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CHILLI VEINAL MOTTLE VIRUS BIOLOGY, MOLECULAR DIVERSITY, EPIDEMIOLOGY, AND DISEASE MANAGEMENT

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ABSTRACT

Chilli veinal mottle virus (ChiVMV) is an economically destructive *potyvirus* that infects chilli production in Asia resulting in severe losses in yield and quality. Contributions in the field of molecular virology, high-throughput sequencing, and bioinformatic tools have made major contributions to the existing knowledge of ChiVMV biology, genetic diversity and the interaction of host and virus in the last decade. New phylogenetic studies using the full sequences of the nucleotides and the polyprotein sequences have shown well defined lineage divisions amongst geographically differentiated isolates, showing ongoing viral evolution by mutation, recombination, and local adaptation. A characteristic pattern of the ChiVMV infection cycle includes aphid-mediated infection transmission, polyprotein processing, cytoplasm replication, and cell-to-cell and systemic local movements. Host RNA silencing is the main antiviral immunity at the molecular level, but ChiVMV overcomes this effect via RNAi suppression via HC-Pro. The management strategies that are currently in place use integrated plant disease management (IPDM) such as the use of vector control, certified seed, cultural practices, resistant germplasm and the use of biological agents. The review combines modern information on the epidemiology of the ChiVMV, its genome structure, molecular interactions, development of resistance, and evolutionary processes, which will form the basis of future studies and the development of long-term and sustainable control mechanisms.

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INTRODUCTION

Vegetables represent a substantial source of revenue and are considered high-value crops for small-scale farmers (Dlamini, 2023). Chilli is an economically important solanaceous crop cultivated worldwide for its pungency, flavor, and nutritional value and ranks third after tomato and potato within the Solanaceae family (Iqbal *et al.*, 2012; Saba *et al.*, 2022). There are about 90 genera, 3000 to 4000 species in *solanaceous* family and approximately 27 species of genus *Capsicum* from which

only five being domesticated viz: *Capsicum baccatum*, *C. annuum*, *C. chinense*, *C. pubescens*, and *C. frutescens*. Among these species, *C. annuum* is the most widely cultivated species, with significant economic importance and a range from mild to spicy cultivars (Ahmad and Ashfaq, 2017; Barboza *et al.*, 2022; Kumar *et al.*, 2024). Chilli is an economically important and highly profitable cash crop cultivated worldwide, and its global production has increased considerably in recent years (Ahmad and Ashfaq, 2018).

Table 1. Major viral diseases reported in chilli and their associated vectors, host range, yield losses, diagnostic methods, and geographical distribution.

Virus	Genus/ Family	Genome Type	Vector	Major Hosts	Yield Loss (%)	Yield Loss Source	Diagnostic Methods	Region Reported	References
Chilli ringspot virus (ChiRSV)	Potyvirus / Potyviridae	ssRNA	Aphids	Chilli, pepper	100%	Literature reports	PTA-ELISA; RT-PCR	China, Pakistan	Ahmad <i>et al.</i> (2017); Wang <i>et al.</i> (2012); Hua <i>et al.</i> (2022)
Chilli veinal mottle virus (ChiVMV)	Potyvirus / Potyviridae	ssRNA	Aphids	Chilli, tomato, African eggplant	55–65%	Literature reports	PTA-ELISA; RT-PCR	China, Pakistan, India, Taiwan	Banerjee <i>et al.</i> (2014); Chen <i>et al.</i> (2022);
Potato virus Y (PVY)	Potyvirus / Potyviridae	ssRNA	Aphids	Potato, chilli, tomato, tobacco	60–100%	Literature reports	PTA-ELISA; RT-PCR	Worldwide	Naveed <i>et al.</i> (2017); Abd El-Aziz (2020); Ghanaïm <i>et al.</i> (2025); Dupuis <i>et al.</i> (2024)
Cucumber mosaic virus (CMV)	Cucumovirus / Bromoviridae	ssRNA	Aphids	Chilli, tomato, and several other hosts	20–100%	Literature reports	High-throughput sequencing (HTS); RT-PCR	Worldwide	Netla <i>et al.</i> (2025); Fadly <i>et al.</i> (2025); Kwon <i>et al.</i> (2025); Jeevarathinam <i>et al.</i> (2025)
Alfalfa mosaic virus (AMV)	Alfamovirus / Bromoviridae	ssRNA	Aphids, pollen, seed	Alfalfa, chilli, pulses, potato, tomato, pea	22–46%	Literature reports	ELISA; RT-PCR; RT-RPA-CRISPR/Cas12a; RNA-Seq	China, Argentina, Chile	Dawoud (2025); Yan <i>et al.</i> (2025); Yang <i>et al.</i> (2025); Peña <i>et al.</i> (2025); Trucco <i>et al.</i> (2026)
Chilli leaf curl virus (ChiLCV)	Begomovirus / Geminiviridae	ssDNA	Whitefly (<i>Bemisia tabaci</i>)	Chilli, tomato, potato, amaranth	≤53%	Literature reports	PCR; Rolling Circle Amplification (RCA); CRISPR/Cas12a	India, Pakistan	Navyatejaswini <i>et al.</i> (2025); Krishnan <i>et al.</i> (2025); Ullah <i>et al.</i> (2025)

Chilli originated in tropical regions of South America, particularly Mexico. Prior to 1585, Portuguese traders brought chilli to the Indo-Pak from Brazil (Hancock, 2022; Villalón-Mendoza *et al.*, 2023).

After black pepper, chilli accounts for 16% of global spice commerce. China is the world's largest producer of all types of chilli, while India is the world's largest producer of dried whole chilli. Major chilli-producing countries include China, India, Mexico, Turkey, Bangladesh, Peru, and Pakistan, where chilli cultivation forms a major component of vegetable production (Ashfaq *et al.*, 2014). In Pakistan and other Asian countries, chilli plays a vital role in the agro-economy and food industries. However, its production is severely constrained by several abiotic and biotic factors. Primarily abiotic factors are salinity, metal contamination, extreme cold, heat, drought and biotic factors include viral, bacterial and fungal infection (Chhapekar *et al.*, 2018). Plant viruses are pathogens that lead to yield reductions in economically important crops. Annually, viruses impacting fruit and vegetable crops lead to global financial losses amounting to several billion dollars (Tatineni and Hein, 2023). Plant viruses are classified into two categories based on their genetic material: RNA and DNA viruses. RNA viruses account for the majority of plant diseases, with over 80% of plant viruses being RNA-based. Additionally, more than 75 distinct and well-documented viruses affecting chilli plants have been identified worldwide (Bimrew and Abera, 2023; Netla *et al.*, 2025). Among these, the genus *Potyvirus* (family Potyviridae) represents one of the most significant and destructive groups of plant viruses. *Potyvirus* was first identified during a study of viruses affecting potatoes in the United Kingdom in the late 1920s (Inoue-Nagata *et al.*, 2022; Chakrabarti *et al.*, 2022). *Chilli vein mottle virus* (ChiVMV), a member of the genus *Potyvirus* within the family Potyviridae, is considered one of the most destructive viruses affecting chilli crops and other *solanaceous* crops (Kumari *et al.*, 2023).

METHODOLOGY OF LITERATURE SEARCH

A systematic literature review was conducted to compile and synthesize published information on Chilli vein mottle virus (ChiVMV), followed by preparation of PRISMA flowchart for transparent reporting. Scientific articles were retrieved from major databases including Scopus, Web of Science (WoS), PubMed, and Google Scholar. ResearchGate was used only as a supplementary source for retrieving full-text versions of articles that had already been

identified through indexed databases and was not considered a primary bibliographic database for literature screening. The literature search covered publications from 1885 to 2026. A small number of early foundational studies (1885–1990) were included to provide historical context, while 23 relevant studies published between 2008 and 2020 were also incorporated. However, the majority of the cited literature was published within the last five years to ensure that the review reflects the most recent development in ChiVMV research. Keywords used in the search included “First report of Chilli vein mottle virus”, “ChiVMV evolutionary genetics”, “ChiVMV aphid transmission”, “ChiVMV management” and “Potyvirus resistance breeding”, with Boolean operators applied where appropriate to fine-tune the search results. The inclusion criteria prioritized peer-reviewed research articles and relevant scholarly reviews, book chapters, and other authoritative sources published in English and studies with confirmed molecular evidence of ChiVMV infection (RT-PCR, sequencing or complete genome data) were prioritized. However, conference abstracts, non-peer-reviewed sources, newspaper reports, popular articles, annual regulatory reports and articles lacking molecular confirmation were excluded. The extracted data included information on geographic distribution, host range, genome organization, strain diversity, phylogenetic relationships, reported yield losses and management strategies which were critically analyzed and synthesized to provide a comprehensive overview of ChiVMV biology, evolution, and sustainable disease control. Tables and figures were designed to synthesize and present the most relevant information in a concise and accessible format. The illustrations for this review were prepared by the authors using original data from publications and appropriately sourced open-access materials.

DISTRIBUTION AND TRANSMISSION

ChiVMV was initially reported in Malaysia (Ong *et al.*, 1979) and has since been reported in Asia, such as China, India, Thailand, Japan, Korea, Pakistan and Africa in chilli and other crops. It is highly spread by the international trade of infected plant materials and effective transmission by aphid vectors (Wang *et al.*, 2025; Lee *et al.*, 2025; Lakshminarayana Reddy *et al.*, 2024; Moya-Ruiz *et al.*, 2023; Chen *et al.*, 2022; Phatsaman *et al.*, 2021). The virus is primarily transmitted by several aphid species in a non-persistent, stylet-borne manner, especially by *Myzus persicae* also referred to as the green peach aphid.

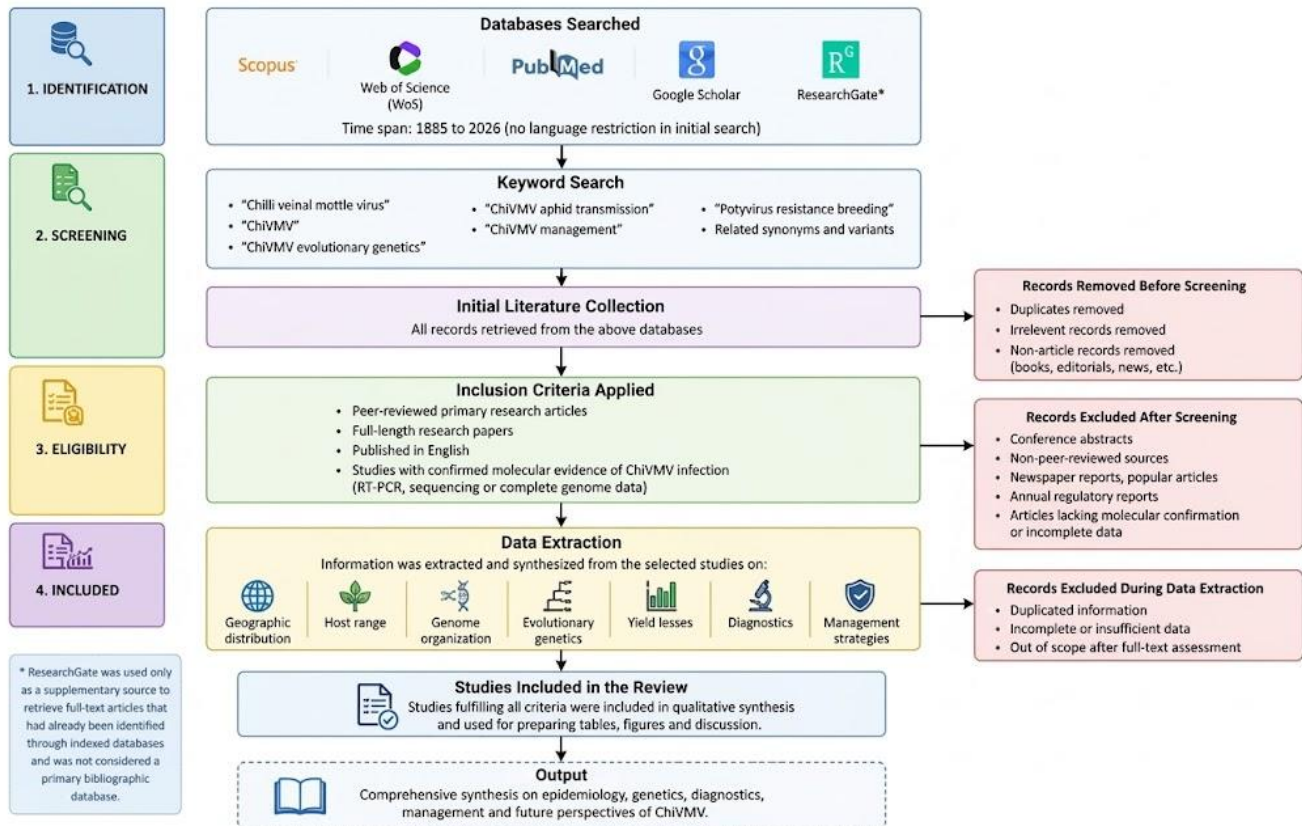


Figure 1. Literature search and study selection workflow used for identification, screening, eligibility assessment, and synthesis of publications related to *Chilli vein mottle virus* (ChiVMV).

Other species such as the rusty plum aphid, brown and green citrus aphid, black legume aphid, cotton aphid and corn leaf aphid facilitate the spread of ChiVMV to other hosts (Zohoungbogbo *et al.*, 2024).

Aphids generally retain non-persistently transmitted viruses for only a short period after acquisition from infected plants (Guo *et al.*, 2022). Due to the non-persistent transmission behavior of aphids, viruses are usually transmitted over short distances. However, strong winds and storms may facilitate long-distance dispersal of viruliferous aphids (Falla and Cuniffe, 2024). The helper component-proteinase (HC-Pro) of ChiVMV plays an important role by facilitating the attachment of virions to receptors on the aphid stylet (Mubashir, 2022). Both the growth of aphid populations and the spread of viruses are facilitated by environmental elements including high humidity and moderate temperatures (Li *et al.*, 2025b). Other methods of virus transmission include grafting and mechanical inoculation; however, the virus cannot be transmitted through seeds (Reddy *et al.*, 2022).

HOST RANGE AND SYMPTOMS

ChiVMV has a relatively narrow but agriculturally significant host range, largely confined to the Solanaceae family (Lakshminarayana Reddy *et al.*, 2024). Natural hosts for this virus include chilli, pepper, tomato, and African eggplants. The documented host range encompasses *Capsicum frutescens*, *C. annuum*, *Physalis floridana*, *Solanum melongena*, various *Chenopodium* species, *Lycopersicon esculentum*, *Solanum nigrum*, *Datura metel*, *Datura stramonium*, and *Nicotiana* species. Experimental studies have demonstrated successful infection of several *Nicotiana* and *Chenopodium* species, which develop local chlorotic lesions and serve as useful diagnostic hosts for biological indexing (Rao *et al.*, 2020; Shonazarova *et al.*, 2025).

Symptoms caused by ChiVMV vary depending on the chili cultivar, plant age at infection, viral strain, environmental conditions, and the presence of other co-infecting viruses (Nalla *et al.*, 2023). Generally, the disease is characterized by vein clearing, mosaic mottling, and distorted leaves that can lead to considerable growth retardation and fruit

malformation. The earliest symptom observed on young chilli leaves is vein clearing and then light or dark green mottling and interveinal chlorosis (Ahmad and Ashfaq, 2018). As infection progresses, leaves become elongated, narrow, and curled as the infection advances thus making the plants look bushy and stunted. In extreme infections, the plant can have low branching, shortened internodes and small, deformed fruits that have poor coloration and low market value. In cultivars that are tolerant, the symptoms can be mild, and recovery can be partial in later stages of growth, although the presence of the virus can still decrease yield (Naresh *et al.*, 2016; Bu *et al.*, 2025). High temperature (above 30°C) and intense sunlight tend to increase the expression of symptoms, whereas low temperatures tend to suppress the expression of visible symptoms. In dual infections between Cucumber mosaic virus (CMV) and Potato virus Y (PVY) or Pepper vein mottle virus (PVMV), plants exhibit severe systemic mosaic, leaf blistering, defoliation and fruit drop as a manifestation of a synergistic effect which enhances viral replication and symptom severity (Bu *et al.*, 2025). In experimental host plants such as *Nicotiana tabacum*, *Nicotiana benthamiana*, and *Datura stramonium*, ChiVMV produces systemic mosaic and chlorotic ring spots, making these species useful diagnostic hosts. On local lesion hosts like *Chenopodium amaranticolor* or *C. quinoa*, the virus induces chlorotic or necrotic lesions within 3-5 days post-inoculation, which are useful for bioassay confirmation and isolate differentiation (Riaz *et al.*, 2021; Zeng *et al.*, 2026; An *et al.*, 2025).

Genome organization and Phylogenetic analysis

The ChiVMV genome begins with a non-translated region (NTR) that is less than 200 base pairs long. A genome-linked protein, VPg, is covalently bound to the 5' end (Ponnam *et al.*, 2023), and a poly(A) tail is present at the 3' terminus (Wan *et al.*, 2023). The virus features flexuous filamentous particles with a width of 11-13 nm and a length of 680-900 nm. The virion contains a monopartite, positive-sense, single-stranded RNA (ssRNA) genome that is 9.7-10 kb in length (Zhang *et al.*, 2025). The open reading frame (ORF) encodes a large polyprotein, which is subsequently cleaved into functional proteins by viral proteinases such as CP, PI, P3, NIa, NIb, 6K1, 6K2, HC-Pro, and VPg (Ahmad *et al.*, 2017; Ji *et al.*, 2023).

The HC-Pro protein, with a molecular weight of approximately 50 kDa, performs multiple biological functions. It is cleaved from a polyprotein and is essential for viral transmission by aphids as well as for cell-to-cell

movement within host plants. Transmission efficiency varies among aphid species due to differences in interactions between HC-Pro and aphid stylet components with various results where each species had a different contact with the feeding canal of HC-Pro, which also had an effect in terms of the ability of the aphids to harbor the virus in the mouthparts (Mubashir, 2022; Rao *et al.*, 2024). In addition to this, Hýšková *et al.* (2024) demonstrated that the central region of the TEV HC-Pro is presumed to contribute to systemic movement, synergism and amplification of the genome in the host plants. The potyvirus has been studied and found that HC-Pro is a powerful inhibitor of RNA silencing that can be effective in reducing transient gene silencing in experiments (Choi *et al.*, 2025).

In *Arabidopsis thaliana*, expression of P1-HC-Pro fusion protein leads to the decrease of accumulation of microRNAs (miRNAs) (Pan *et al.*, 2025). P3 is the third protein encoded by the potyviral genome and has an approximate molecular weight of 40 kDa. It is a protein that is least known and most diverse in the family Potyviridae (Hýšková *et al.*, 2024). Moreover, the P3 protein also interferes with other viral proteins and it is the main cause of pathogenicity. The C-terminal region of the P3-6K1 complex has a pathogenicity determinant of *Plum pox virus* (PPV) (García *et al.*, 2025). P3 is next to the 6K1 protein, a small extra protein produced by the open reading frame (ORF). Nevertheless, no clear cleavage between 6K1 and P3 in potyviruses, including TEV has been found (Hu *et al.*, 2025).

Studies on Tobacco vein mottling virus have demonstrated that a viral protein genome-linked (VPg) is involved in viral replication. It was also revealed that the particular residue that links VPg to the viral genome, tyrosine was not found in large amounts in the mutant virus. It has also been discovered that eIF4E and other plant translational initiation factors interact with VPg. Recent studies also show that VPg plays a major role in the extensive transport of the virus (Pandiaraj *et al.*, 2025; Schein, 2025).

The Nuclear Inclusion protein a (NIa) has structural similarities to serine proteases and has a cysteine residue at the active site. Also, NIa has nonspecific RNA-binding of P1 and HC in its protease domain (Xiao *et al.*, 2022). Next in line of order of nuclear inclusion components is NIb which is a RNA-dependent RNA polymerase (RdRp) with a molecular weight of 58 kDa.

Table 2. Functional roles of major potyviral proteins and their relevance to the evolution, epidemiology, and management of Chilli veinal mottle virus (ChiVMV).

Protein	Functional Role	Epidemiological Consequence	Evolutionary Mechanism	Management Implication	References
P1	Host adaptation and symptom modulation	Adaptation to diverse host species	High sequence variability	Monitor emergence of novel ChiVMV variants affecting host adaptation	(Huang <i>et al.</i> , 2025)
HC-Pro (Helper component-protease)	Aphid transmission, RNA silencing suppression	Host range expansion	Recombination, positive selection	Vector management	(Choi <i>et al.</i> , 2025)
P3	Pathogenicity determinant	Resistance erosion	Point mutations	Durable resistance breeding	(Mäkinen, 2020)
6K1	Replication stabilization	Replication efficiency	Minor variation	Development of host-targeted antiviral strategies	(Yu <i>et al.</i> , 2025)
CI (Cylindrical inclusion protein)	Helicase and movement	Systemic infection	Amino acid substitutions	Movement-blocking strategies	(Bu <i>et al.</i> , 2025)
CP (Coat protein)	Encapsidation, vector interaction	Diagnostic escape	Genetic drift & selection	Primer redesign and surveillance	(Devi <i>et al.</i> , 2022)
6K2	Replication vesicle formation	Increased viral fitness	Adaptive mutations	Exploration of replication-associated host interactions for improved disease management	(Xue, 2023)
NIa-VPg	eIF4E interaction	Resistance breakdown	Selection-driven mutations	eIF4E-based resistance deployment	(Zlobin and Taranov, 2023)
NIa-Pro (Protease)	Polyprotein processing	Viral maturation efficiency	Conserved catalytic core	Investigation of conserved protease functions for future antiviral intervention strategies	(Wang <i>et al.</i> , 2025)
NIb (RNA-dependent RNA polymerase)	Genome replication	Quasi-species diversity	Error-prone replication	Long-term monitoring of viral evolution and emergence of adaptive variants	(Ge <i>et al.</i> , 2025; Singh <i>et al.</i> , 2023)

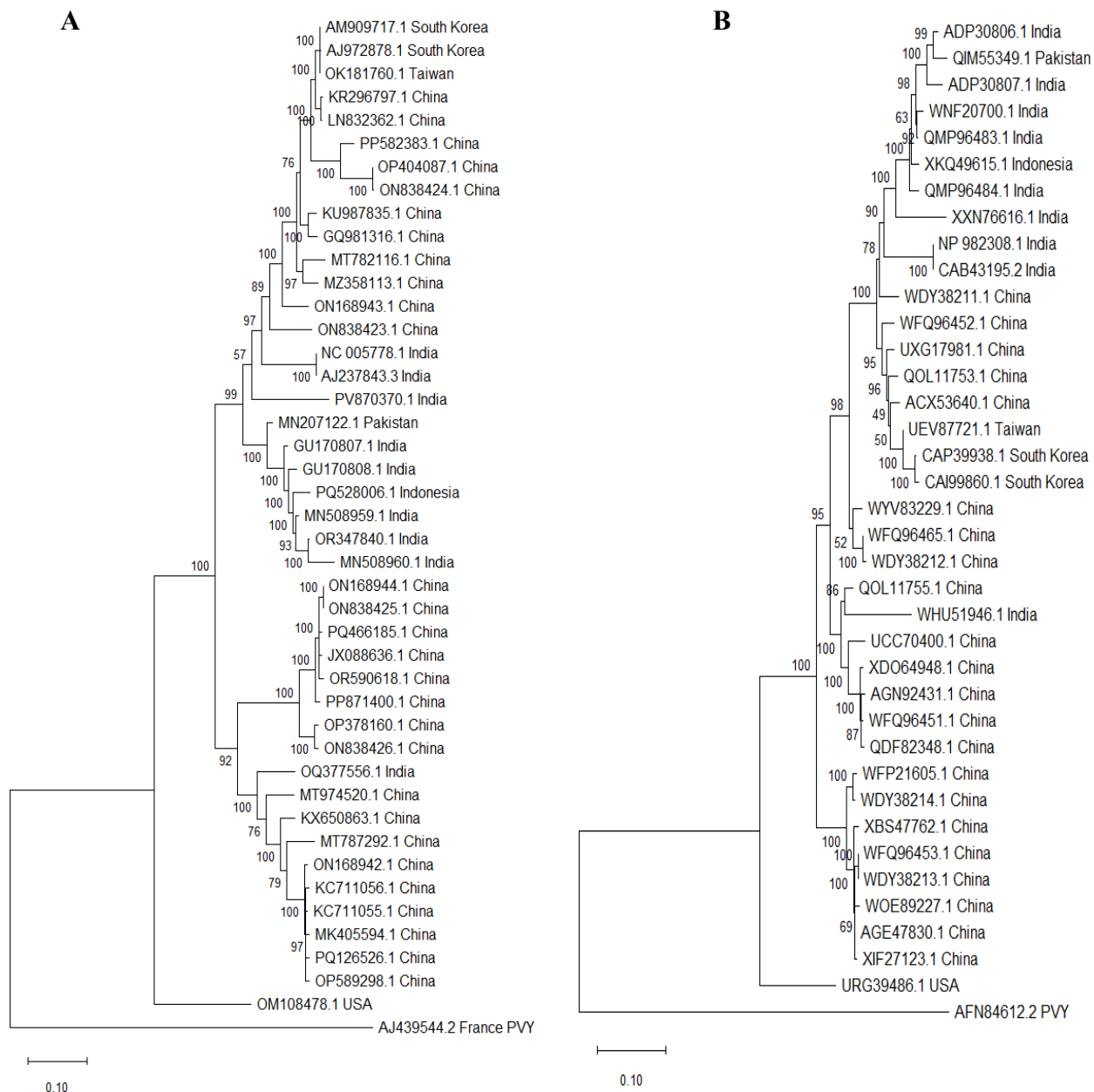


Figure 2. Phylogenetic relationships of Chilli veinal mottle virus (ChiVMV) isolates based on complete nucleotide genome sequences (A) and coat protein sequences (B) retrieved from the NCBI GenBank database.

Representative isolates were selected according to sequence completeness and geographical diversity. Sequence alignments were performed using ClustalW in MEGA 12, and phylogenetic trees were reconstructed using the Neighbor-Joining method with 1000 bootstrap replications. Potato virus Y (PVY) was used as an outgroup. The analyses resolved ChiVMV isolates into distinct clades largely corresponding to their geographical origin, indicating

regional diversification and evolutionary divergence among virus populations across Asia.

The GDD motif is one of the most conserved motifs in the enzyme activity of Tobacco vein mottle virus (TVMV) NIB where any change in the motif leads to harmful effects (Li *et al.*, 2025a; Niraula *et al.*, 2026). In potyviruses the CP is the final product of polyprotein, located at the 3'-terminal of the single large open reading frame (ORF). Its molecular

mass typically ranges between 30 to 40 kDa and has many different functions including building the viral particle,

nucleic acid protection, cell-to-cell movement and vector transmission (Gaur *et al.*, 2023; Xue *et al.*, 2023).

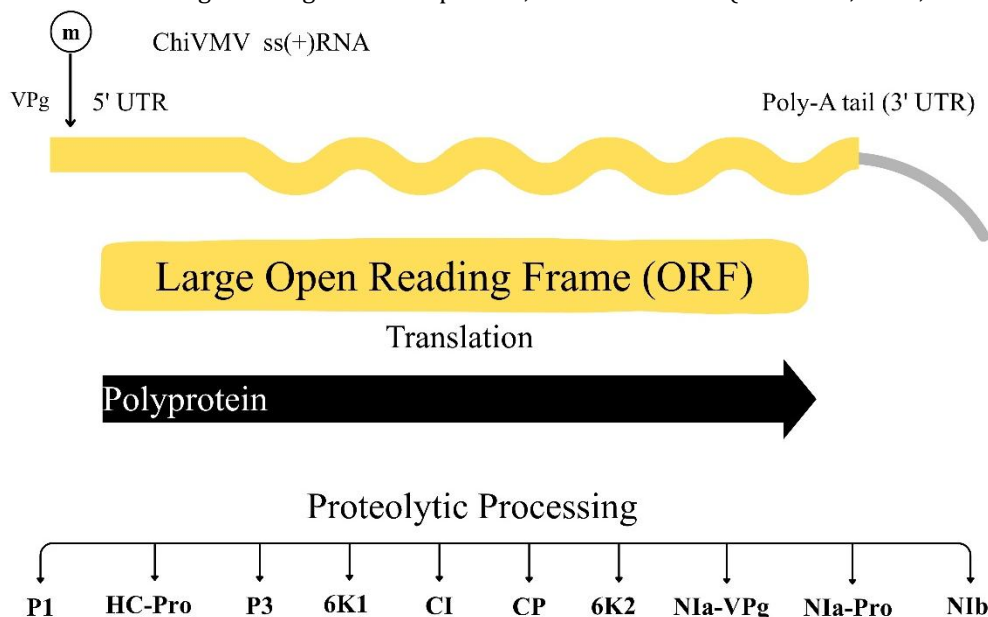


Figure 3. Genome organization of Chilli veinal mottle virus (ChiVMV).

A further short open reading frame (ORF), termed PIPO, has been discovered in all family members and is crucial for the transmission of the virus between cells. The functions of many potyviral genes are not well known, and they can have one or more other functions. Their exact roles may be of value in understanding the role they play in the development of virus-resistant plants (Mingot *et al.*, 2016; Xue *et al.*, 2023). ChiVMV can be detected and confirmed using RT-PCR, ELISA, and LAMP assays. It emphasizes genetic diversity, recombination and useful diagnostic techniques, which are helpful in crop protection and controlling disease (Lakshminarayana Reddy *et al.*, 2024; Netla *et al.*, 2025).

MOLECULAR DETECTION AND DIAGNOSTIC TECHNIQUES

Early and accurate detection of ChiVMV is crucial for disease management, certification of planting materials, and epidemiological surveillance. Visual diagnosis is unreliable due to the existence of symptomless infections, mixed virus complexes and environmental factors that lead to the expression of symptoms. Therefore, serological and molecular detection methods have also been established to detect ChiVMV in a sensitive and specific way. Preliminary diagnosis of ChiVMV was based on the use of enzyme-linked immunosorbent assay (ELISA) with polyclonal and monoclonal antibodies

against the ChiVMV coat protein (CP) (Jiao *et al.*, 2020). Double antibody sandwich (DAS-ELISA) and indirect ELISA formats have been successfully used for large-scale screening of field samples and seed health testing (Ahmad and Ashfaq, 2018). These assays are cost-effective, relatively simple and suitable for high-throughput screening; however, their sensitivity can be limited in cases of low virus titer or antigenic variation among isolates (Cassedy *et al.*, 2021). The development of immunostrip or lateral flow devices (LFDs) has provided a rapid, on-site diagnostic option for farmers and quarantine officials (Cavalera, 2021). Nevertheless, the high cost of antibody production and possible cross-reactivity with related potyviruses restrict their universal application (Liu *et al.*, 2015).

Reverse transcription polymerase chain reaction (RT-PCR) remains the gold-standard technique for ChiVMV detection due to its high specificity and sensitivity. Primers targeting conserved regions of the coat protein (CP), nuclear inclusion b (Nib), or polymerase (Pol) gene are commonly used. Among the well-established primers are the CVMV1037Pol set (Tsai *et al.*, 2008), which amplifies a region of the Nib-CP junction, and several newer sets designed to differentiate ChiVMV from closely related Potyvirus species. RT-PCR allows not only virus detection but also sequence-based characterization, enabling phylogenetic and recombination analyses. In

field diagnostics, one-step RT-PCR kits simplify workflow by combining reverse transcription and amplification in a single tube, reducing contamination risks (Tripathi and Rathinam, 2025). Despite its accuracy, RT-PCR requires laboratory infrastructure, RNA extraction, and thermal cycling, which limit its application in resource-poor settings (Chakraborty, 2024).

RT-qPCR offers exceptional sensitivity (detecting as few as 10 viral copies per reaction) and allows comparison of viral load among cultivars or treatment conditions. However, the high cost of reagents and need for advanced instrumentation restrict their use mainly to research and

reference laboratories (Pereira *et al.*, 2022).

Recent advances in isothermal nucleic acid amplification have expanded the diagnostic options available for ChiVMV. Among these, reverse transcription loop-mediated isothermal amplification (RT-LAMP) and reverse transcription recombinase polymerase amplification (RT-RPA) have emerged as rapid and field-deployable alternatives to conventional RT-PCR. These techniques operate under isothermal conditions and are particularly suitable for on-site diagnosis in resource-limited settings. Their individual principles, advantages, and applications are described below.

Table 3. Comparative overview of diagnostic techniques used for detection of Chilli veinal mottle virus (ChiVMV).

Diagnostic Method	Sensitivity	Specificity	Cost	Field Applicability	Major Limitations
ELISA	Moderate	Moderate–High	Low	Suitable for large-scale screening	Lower sensitivity at low virus titre; requires antibodies
RT-PCR	High	High	Moderate	Laboratory-based	Requires thermal cycler and trained personnel
RT-qPCR	Very High	Very High	High	Laboratory-based	Expensive equipment and reagents
RT-LAMP	High	High	Low–Moderate	Suitable for field and resource-limited conditions	Primer design is complex; risk of non-specific amplification
RT-RPA	High	High	Moderate	Rapid field detection	Reagent cost and limited commercial availability
NGS	Extremely High	Very High	Very High	Research and surveillance applications	High cost, bioinformatics expertise required

The available diagnostic methods for ChiVMV differ considerably in terms of sensitivity, cost, turnaround time, and field applicability. While ELISA remains useful for large-scale screening, nucleic acid-based methods such as RT-PCR and RT-qPCR provide greater sensitivity and specificity. Isothermal amplification techniques, including RT-LAMP and RT-RPA, offer rapid detection under field conditions without the need for sophisticated laboratory infrastructure. In contrast, next-generation sequencing (NGS) enables comprehensive virus identification and evolutionary analyses but remains comparatively expensive and technically demanding (Table 3). Therefore, selection of an appropriate diagnostic approach should be guided by the intended application, available resources, and required level of sensitivity.

REVERSE TRANSCRIPTION LOOP-MEDIATED ISOTHERMAL AMPLIFICATION (RT-LAMP)

RT-LAMP was developed for ChiVMV detection by Banerjee *et al.* (2016) and subsequently optimized in later studies. The assay employs four to six primers targeting conserved regions of the NlB or coat protein genes and amplifies viral RNA under isothermal conditions (60–65 °C). RT-LAMP enables reliable detection of ChiVMV within 30–45 minutes and exhibits sensitivity comparable to, or greater than, conventional RT-PCR, making it suitable for rapid field diagnosis.

REVERSE TRANSCRIPTION RECOMBINASE POLYMERASE AMPLIFICATION (RT-RPA)

RT-RPA is a more recent isothermal amplification

technique for ChiVMV detection. Developed by Jiao *et al.* (2020), the assay targets the coat protein gene and operates efficiently at 37–42 °C, producing results within approximately 20–25 minutes. Because it requires only minimal equipment and tolerates crude plant extracts, RT-RPA is particularly well suited for field surveillance, quarantine inspections, and rapid disease diagnosis in resource-limited environments.

The introduction of next-generation sequencing (NGS) has enabled full-genome sequencing of ChiVMV isolates, and novel variants and recombination events could be discovered (Zhou *et al.*, 2021). NGS facilitates unbiased detection of mixed infections and has disclosed substantial intra-species diversity of ChiVMV populations. In combination with bioinformatics tools, NGS helps to design more robust diagnostic primers and probes that are able to manage the sequence diversities among global isolates (Hilt and Ferrieri, 2022). Primer-BLAST and AmpliX and OligoAnalyzer *in silico* tools are now commonly being utilized to design and test ChiVMV-specific primers prior to lab work. These methods also guarantee specificity of the targets, avoid off-target amplification and will assist in calculating the anticipated amplicon sizes using reference genome accessions. Altogether, the development of ChiVMV diagnostics could be described as a shift toward the laboratory-based serological tests toward the rapid field-deployable molecular devices. The emerging trends in diagnostic approaches will probably be a combination of portable detection systems and smartphone-based imaging or microfluidic biosensors in the real-time monitoring of viral outbreaks (Kozyreva *et al.*, 2021; Jullien, 2013).

MANAGEMENT

Management of ChiVMV traditionally relies on host resistance, cultural practices, and vector control. However, ChiVMV populations exhibit substantial genetic variation, and this evolutionary diversity has direct implications for the efficacy of integrated pest management (IPM) and host resistance programs (Zhoungbogbo *et al.*, 2024; Shilpha and Kang, 2025). Genetic differences among viral isolates, particularly in key genomic regions such as the coat protein (CP) and the helper component–proteinase (HC-Pro), can modulate aphid transmission efficiency and symptom expression, thereby influencing epidemiological outcomes under field conditions (Bhoi *et al.*, 2022; Jiang *et al.*, 2023).

Genetic mapping studies in chilli have identified specific

resistance loci, including both dominant (Cvr1) and recessive (cvr4) genes that confer partial resistance to ChiVMV. Fine-mapping and functional validation of these loci demonstrate that host resistance deployment must consider the prevailing viral genotypes to maintain long-term effectiveness, as distinct ChiVMV lineages may interact differentially with plant defense pathways (Ponnam *et al.*, 2023; Lee *et al.*, 2025). Host resistance programs that do not account for viral genetic diversity risk resistance breakdown due to the adaptive potential of high nucleotide diversity in viral populations, which may facilitate the emergence of variants capable of overcoming specific resistance alleles (LaTourrette and Garcia-Ruiz, 2022).

RNA viruses in general, including potyviruses such as ChiVMV, have high mutation rates due to error-prone replication, resulting in diverse nucleotide variants within local populations (Anuradha *et al.*, 2023). Although the degree of genetic diversity varies by region and isolate, increased nucleotide diversity can expand the adaptive landscape of the virus, affecting both pathogenicity and interactions with host resistance mechanisms (LaTourrette and Garcia-Ruiz, 2022). While recombination has not been universally detected in all ChiVMV populations, it remains a potential evolutionary mechanism that can generate novel genotypic combinations when co-infection by multiple variants occurs (Lakshminarayana Reddy *et al.*, 2024). Such recombination events, if confirmed with robust bioinformatics analyses, may further contribute to genetic diversification and complicate management strategies (Chavhan *et al.*, 2024).

Given this context, disease management must transcend broad descriptions and integrate molecular insights into IPM frameworks (Rai and Rai, 2025). Phytosanitary measures remain fundamental: the use of certified virus-free seed, prompt removal of symptomatic plants, and elimination of weed hosts reduce primary inoculum. Cultural practices such as crop rotation with non-solanaceous hosts and maintenance of field hygiene diminish local virus reservoirs and vector attractants (Tatineni and Hein, 2023; Singh *et al.*, 2025).

Advances in molecular tools, including pathogen-derived resistance strategies, RNA interference and RNA silencing-based technologies, provide additional avenues for developing robust resistance to RNA viruses (Rout *et al.*, 2022). These approaches, when coupled with an understanding of viral genetic variation and host defense

network dynamics, can enhance the durability of engineered resistance (Bonachela, 2024). Periodic molecular surveillance of ChiVMV populations is also recommended to detect shifts in lineage prevalence, emergent variants, and potential recombination signals that could undermine existing management practices or resistance deployment (Chen *et al.*, 2026).

RESISTANCE DEVELOPMENT

Plant viruses cause severe yield losses globally, and the development of resistant cultivars remains the most effective, long-term strategy for their management. Viral diseases have had a long history of research to be controlled since the nineteenth century and the breeding of resistance turned out to be one of the most sustainable methods (Zuo *et al.*, 2024). Resistance can be developed through conventional breeding or genetic engineering approaches (Limenie and Alehegn, 2025; Abebe and Tafa, 2022). Sanford and Johnston (1985) were the pioneers in the idea of developing virus-resistant crops, when they coined the concept of pathogen-derived resistance (PDR). This methodology is one of the significant breakthroughs in the creation of transgenic plants resistant to viruses that now forms one of the foundations of plant virology and molecular breeding (Akhtar *et al.*, 2023).

The basic principle of PDR is to insert the viral genes into the host plants in order to interrupt viral replication or interrupt viral-host interactions. Expression of viral genes in transgenic plants can interfere with viral replication or host-virus interactions and they express proteins or RNA molecules that prevent the replication cycle of invading viruses, therefore, providing protection to the plant (Kasi Viswanath *et al.*, 2023; Zahoor *et al.*, 2025). This method was first proven in tobacco against the Tobacco mosaic virus (TMV) with the help of transformation of tobacco even with the aid of the coat protein (CP) gene. As plant viruses have small genomes, and rely nearly solely on host machinery to replicate, most of their genes can be exploited to produce resistance by either protein-mediated or RNA-mediated processes (Huang *et al.*, 2024; Baulcombe, 2022).

PATHOGEN-DERIVED AND ENGINEERED RESISTANCE

Engineered resistance is a modern and efficient alternative to conventional breeding and relies on the introduction of specific viral or non-viral genes into plant genomes. This approach was pioneered in 1986 when Roger Beachy and colleagues developed TMV-resistant tobacco plants expressing the viral coat protein gene

(Nelson *et al.*, 1987). Transgenic plants expressing these genes exhibited delayed infection or enhanced resistance. Subsequent experiments showed that antiviral resistance could be conferred even by non-translatable viral RNA sequences, and thus RNA-mediated resistance was identified as a powerful antiviral response (Sun *et al.*, 2020).

Resistance can be engineered using pathogen-derived transgenes, natural resistance (R) genes or even non-pathogenic source genes. The expression of genes of viral coat protein, replicase or movement proteins may directly interfere with viral disassembly, translation or replication and lead to delayed or suppressed infection. However, RNA-mediated mechanisms that entail post-transcriptional silencing of genes have been the most favored one owing to their high efficiency and heritability (Gaucherand and Gaglia, 2022; Prasad *et al.*, 2024).

RNA SILENCING MECHANISMS

The RNA silencing mechanism is an essential antiviral defense in plants, and it operates by the sequence-specific degradation of the viral RNA by small RNAs. Napoli and Van der Krol were the first researchers to observe this phenomenon in transgenic petunia plants when overexpression of chalcone synthase surprisingly resulted in flower color loss a process also known as “cosuppression” (Van der Krol *et al.*, 1988; Napoli *et al.*, 1990; Okuda *et al.*, 2026). RNA silencing was subsequently discovered as a sequence-specific mechanism which degrades viral RNA and it acts as a plant immune system (Baulcombe, 2022). It is a pathway which includes Dicer-like (DCL) enzymes recognizing viral double-stranded RNA intermediates and cleaving them into small interfering RNAs (siRNAs). These siRNAs are integrated into RNA-induced silencing complexes (RISC) that contain Argonaute (AGO) proteins that in turn mediate the destruction of matching viral RNAs and hence limit the accumulation of the virus (Akbar *et al.*, 2022). Recent works on the Chilli veinal mottle virus (ChiVMV) have shown numerous layers of host-virus interactions that come to convergence or are affected by the defence mechanisms of RNA silencing (Shingote *et al.*, 2022).

As it was proven by Riaz *et al.* (2021), a partial resistance to the virus was obtained in *Nicotiana benthamiana* with the help of the stable expression of the ChiVMV gene of the coat protein (CP). This resistance is attributed to pathogen-derived resistance (PDR), whereby the

expression of viral sequences induces the RNA silencing machinery leading to an increase in the formation of siRNAs that is similar to the viral genome. These siRNAs

precondition plant to respond more quickly to silencing under viral challenge which leads to less accumulation and no severe symptoms.

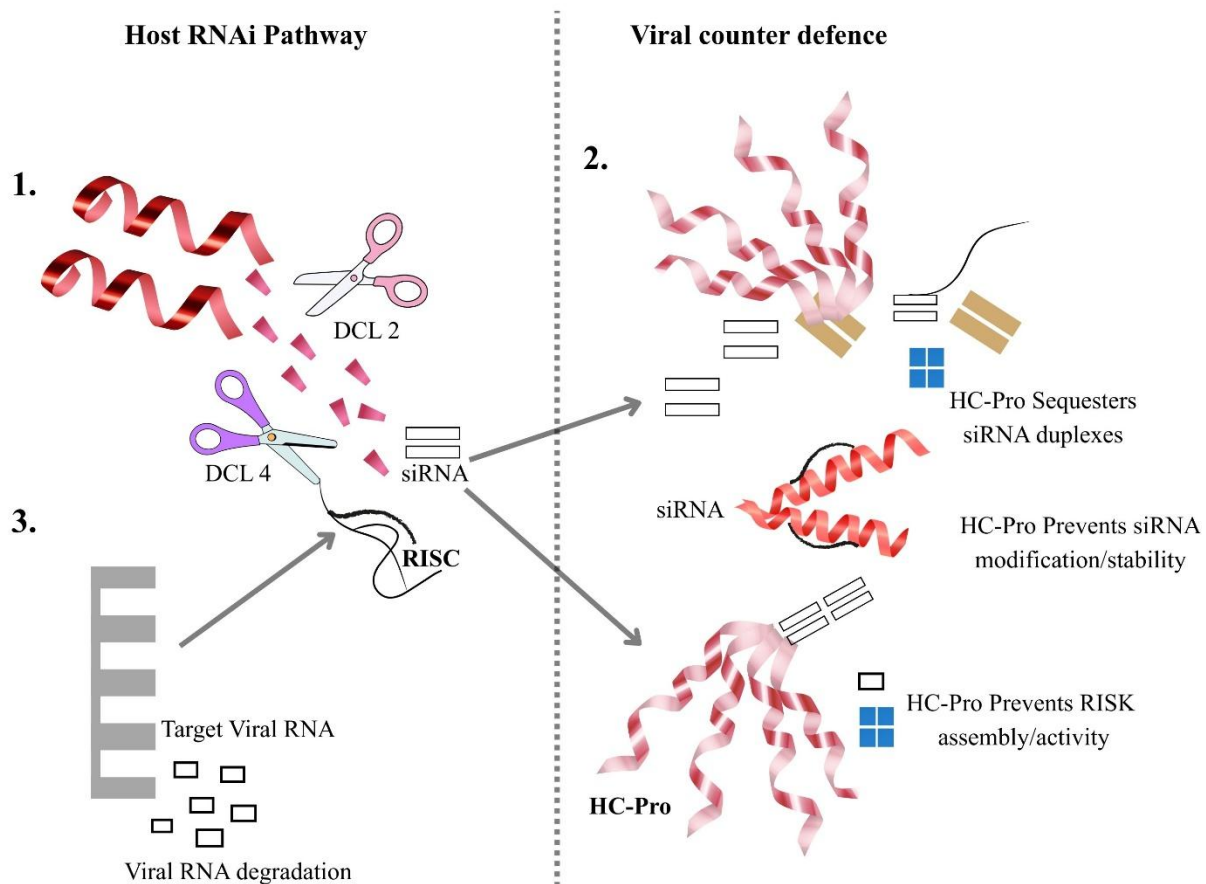


Figure 4. Host RNAi pathway and HC-Pro-mediated suppression of antiviral defense.

Additional information on the host defense network by discovering miR827 as a favorable regulator of antiviral defense. MiR827 overexpression in *N. benthamiana* improved resistance to ChiVMV and suppression leads to susceptibility. miR827 antiviral property was associated with reactive oxygen species (ROS) and salicylic acid (SA) signaling, and was indicated to target fructose-1,6-bisphosphatase (FBPase), which is an important enzyme in carbon metabolism (Tang *et al.*, 2024). miR827-mediated regulation was suggested to combine RNA silencing with metabolic and hormonal pathways to boost immunity because silencing FBPase augmented resistance (Chen *et al.*, 2024). This demonstrates the complicated cross-communication between the RNA silencing and SA/ROS-mediated defense signals in infection of ChiVMV (Val-Torregrosa *et al.*, 2022). Further post-transcriptional regulation has been found to

be involved in viral restriction by other studies. Ji *et al.*, (2023) also stated that the infection of ChiVMV triggers the activation of autophagy-related genes (ATGs) and direct interaction of ATG8f with the viral protein 6K2, which causes autophagic degradation. Inhibition of autophagy by silencing ATG8f or inhibitors of autophagy augmented the virus accumulation and autophagy activation decreased infection, respectively. In a similar manner, NtG3BPL1, which is a G3BP-like protein, was also found by Peng *et al.*, (2024) to be a positive regulator of antiviral response that can interact with the ChiVMV 6K2 protein and induce its degradation via autophagy pathway. These findings suggest that autophagy, which tends to co-operate with RNA silencing, is a key factor in the breakdown of viral components and inhibition of ChiVMV growth.

Along with these mechanisms, there are also host

metabolic enzymes and proteins concerning defense factors and their influence on the outcome of infection. Yang *et al.* (2022) discovered that Glucose-6-phosphate dehydrogenase (G6PDH) negatively regulates viral accumulation. In the meantime, Huang *et al.*, (2025) demonstrated that overexpression of CaPR1 classic pathogenesis-related (PR) gene-enhanced ChiVMV resistance, which reduced viral accumulation and disease severity. This supports the relationship between RNA silencing, hormonal signaling and defense gene activation in resistance mediation as RNA silencing can be activated by SA signaling as well as PR1 expression.

Collectively, such studies indicate that the interactions between ChiVMV and plants can be characterized as complex and multilayered defense mechanisms. The molecular insights discussed above provide a foundation for practical disease management strategies against ChiVMV. RNA silencing is a key antiviral response, which is facilitated and regulated by miRNA, ROS, SA signaling and autophagy-mediated viral protein degradation. Understanding the molecular crosstalk among these pathways may facilitate the development of sustainable and broad spectrum resistance to ChiVMV in chilli and other related crops. However, these insights support the development of durable resistance strategies, improve molecular diagnostic tools for early detection and guide surveillance efforts to anticipate resistance breakdown in chilli infected with this virus.

INTEGRATED DISEASE MANAGEMENT FRAMEWORK FOR CHIVMV

Effective management of Chilli veinal mottle virus (ChiVMV) requires the integration of multiple complementary approaches rather than reliance on a single control strategy. Sustainable disease suppression is best achieved through an integrated disease management (IDM) framework (Nalla *et al.*, 2023; Shilpha and Kang, 2025).

The foundation of this approach involves the deployment of resistant cultivars whenever available, coupled with the use of virus-free planting material to minimize primary inoculum sources. Recent advances in molecular mapping and resistance breeding have identified promising resistance loci that may contribute to the development of durable ChiVMV-resistant cultivars (Ponnam *et al.*, 2023; Lee *et al.*, 2025). Regular field surveillance and early diagnosis using serological and molecular techniques facilitate timely detection of infections and support informed management decisions

(Jiao *et al.*, 2020; Lakshminarayana Reddy *et al.*, 2024).

Vector management remains a critical component of ChiVMV control and should include monitoring of aphid populations, elimination of alternative host plants, and implementation of environmentally responsible vector suppression strategies. Since aphid-mediated transmission plays a central role in disease spread, effective vector management can substantially reduce secondary infections within crop fields (Guo *et al.*, 2022; Falla and Cunniffe, 2024). Cultural practices such as rouging infected plants, weed management, crop sanitation, and adjustment of planting schedules further contribute to limiting virus dissemination and reducing inoculum pressure (Nalla *et al.*, 2023).

Emerging biotechnological approaches, including RNA interference (RNAi), CRISPR/Cas-based technologies, and marker-assisted breeding, offer additional opportunities for enhancing resistance and strengthening long-term disease management programs (Akbar *et al.*, 2022; Kasi Viswanath *et al.*, 2023; Shilpha and Kang, 2025). The successful implementation of IDM depends on the coordinated interaction of these approaches under field conditions. Integrating resistant cultivars, early diagnostics, vector management, cultural practices, and advanced breeding technologies can reduce disease pressure, delay the emergence of new viral variants, and improve the sustainability of chilli production systems affected by ChiVMV.

EVOLUTIONARY IMPLICATIONS AND FUTURE RESEARCH DIRECTIONS

Despite considerable advances in the characterization of Chilli veinal mottle virus (ChiVMV), important questions regarding its evolutionary dynamics remain unresolved. Similar to other RNA viruses, ChiVMV exhibits a high evolutionary potential owing to the error-prone nature of viral RNA-dependent RNA polymerases, which continuously generate genetic variation within virus populations. This genetic variability provides the raw material for adaptation to different hosts, ecological conditions, and management interventions, ultimately influencing virus fitness, pathogenicity, and epidemiological success (Riaz *et al.*, 2018; LaTourrette and Garcia-Ruiz, 2022; Singh *et al.*, 2023).

Phylogenetic analyses have consistently demonstrated the presence of geographically structured ChiVMV populations across Asia, suggesting that regional diversification and local adaptation have contributed to

the emergence of distinct viral lineages (Tsai *et al.*, 2008; Rao *et al.*, 2020; Devi *et al.*, 2022). The clustering of isolates according to their geographical origin may indicate restricted gene flow among some populations and highlights the importance of regional epidemiological surveillance for monitoring the emergence and spread of novel variants. Population structure analyses have been increasingly used to investigate viral genetic differentiation, evolutionary dynamics, and potential patterns of virus spread (Çelik *et al.*, 2022).

In addition to mutation, recombination represents a major evolutionary force shaping the diversity of plant RNA viruses. Evidence of recombination has been reported in several ChiVMV isolates, indicating that exchange of genetic material may contribute to the emergence of novel genotypes with altered biological properties (Ahmad and Ashfaq, 2018; Rao *et al.*, 2020). Recombination can accelerate viral adaptation by generating new genetic combinations that may influence virulence, host range, and transmission efficiency. However, the frequency of recombination events and their contribution to long-term ChiVMV evolution remain poorly understood and warrant further investigation.

Selection pressures imposed by resistant cultivars, host defense mechanisms, and environmental conditions may further influence the evolutionary trajectory of ChiVMV populations. Positive selection acting on viral proteins involved in replication, movement, and host interactions could facilitate the emergence of adaptive variants capable of overcoming resistance barriers. This possibility is particularly relevant given the increasing deployment of ChiVMV resistance genes such as Cvr1 and cvr4 in pepper breeding programs (Lee *et al.*, 2025). The long-term durability of resistance therefore depends not only on the effectiveness of resistance loci but also on the evolutionary capacity of virus populations to generate resistance-breaking variants.

Future research should focus on genome-wide population analyses, estimation of mutation rates, identification of recombination hotspots, and assessment of selection signatures across ChiVMV genomes. Furthermore, climate-driven changes in temperature regimes, vector abundance, and host distribution may alter virus epidemiology and accelerate evolutionary processes. Integrating genomics, population genetics, epidemiology, and resistance breeding will be essential for predicting future disease risks and developing durable management strategies against ChiVMV.

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