed variability in seed transmission rates.

The complexity of this phenomenon is highlighted by the various factors influencing seed transmission, which include host cultivar characteristics, virus isolates, environmental conditions, infection timing, and potential viral synergism. Recognising the impact of these factors is critical for developing effective crop-virus disease management strategies. In essence, the findings of these studies highlight the ongoing need for research into the determinants of seed transmissibility, viral interactions with host genes, and the ecological dynamics of plant viruses in reproductive organs, with a focus on potyviruses. These findings are critical for improving our understanding of epidemiology, evolution, and developing long-term strategies to mitigate the impact of seed-transmitted plant viruses on global agriculture.

Authors' Contributions

The contributions of the authors are as follows: Conceptualization: RP; Data curation and formal analysis: RP; Funding acquisition: KS, RP and RO; Investigation and supervision: RP, RO and HC. Writing-original draft.: KS. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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