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Potato leafroll virus: A re-emerging threat to sustainable potato production

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Abstract

Potato leafroll virus (PLRV, species *Polerovirus PLRV*) is a positive-strand RNA virus, a member of the genus *Polerovirus* within the family *Solemoviridae*. Virus particles of PLRV are isometric, 24 nm in diameter. PLRV is the causal agent of leafroll disease in potato (*Solanum tuberosum* L.) which is present in all potato-growing regions worldwide and causes significant losses in yield and quality of potato tubers. PLRV is transmitted in a persistent, non-replicative manner by aphid vectors and via infected tubers produced by PLRV-infected potato plants. In the past, PLRV incidence has been contained by applying insecticides to control vector aphids; however, changes in agronomic practices and a warmer environment have led to the re-emergence of PLRV as a threat to potato production systems.

KEYWORDS
Polerovirus PLRV, *Solanum tuberosum*, Solemoviridae

1 | INTRODUCTION

Potato leafroll virus (PLRV, species *Polerovirus PLRV*) is a positive-strand RNA virus which belongs to the genus *Polerovirus* within the family *Solemoviridae* (Sõmera et al., 2021; Harrison, 1984). It is the causal agent of potato leafroll disease which affects potato, *Solanum tuberosum*, worldwide. PLRV was among the first plant viruses to be identified and its genome sequenced (Mayo et al., 1989). Research on PLRV has provided major insights into aphid vectoring of plant viruses, the organisation and expression of viral RNA genomes and virus–vector interactions. The infectious nature of potato leafroll disease and its transmission via grafting were revealed in 1916 (Quanjer et al., 1916). Later, aphid transmission was shown to be circulative, involving passage of the virus from the midgut to the salivary glands via hemocoel (Day, 1955), and to be non-replicative in aphids (Harrison, 1958).

Subsequent sequencing and analysis of expression of PLRV genomic RNA revealed a range of gene expression strategies used by RNA viruses, including subgenomic (sg) RNA production (sgRNA1 and sgRNA2), internal ribosome entry, translational frameshifting and readthrough. These mechanisms maximise the coding capacity of the compact PLRV genome (Figure 1a) (Jaag et al., 2003; Taliansky et al., 2003). More recently, a role of PLRV in modulating aphids' behaviour and reproduction rates was revealed (Patton et al., 2020).

2 | MAIN DISEASES AND SYMPTOMOLOGY

PLRV is a major viral pathogen of potatoes (*Solanum tuberosum*) in all potato growing regions worldwide (Harrison, 1984). PLRV infection can cause up to 70% of tuber yield losses and may induce tuber necrosis in some potato varieties, affecting tuber quality (Killick, 1979; Manzer et al., 1982). In some cultivars, such as Golden Wonder and Russet Burbank, tubers on plants with either primary (aphid-transmitted) or secondary (tuber-transmitted) PLRV infections may develop internal net necrosis (Douglas & Pavek, 1972). Symptoms of primary infection include yellowing and upward rolling of young leaves,

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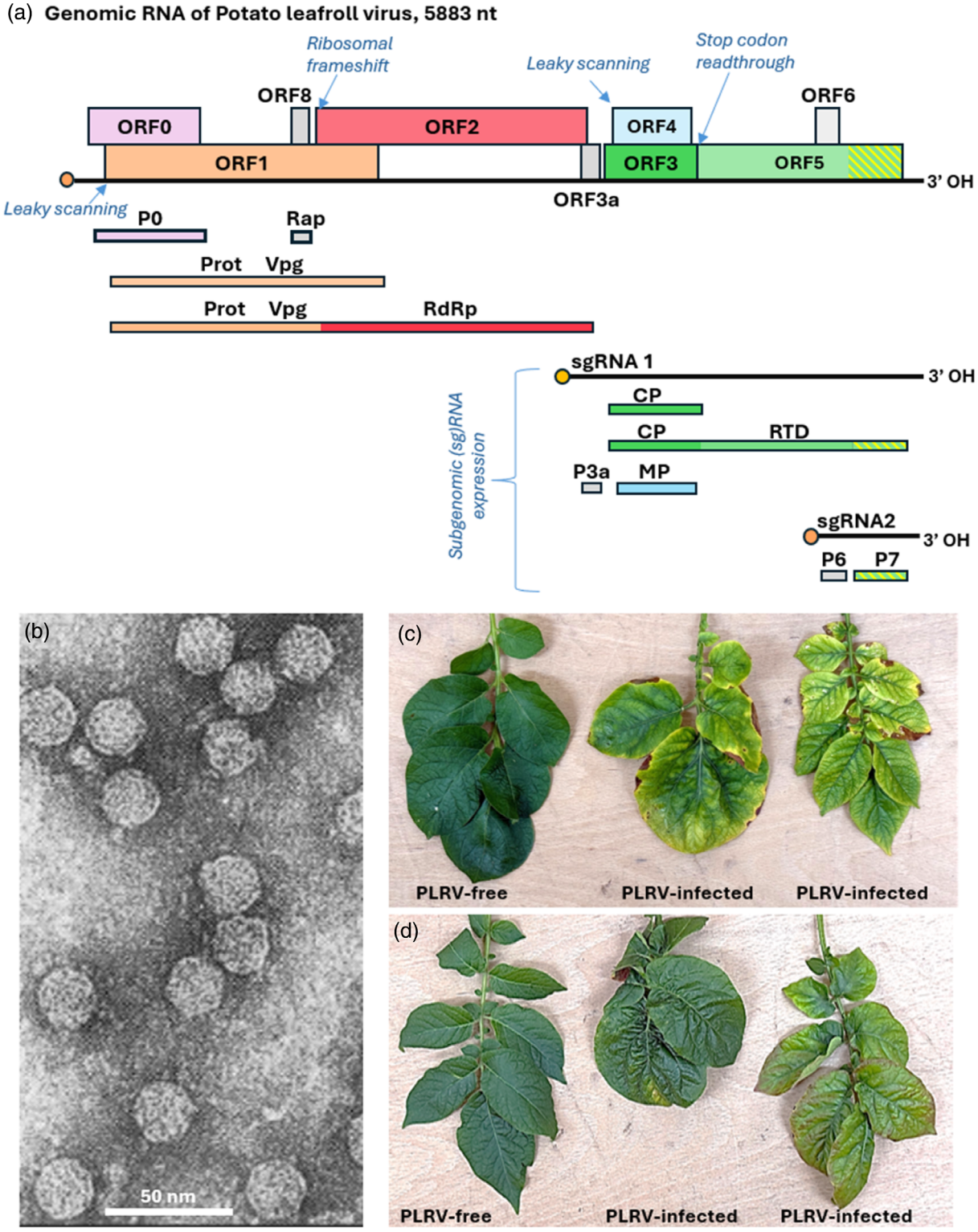


FIGURE 1 Potato leafroll virus (PLRV) genome organisation, particle morphology and symptoms in potato. (a) Schematic representation of the genomic RNA organisation and gene expression strategy of PLRV (5883 nt). Open reading frames (ORFs) are indicated by boxes. ORF0 encodes the RNA silencing suppressor (P0). ORF1 encodes a polyprotein containing a protease (Prot) and viral genome-linked protein (VPg). ORF2 is expressed via a-1 ribosomal frameshift and encodes the RNA-dependent RNA polymerase (RdRp). ORF3 encodes the coat protein (CP), while translational readthrough produces the readthrough domain (RTD). ORF4 encodes the movement protein (MP). ORF3a encodes a small protein (P3a) involved in long-distance movement. ORFs 6 and 7 encode small proteins (P6 and P7) of unknown or regulatory function. Viral proteins are expressed via leaky scanning and subgenomic (sg) RNAs (sgRNA1 and sgRNA2). (b) Transmission electron micrograph of purified PLRV particles. Scale bar = 50 nm. Reproduced with permission from AAB. (c, d) Symptoms of PLRV infection in potato cultivars 'Elland' (c) and 'Maris Piper' (d). Left: Leaves from uninfected plants. Middle and right: Leaves from PLRV-infected plants (lower/older and upper/younger leaves, respectively) showing typical symptoms. Infection shown represents secondary infection following tuber transmission.

especially at the base, and plants have an upright habit. The edges of young leaflets of some cultivars may develop reddening. Secondary symptoms appear in plants grown from infected tubers, such as stunting of the shoots and upward rolling of leaflets, especially of basal leaves which become rigid and leathery (Figure 1c,d) (Loebenstein, 2001).

Most potato varieties are susceptible to PLRV. However, resistance to PLRV has been reported in *S. tuberosum* ssp. *andigena* landrace LOP-868 (Velásquez et al., 2007) as well as in *S. tuberosum* clones G7445 and G7032 (Barker et al., 1994). Potato cultivars susceptible to PLRV vary significantly in PLRV symptom development. This complicates detection of PLRV-infected plants in cultivars with low propensity for development of PLRV symptoms. Furthermore, varietal differences of PLRV may affect symptom development; for example, a symptomless isolate of PLRV was reported in Germany (Hühnlein et al., 2016). In tomato, tomato yellow top strains of PLRV cause stunting of plants, marginal yellowing and curling of leaflets and death of flower buds (Braithwaite & Blake, 1961).

3 | GEOGRAPHICAL DISTRIBUTION

Despite its global presence, PLRV shows relatively little sequence variation compared to other plant RNA viruses. Recent analysis of all 117 full-length PLRV genomes sequenced worldwide by 2025 showed an overall nucleotide identity of at least 94% (Cowan et al., 2025). Phylogenetic analysis showed no clear geographic connection, with the highest diversity found in the Americas where all phylogenetic lineages are present (Figure 2). This suggests that PLRV originated in South America and was distributed globally in infected tubers.

Analysis of genetic diversity of PLRV proteins showed that the C-terminal section of the ORF5-encoded RTD and the P0 RNA silencing suppressor had the greatest variability (Farooq et al., 2022). The relatively low global genetic diversity may be explained by recent divergence of PLRV from an ancestral virus and/or the result of very strong selection constraints due to restricted host range and relatively narrow genetic base of its host plant (Guyader & Ducray, 2002). There are indications that tuber transmission and aphid transmission may impose different selection pressures on the structural proteins of PLRV, with limited scope for genetic diversity due to the circulative transmission within aphids (Cowan et al., 2025). Little is known about the effect of PLRV sequence diversity on the virus biology, but the changes in ORF5 protein, which is involved in virus systemic movement in plant and aphid transmission (Peter et al., 2008; Schiltz et al., 2022), are likely to affect both virus infection dynamics in plants and interactions with aphids. For example, an emerging PLRV variant which recently replaced the historic PLRV type in Scotland (Cowan et al., 2025) is phylogenetically related to a German variant (Hühnlein et al., 2016), which contains most of the amino acid changes in the C-terminus of the ORF5 protein.

4 | HOST RANGE

PLRV has a relatively limited host range, causing economic losses principally in potato (*Solanum tuberosum*), with infection reported in all potato cultivation areas worldwide. In the Americas and Australasia, PLRV was occasionally found in tomato plants, *Solanum lycopersicum*, where it caused yellow top disease, but no other crops were found to be affected. Most known wild hosts of PLRV are *Solanaceae* species (Harrison, 1984) (including *Solanum nigrum* (Black nightshade), *Datura stramonium* (Jimson weed), *Physalis floridana*, *Physalis minima* (ground cherry), *Withania somnifera* (winter cherry)) (Singh, 2016). Non-solanaceous hosts include *Amaranthus caudatus*, *Amaranthus viridis*, *Celosia argentea*, *Gomphrena globosa* (Amaranthaceae), *Chenopodium album* (Chenopodiaceae), *Nolana lanceolata* (Nolanaceae), *Capsella bursa-pastoris* (Brassicaceae), *Montia perfoliata* (Portulacaceae) (Harrison, 1984; Natti et al., 1953; Singh, 2016). Although there is a possibility that PLRV could be transmitted between these wild species and potato crop by viruliferous aphids, the impact of potential wild hosts of PLRV on its circulation remains unknown.

5 | GENOME ORGANISATION

PLRV consists of ~24 nm diameter isometric virus particles (Figure 1b), composed of major (23 kDa) and minor (80 kDa) coat proteins (CPs) which encapsidate 6 kb positive-strand RNA genomes that have a virus genome linked protein (VPg) covalently linked to the 5′ terminus (Van der Wilk et al., 1997, Taliansky et al., 2003). PLRV genomic RNA contains eight open reading frames (ORFs) coding for proteins involved in key virus functions such as genome replication in plant cells, movement within plants, suppression of plant antiviral defences and aphid transmission. Expression of tightly packed and sometimes overlapping PLRV ORFs involves a range of strategies including translational frameshift, readthrough, leaky scanning and ribosome scanning. The 5′-proximal ORFs 0, 1, 2 and 8 are expressed from the genomic RNA, while expression of the 3′-proximal ORFs 3a, 3, 4, 6 and 7 occurs from two sg RNAs sharing the same 3′ as the genomic RNA (Figure 1c). The larger sgRNA is required for translation of ORF3, ORF3a, ORF4 and ORF5 (Ashoub et al., 1998; Farooq et al., 2022; Taliansky et al., 2003). The C-terminal 125 amino acid portion of the ORF5-encoded protein could be expressed as the ORF7 protein from the shorter sgRNA (Ashoub et al., 1998).

The ORFs P1 and P2 encode a proteinase, a genome-linked protein (VPg) and an RNA-dependent RNA polymerase (RdRp), a key viral protein involved in replication of genomic RNA and synthesis of two sg RNAs for the expression of the 3′ proximal ORFs (Taliansky et al., 2003). Expression of the RNA replicase occurs from genomic RNA and involves ribosomal frameshifting, enabling production of an extended protein by translating ORF1 and ORF2. The 5′ proximal ORF0 encodes a suppressor of RNA silencing, which allows PLRV to withstand plant antiviral RNAi defences (Pazhouhandeh et al., 2006).

The ORF3 and ORF5 encode PLRV structural proteins. The major CP encoded by ORF3 and the ORF3-ORF5 readthrough protein (RTP)

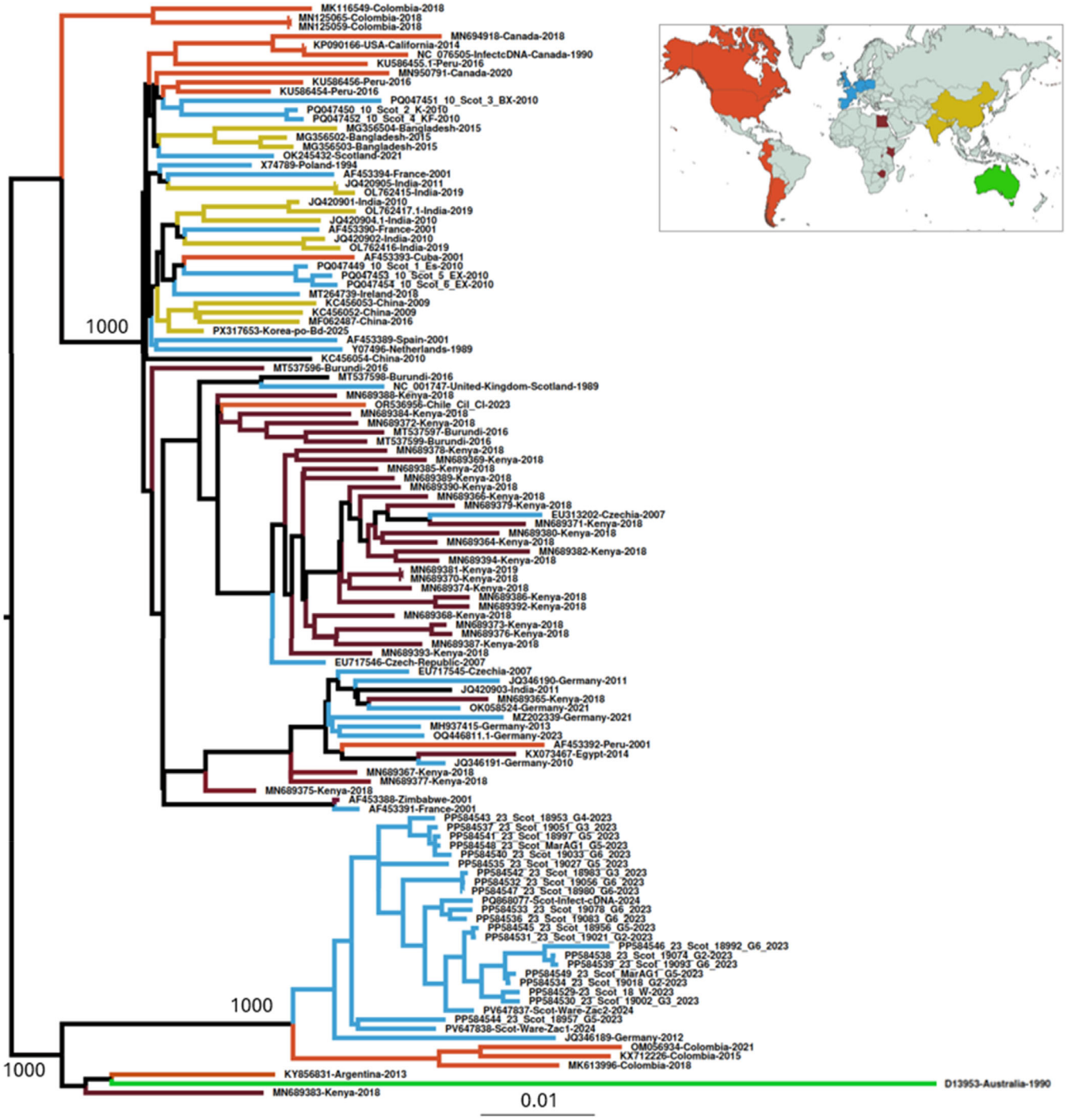


FIGURE 2 Phylogenetic analysis of full-length genomic RNA of Potato leafroll virus (PLRV) inferred using the maximum likelihood (ML) method. Branches are coloured according to the geographic origin of the isolates, using the same colour scheme as the world map (insert). Node labels include GenBank accession number, country of origin and year of isolation. Bootstrap values obtained after 1000 re-samplings are shown for selected nodes. Scale bar below indicates nucleotide differences.

is translated via a leaky amber stop codon at the 3′ end of ORF 3 and is incorporated into virions as a minor CP (DeBlasio et al., 2015, Taliansky et al., 2003). The amino-terminal part of the ORF5-encoded peptide of the RTP is essential for phloem movement and aphid transmission of the PLRV virus particles (Schiltz et al., 2022).

The ORF4 encodes a phloem movement protein that facilitates transport of PLRV between companion cells and sieve elements (Schmitz et al., 1997). The protein encoded by ORF3a is known to be associated with the PLRV virion and involved in viral phloem movement together with the ORF4 protein and both structural proteins encoded by ORF3 and ORF5 (DeBlasio et al., 2018). ORF6 has an unknown function but possesses nucleic acid-binding properties and ORF7 has been shown to increase aphid fecundity when expressed in plants (Patton et al., 2020).

6 | PARTICLE STRUCTURE AND COMPOSITION

PLRV encodes two structural proteins (Miller et al., 1995) (Figure 1a), which encapsidate genomic RNA and form 24 nm spherical particles (Figure 1b). The CP, derived from ORF3, constitutes the major component of the viral capsid. The minor capsid component, the RTP, is generated as a result of ribosomal readthrough of the leaky stop codon of ORF3 coding for the CP and translation of the ORF5, coding for the readthrough domain (RTD) (Bahner et al., 1990). Cryo-electron microscopy and crystallographic studies showed that PLRVCP assembles with T = 3 icosahedral symmetry (Adams et al., 2022; Byrne et al., 2019), which arranges 180 CP monomers into closed particles with twofold, threefold and fivefold symmetry. The RTP is incorporated into the capsid sub-stoichiometrically with the RTD exposed at the virion surface. The N-terminal parts of RTD are situated on the twofold symmetry axis of the icosahedral viral capsid and form dimers stabilised by a C-terminal peptide (Schiltz et al., 2022).

7 | PURIFICATION

Purification of PLRV is based on enzymic digestion of plant cell walls with Driselase (a mixture of fungal carbohydrolases), followed by the organic solvent extraction to remove pigments and lipids and recovery of virus particles by ultracentrifugation (Takanami & Kubo, 1979). Method: freeze PLRV-infected *Physalis floridana* or potato leaves for a week or more at −70°C. Grind 500 g of leaf material at room temperature with 1 litre 0.1 M sodium citrate buffer, pH 6.0, containing 0.5% 2-mercaptoethanol supplemented with 1% Driselase, then incubate at 25°C for 2–3 h with shaking. Adjust extract to pH 7.0 by adding 0.2 M Na_2HPO_4, emulsify with a 0.67 volume of chloroform/butanol mixture (1:1, v/v) and centrifuge at 3000 ×*g* for 15 min. To the aqueous phase, add polyethylene glycol M.Wt. 6000, to 8% (w/v) and NaCl to 0.2 M. Stir for 1 h at 4°C, incubate at room temperature for 1–2 h, then centrifuge at 20,000 ×*g* for 15 min. Resuspend sedimented pellets in 100 mL 0.02 M sodium phosphate buffer, pH 7.5, containing 1% Triton X-100 and centrifuge at 10,000 ×*g* for 15 min. Further purify by two cycles of high-speed centrifugation at 100,000 ×*g* through 20% sucrose cushion for 2–3 h and low-speed centrifugation at 3000 ×*g*, resuspending the final high-speed sediments in 2 mL phosphate buffer. Further purification may be achieved by centrifugation, 10,000 ×*g* for 3 h in 10%–40% sucrose gradient. Purified virus particles can be stored frozen but they precipitate reversibly at about 4°C. All centrifugation is therefore done at 15°C. Virus yields are about 0.7 mg/kg potato leaves and 1 mg/kg P. *floridana* leaves.

8 | TRANSMISSION

PLRV is a phloem-limited virus and not mechanically transmissible. It is transmitted between plants by aphids, principally by *Myzus persicae* and *Macrosiphum euphorbiae*, but could be transmitted by grafting or by dodder (*Cuscuta* spp.) plants (Stevens, 2013). Vectoring of PLRV by its aphid vectors occurs in a persistent, circulative, non-replicative manner. The virus is acquired by aphids from infected plants during feeding on the phloem; it moves from gut to salivary glands via the haemolymph. Aphids remain capable of transmitting PLRV and infecting potato plants for their entire lifespan (Taliansky et al., 2003). PLRV replicates exclusively in the phloem tissue of infected plants, and in the case of mixed infection with an umbravirus, for example, Pea enation mosaic virus-2, PLRV can invade mesophyll cells (Ryabov et al., 2001; Taliansky et al., 2003). The systemic movement of PLRV within plants requires structural proteins encoded by ORF3 and ORF5, as well as the movement protein encoded by the ORF4 and the ORF3a. The systemic movement through the phloem of potato plants also allows PLRV infection to reach developing tubers via the stolon phloem, thereby enabling vertical transmission of the virus to the next vegetative generation. Virion assembly is essential for both phloem movement and for the aphid transmission of PLRV. Both the CP and minor RTP are required for the systemic movement of PLRV through the phloem and aphid transmission, which involves transition of the virus particles through midgut and salivary gland epithelial cells and circulation in the haemolymph (Olmedo-Velarde et al., 2023; Schiltz et al., 2022).

9 | SEROLOGICAL AND MOLECULAR DETECTION

Serological assays for PLRV based on detection of PLRV structural proteins (ELISA) (Tamada & Harrison, 1980; Torrance, 1992) were developed in the 1970s and are commercially available. The advent of monoclonal antibodies and development of assays based on fully recombinant immunoglobulins has allowed an enduring supply of serological reagents (Al-Mrabeh et al., 2009). Detection of PLRV RNA by reverse transcription RT-PCR offers higher sensitivity and specificity in both plant and aphid vectors (Robertson et al., 1991; Singh et al., 1995). The relatively low genetic diversity of PLRV and information on distribution of conserved and divergent regions in the PLRV genome have made it possible to design RT-PCR assays using primers capable of amplifying all genetic variants of the virus (Cowan et al., 2025).

10 | ECOLOGY AND CONTROL

PLRV is transmitted both horizontally (between plants by its aphid vectors) and vertically by tubers produced by the infected plants. Therefore, control of PLRV includes the following strategies:

1. Production of virus-free seed tubers by meristem culture propagation (Gong et al., 2019). This ensures virus-free status of seed potato at the start of the production cycles, which usually includes up to six field generations.

2. Control of aphid vectors by chemical pesticides (Robert et al., 2000).
3. Removal of infected plants in seed potato crops by roguing based on symptoms (Thomas-Sharma et al., 2016). However, the efficiency of roguing ultimately depends on recognition of symptoms, which can be mild or less pronounced or delayed in some cultivar–PLRV variant combinations, making it more difficult to identify and eliminate PLRV-infected plants.
4. The development and introduction of PLRV-resistant potato varieties could provide a sustainable solution to PLRV management by reducing reliance on insecticides as well as on monitoring and elimination of the virus-infected seed tubers. Several sources of PLRV-resistance have been identified in *Solanum* species which could potentially be incorporated into potato breeding programmes (Barker, 1987; Barker et al., 1994; Velásquez et al., 2007).

11 | CONCLUSIONS AND FUTURE PROSPECTS

Research on PLRV has played a fundamental role in the advance of our understanding of plant virus biology, particularly in relation to aphid transmission and the mechanisms underlying persistent, circulative virus–vector interactions. PLRV was among the first plant viruses to be fully sequenced and subsequent analyses of its genome and gene expression (Mayo et al., 1989) have provided important insights into viral replication, movement within host phloem tissues and long-distance infection processes.

Moving forward, it's clear that PLRV poses a continuing threat to potato production systems and research on factors affecting emergence and spread of this virus is critically important.

Recent restrictions on chemical control of aphid vectors (Blake, 2018), combined with increasingly mild winters in regions such as Northern Europe, have contributed to a renewed risk of virus re-emergence and spread (Skelsey, 2024; Trebicki, 2020). These changing environmental and agronomic conditions highlight the need for more resilient and integrated disease management strategies.

A key consideration for future research is the importance of understanding the effects of PLRV infection on behaviour and reproduction of its aphid vectors, which are likely to impact the efficiency of virus spread and the virus epidemiology (Patton et al., 2020). In addition, priority should be given to identifying and deploying natural resistance genes in potato or genome editing approaches (Barker, 1987; Velásquez et al., 2007) and the accurate identification and monitoring of PLRV incidence within seed and ware potato crops. Given the changing environment with warmer winters allowing earlier build-up of aphids in crops, virus monitoring and seed tuber certification could be expanded to ensure elimination of virus-infected seed tubers. In future, field inspections could be supplemented with laboratory tests on field samples to track virus incidence more precisely and prevent spread through seed tubers.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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