



Virome of major seed spice crops: current status, disease surveillance, and biosecurity

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Abstract

High-throughput sequencing (HTS) has changed how researchers detect and characterise plant viruses, shifting from single pathogens to whole viral communities, or viromes, associated with a crop. The major seed spice crops cumin (*Cuminum cyminum*), coriander (*Coriandrum sativum*), fennel (*Foeniculum vulgare*) and fenugreek (*Trigonella foenum-graecum*) are grown on more than four million hectares worldwide and account for over USD 3 billion in annual trade. Yet their viral diseases and viromes remain poorly documented. This review synthesises published research from 1972 to 2025, emphasising recent HTS-enabled discoveries, and provides a consolidated overview of the viruses reported in these crops to date. To date, researchers have recorded more than 22 virus species from eight viral families. Recent additions include Beet curly top virus in coriander in the USA, three novel viruses in Indian coriander (among them the first enamovirus reported from the Apiaceae), the carrot motley dwarf complex in cilantro and fennel, Coriander cytorhabdovirus 1 in Chile, Vanilla distortion mosaic virus as the first virus reported in cumin, and four begomovirus complexes in fenugreek across South Asia. We also consider pea seed-borne mosaic virus in Australian fenugreek a specific biosecurity concern. However, seed transmission rates in this host are unknown; in pea, seed transmission approaches 100%. The contributions of dsRNA enrichment, small RNA sequencing and AI-assisted analytical tools to virus discovery are discussed. The main gaps are the absence of HTS-based virome surveys in several major producing countries, limited knowledge of vectors and epidemiology, and scarce data on seed transmission. We argue that seed spice virology should be reframed as a seed-trade biosecurity problem, and that virome data should be part of phytosanitary risk assessment and seed health certification, not surveillance alone. Priorities include virome-guided resistance breeding, stronger surveillance, and integrating HTS into seed certification systems.

Keywords: virome, seed spices, biosecurity

Introduction

Advances in high-throughput sequencing (HTS) have reshaped plant virology by enabling rapid, sensitive detection of both known and previously unknown viruses (Kreuze *et al.*, 2009; Adams *et al.*, 2009). These technologies extended virus research beyond individual pathogens to entire viral communities, known as viromes, and have improved understanding of virus diversity, evolution and epidemiology in agricultural systems (Kreuze *et al.*, 2009). Plant viruses are an increasing constraint on crop production worldwide. Climate change, agricultural intensification, international trade and the

movement of planting material all create new openings for virus emergence and spread (Jeger, 2020; Uke *et al.*, 2022). Interactions among multiple viruses within a single host can also alter disease development and epidemic dynamics, although these relationships are still poorly understood in most cropping systems (Syller, 2012; Tollenaere *et al.*, 2016). The concept of the plant virome emerged from microbiome research and refers to the full set of viruses present in a host or environment (Berg *et al.*, 2020). Virome studies can cover individual plants, insect vectors, weeds, whole fields, and environmental reservoirs such as soil and water (Rosario *et al.*, 2015; Fontenele *et*

al., 2021). Applying HTS and viral metagenomics has improved understanding of viral diversity and has revealed many previously undetected viruses in agricultural systems (Al Rwahnih *et al.*, 2011).

Seed spice crops, in particular coriander (*Coriandrum sativum*), cumin (*Cuminum cyminum*), fennel (*Foeniculum vulgare*) and fenugreek (*Trigonella foenum-graecum*), are agricultural commodities of substantial economic and nutritional value. They are grown on more than four million hectares worldwide and contribute over USD 3 billion annually to global trade (Spice Board of India, 2021). India is the largest producer and exporter of seed spices and is therefore central to the global seed spice supply chain (Spice Board of India, 2021). Despite this, plant virologists have paid limited attention to seed spice crops. Most earlier studies relied on symptom-based diagnosis, serology and targeted PCR, and reported only a small number of known viruses (Jones and Kehoe, 2016). As a result, the diversity, distribution, transmission biology, and epidemiological significance of viruses infecting these crops remain poorly understood. HTS has exposed a large fraction of viruses that escape conventional diagnostics. A recent meta-transcriptomic study of *Cnidium officinale* (Apiaceae) identified 31 viruses, including 22 novel species, which reveals the extent of viral diversity within apiaceous crops (Kang *et al.*, 2025). Similar HTS-based work has uncovered several previously unknown viruses in coriander, fennel and fenugreek, showing that seed spice viromes are more complex than earlier surveys suggested (Sidharthan *et al.*, 2023; Alcalá-Briseño *et al.*, 2023). Important gaps remain. No HTS-based virome survey has been reported for cumin, and comprehensive RNA virome studies in fenugreek are still lacking. Data on seed transmission, vector ecology, virus-host interactions and resistance sources are also limited. Information in these aspects is crucial as seed spices are traded globally, and seed movement can carry viruses over long distances between production regions (Jones and Naidu, 2019). Better knowledge of seed spice viromes is therefore needed for disease surveillance, resistance breeding, seed health testing and biosecurity planning.

This review has five aims. First, to compile and synthesise published information on viruses reported from coriander, cumin, fennel and fenugreek, with an emphasis on recent HTS-enabled discoveries. Second, to trace the shift from conventional diagnostics to HTS and AI-assisted bioinformatics for virus detection. Third, to review current knowledge of seed transmission, vector relationships and epidemiology in these crops. Fourth, to assess how virome data and HTS diagnostics can inform seed health testing, pest risk assessment and phytosanitary decisions. Fifth, to identify the main research gaps and future priorities for virome surveys, biological characterisation, resistance breeding and biosecurity in seed spice production systems. Throughout, seed-trade biosecurity is the central theme, as

virome data have the greatest practical relevance here and existing knowledge gaps pose the most significant regulatory challenges.

Botanical and epidemiological context of seed spice crops

Coriander, cumin, fennel and fenugreek are grouped as seed spices for culinary and economic reasons, but they differ considerably in botanical relationships and virus associations. Coriander, cumin and fennel belong to the Apiaceae (*Umbelliferae*), whereas fenugreek is a member of the Fabaceae (*Leguminosae*) (Peter and Nybe, 2006). Within the Apiaceae, coriander, cumin and fennel fall under the subfamily Apioideae; fenugreek is included among seed spices for agronomic and culinary reasons rather than taxonomic affinity (Peter and Nybe, 2006). These differences directly affect virus diversity and epidemiology. The three apiaceous crops share several closely related virus groups, particularly potyviruses such as Celery mosaic virus (CeMV), Carrot virus Y (CarVY), and apium virus Y (ApVY), which are common across Apiaceae (Latham and Jones, 2004). Aphids, especially *Cavariella aegopodii* and related species, mainly transmit these viruses and act as efficient non-persistent vectors among apiaceous hosts (Latham and Jones, 2004). Fenugreek, by contrast, is exposed to a different set of viruses because of its closer relationship to grain legumes, and can host viruses common in legume and mixed vegetable systems, including several begomoviruses (Sattar *et al.*, 2023). Fenugreek may therefore act as an epidemiological bridge between seed spices, legumes and vegetables, moving viruses across agricultural ecosystems. Historically, researchers recorded few viruses from these crops. Before HTS, researchers documented roughly 8 to 10 virus species across the four crops, mostly from Europe and Australia, using ELISA or RT-PCR (Jones and Kehoe, 2016). That apparent simplicity reflected the limits of the available diagnostics rather than the true composition of the virome (Maina *et al.*, 2024).

Research on seed spice viruses lags behind research on viruses affecting major cereal, vegetable, and horticultural crops. Information on virus diversity, distribution, vector relationships, seed transmission and host resistance remains fragmented. Geographic bias has widened this gap, since major producing regions such as India, Iran and Morocco have received comparatively little study (Latham and Jones, 2004). HTS has begun to change this by revealing previously unknown viruses and complex virus associations, which indicates that these viromes are considerably more diverse than once recognised (Massart *et al.*, 2017; Alcalá Briseño *et al.*, 2023). This botanical and epidemiological framing sets up the crop-by-crop virome profiles that follow.

Virome profiles of major seed spices

Cumin (*Cuminum cyminum* L.)

Cumin is the most economically important seed spice by production and trade. Yet, it is one of the least studied from a virological standpoint. Jones *et al.* (2005) reported that Carrot virus Y (CarVY) infects cumin systemically, inducing severe symptoms including reddening, leaf necrosis, stunting, wilting, weak stems, and eventual plant death, indicating its high susceptibility under experimental conditions. Despite this susceptibility, no evidence of seed transmission was detected, and natural field infections in cumin have not been reported. Vanilla distortion mosaic virus (VDMV), reported from Rajasthan, is the only virus formally recognised with cumin as a primary host (Meena *et al.*, 2022). No comprehensive HTS-based virome survey has been carried out in cumin, and no information exists on virus vectors, seed transmission, resistance sources, or the geographic distribution of VDMV. Given the large-scale cultivation of cumin in Rajasthan and Gujarat, India, and in Iran and Morocco, the lack of information on cumin viruses is a major gap for surveillance and biosecurity.

Coriander (*Coriandrum sativum* L.)

Coriander is the most extensively studied seed spice for virus diseases, with reports from Chile, California, India, Iran and Europe (Grimm *et al.*, 2021; Zamorano *et al.*, 2024). Early work identified coriander as a symptomless host of Watermelon mosaic virus (WMV) through mechanical transmission and back-inoculation (Grogan *et al.*, 1959). Natural infection causing disease was not confirmed until Cespedes *et al.* (2022) used HTS to detect WMV in field-grown coriander (*Coriandrum sativum*) with leaf mottling symptoms in California. This case makes two points: HTS improves detection, and viruses can establish in new hosts that share space with, or grow next to, existing crops. Beet curly top virus (BCTV) has caused serious outbreaks in coriander-growing areas of Washington State, USA, where incidence reached 40 to 90 per cent in the Columbia Basin. Circulifer tenellus transmits the virus in a persistent-propagative manner, making management difficult (Grimm *et al.*, 2021). BCTV infection also alters essential oil composition, particularly linalool content, and no resistant source of coriander is currently available (Saadati *et al.*, 2024). Recent HTS work in India identified three novel viruses: CsDPV1, CsDPV2 (Partitiviridae) and CsEV, the first enamovirus reported from an Apiaceae host, whose umbravirus helper has not yet been identified (Sidharthan *et al.*, 2023). In California, a carrot motley dwarf (CMD)-like complex involving FvPV, Pastinaca umbravirus 1, TorCLV, tobamovirus-like associated RNAs and a novel parsley polerovirus showed how complex multi-virus infections can be in Apiaceae crops (Erickson *et al.*, 2024; Latham and Jones, 2004). Coriander cytorhabdovirus 1 (CoCRV1) was recently reported from Chile, the first cytorhabdovirus identified in a seed spice crop, although its host range, transmission biology and distribution remain unknown (Zamorano *et al.*, 2024). Several other insect-borne viruses have been recorded in coriander worldwide. Aphid-transmitted viruses include coriander feathery red-vein virus

(CFRVV), Alfalfa mosaic virus (AMV), Celery mosaic virus (CeMV), Apium virus Y (ApVY), Carrot virus Y (CarVY), Carrot red leaf virus (CaRLV) and Carrot mottle virus (CaMoV) (Pemberton *et al.*, 1974; Alhubaishi *et al.*, 1987; Tian *et al.*, 2008; Smith *et al.*, 2011). Groundnut ringspot virus is thrips-transmitted (Lima *et al.*, 1999), while Lettuce chlorosis virus (LCV) and Beet pseudo-yellows virus (BPYV) are whitefly-transmitted (Alabi *et al.*, 2020). Taken together, these reports indicate that the range of viruses able to infect or co-infect coriander, and our capacity to detect them, is expanding as HTS methods improve. Experimental studies by Jones *et al.* (2005) showed that coriander is a systemic host of Carrot virus Y (CarVY), developing severe symptoms including vein clearing, mosaic, leaf necrosis, weak stems and pronounced stunting after aphid-mediated infection. Field surveys, however, failed to detect natural CarVY infection in coriander, which suggests it is unlikely to act as a significant virus reservoir under field conditions. As in several horticultural crops, poor weed and insect management around coriander may still raise the risk of virus movement from alternative reservoir hosts through aphid vectors.

Fennel (*Foeniculum vulgare* Mill.)

Fennel has received more attention than cumin, mainly through reports of CeMV, CarVY and ApVY in Europe (Latham and Jones, 2004). Data on seed transmission of CeMV, CarVY and ApVY in fennel are missing, which is an important gap for seed certification and international seed trade (Latham and Jones, 2004; International Plant Protection Convention, 2019). The HTS-based transcriptome of the California cilantro disease complex identified *Foeniculum vulgare* polerovirus (FvPV) in this host, linking fennel directly to this emerging association (Sidharthan *et al.*, 2022; Erickson *et al.*, 2024). Researchers first identified FvPV through bioinformatic mining of publicly available NCBI Transcriptome shotgun assembly (TSA) datasets from fennel leaves collected in Italy, which revealed partial viral genome sequences and highlighted the utility of transcriptome-based virus discovery (Sidharthan *et al.*, 2022). FvPV shares 88.5–89.1% nucleotide identity with partial RNA-dependent RNA polymerase (RdRp) sequences previously assigned to Fennel motley virus (FMV), indicating that some earlier FMV detections may actually correspond to FvPV (Erickson *et al.*, 2024). Fennel is recognized as a natural host of Cucumber mosaic virus (CMV), and its potential role was identified in the epidemiology of CMV within diverse cropping systems (Dragich *et al.*, 2014). Parrella *et al.* (2003) and Dikova (2011) reported establishing experimental transmission of Tomato spotted wilt virus (TSWV) on *F. vulgare*. Seasonal monitoring of fennel in Bulgaria by serological methods revealed the occurrence of Alfalfa mosaic virus (AMV), Cucumber mosaic virus (CMV), Tomato spotted wilt virus (TSWV), Tobacco mosaic virus (TMV), and Celery mosaic virus (CeMV), with AMV, CMV, TSWV, and TMV showing higher virus titres during summer than in spring. The increased viral incidence was closely associated with rising aphid populations, highlighting the value of vector management and seasonal surveillance in fennel (Dikova and Lambev, 2014). No HTS-based virome survey of fennel has been reported from major production regions, and the global

distribution and prevalence of FvPV and the CMD-like complex in fennel remain poorly understood.

Fenugreek (*Trigonella foenum-graecum* L.)

Because fenugreek belongs to the Fabaceae, it is exposed to a distinct group of viruses associated with legumes and mixed cropping systems (Peter and Nybe, 2006). It is a natural host for Tobacco streak virus (TSV) (Kaiser *et al.*, 1991), Soybean dwarf virus (SbDV), Faba bean necrotic yellows virus (FBNYV) and Beet western yellows virus (BWYV) (Bekele *et al.*, 2005), and an experimental host for AMV (Latham and Jones, 2001), CMV (Iqbal *et al.*, 2011), FBNYV (Franz *et al.*, 1997), Turnip mosaic virus (TuMV) (Fisher and Lockhart, 1976) and Pea enation mosaic virus (PEMV). In Australia, Cucumber mosaic virus (CMV), Turnip yellows virus (TuYV), and Pea seed-borne mosaic virus (PSbMV) were recorded at 90 per cent, 75 per cent, and 20 per cent incidence, respectively, with PSbMV causing complete yield loss under severe infection (Aftab *et al.*, 2018). Because PSbMV shows nearly 100 per cent seed transmission in pea, its seed transmission potential in fenugreek is a key research priority (Jones and Naidu, 2019; Aftab *et al.*, 2018). Fenugreek has also

become a hotspot for begomovirus diversity, with reports of Fenugreek yellow vein Rajasthan virus (FeYVRaV), Ageratum enation virus (AEV), Tomato leaf curl Kerala virus (ToLCKeV), and the DNA-B molecule of Tomato leaf curl New Delhi virus (ToLCNDV), together with Ageratum yellow leaf curl betasatellite, AEV plus AYLCB, and a fenugreek strain of Pedilanthus leaf curl virus (PeLCV) across South Asia (Ashwathappa *et al.*, 2022; Kumar *et al.*, 2023). The broad host range of PeLCV, which includes several solanaceous crops, suggests fenugreek may act as a reservoir that supports Bemisia tabaci-mediated virus spread (Ashwathappa *et al.*, 2022; Sattar *et al.*, 2023). PCR with degenerate geminivirus primers and Southern hybridisation with a tomato leaf curl begomovirus probe detected a begomovirus molecule causing leaf curl in Paan methi or Nagauri fenugreek (*Trigonella corniculata*) in India (Raj *et al.*, 2001). Leaf curl of fenugreek caused by AEV has been reported in India, Pakistan and Nepal (Swarnalatha *et al.*, 2019; Tahir *et al.*, 2015). Table 1 summarises key viruses and virome components reported from seed spice crops.

Table 1. Documented viruses in coriander, cumin, fennel and fenugreek.

Virus	Family	Genome	Host Crop	Detection Method	Key Reference
Watermelon mosaic virus (WMV)	Potyviridae	ssRNA(+)	Coriander	HTS, RT-PCR	Cespedes <i>et al.</i> 2022
Pea seed-borne mosaic virus (PSbMV)	Potyviridae	ssRNA(+)	Fenugreek	ELISA, RT-PCR	Aftab <i>et al.</i> 2018
Celery mosaic virus (CeMV)	Potyviridae	ssRNA(+)	Coriander, Fennel	ELISA, RT-PCR	Fox <i>et al.</i> 2022
Beet mosaic virus (BtMV)	Potyviridae	ssRNA(+)	Coriander	RT-PCR, sequencing	Fox <i>et al.</i> 2022
Turnip yellows virus (TuYV/BWYV)	Solemoviridae (Ploverovirus)	ssRNA(+)	Coriander, Fennel, Fenugreek	ELISA, RT-PCR	Aftab <i>et al.</i> 2018; Fox <i>et al.</i> 2022
Potato leafroll virus (PLRV)	Solemoviridae (Ploverovirus)	ssRNA(+)	Coriander	ELISA	Fox <i>et al.</i> 2022
Artichoke latent virus (ArLV)	Potyviridae	ssRNA(+)	Coriander	RT-PCR	Fox <i>et al.</i> 2022
Coriander cytorhabdovirus 1 (CoCRV1)	Rhabdoviridae (Cytorhabdo virus)	ssRNA(-)	Coriander	HTS metatranscriptome	Zamorano <i>et al.</i> 2024
Beet curly top virus (BCTV)	Geminiviridae (Curtovirus)	ssDNA	Coriander	PCR, Sequencing	Grimm <i>et al.</i> 2021
<i>Coriandrum sativum</i> deltapartitivirus 1&2 (CsDPV1, CsDPV2)	Partitiviridae (Deltapartitivirus)	dsRNA	Coriander	HTS (transcriptomics)	Sidharthan <i>et al.</i> 2023
<i>Coriandrum sativum</i> enamovirus (CsEV)	Solemoviridae (Enamovirus)	ssRNA(+)	Coriander	HTS (transcriptomics)	Sidharthan <i>et al.</i> 2023
CMD complex: FvPV +PasUV1+TorCLV +tlaRNAs+PaPV	Multi-family complex	ssRNA(+)	Coriander, Fennel, Cilantro	HTS metatranscript	Erickson <i>et al.</i> 2024
Vanilla distortion mosaic virus (VDMV)	Potyviridae	ssRNA(+)	Cumin	RT-PCR, sequencing	Meena <i>et al.</i> 2022
Carrot virus Y (CarVY)	Potyviridae	ssRNA(+)	Fennel, Carrot	RT-PCR	Fox <i>et al.</i> 2022
Apiaceae virus Y (ApVY)	Potyviridae	ssRNA(+)	Fennel, Carrot	RT-PCR	Fox <i>et al.</i> 2022
<i>Foeniculum vulgare</i> polerovirus (FvPV)	Solemoviridae (Ploverovirus)	ssRNA(+)	Fennel, Coriander	HTS	Erickson <i>et al.</i> 2024
Cucumber mosaic virus (CMV)	Bromoviridae	ssRNA(+)	Fenugreek	ELISA, RT-PCR	Aftab <i>et al.</i> 2018
Fenugreek yellow vein Rajasthan virus (FeYVRaV)	Geminiviridae (Begomovirus)	ssDNA	Fenugreek	RCA, sequencing	Kumar <i>et al.</i> 2023
ToLCKeV+ToLCNDV +betasatellite	Geminiviridae (Begomovirus)	ssDNA	Fenugreek	PCR, sequencing	Ashwathappa <i>et al.</i> 2022
Pedilanthus leaf curl virus (PeLCV)-fenugreek strain	Geminiviridae (Begomovirus)	ssDNA	Fenugreek	RCA, sequencing	Sattar <i>et al.</i> 2023

Virus detection: from symptom to sequencer

The pre-HTS era: serology and RT-PCR

Before HTS, virus detection in seed spice crops relied on symptom observation, biological transmission studies, electron microscopy, ELISA and RT-PCR (Jones and Kehoe, 2016). These methods worked for a limited set of known viruses, mainly in coriander and fennel, but could not identify novel, divergent or cryptic viruses. Agents now recognised, such as deltapartitiviruses and enomovirus-umbrovirus complexes in coriander, went undetected in this period. RT-PCR and Sanger sequencing also required prior sequence information for primer design, which restricted discovery and left cumin and fenugreek largely unexplored apart from a few targeted studies (Massart *et al.*, 2017; Meena *et al.*, 2022).

HTS technologies in seed spice virome research

HTS has moved virus detection from single-pathogen diagnosis towards whole-virome analysis in seed spice crops (Maina *et al.*, 2024). Among HTS approaches, dsRNA-enriched Illumina sequencing is well suited to detecting actively replicating RNA viruses, including the low-titre cytorhabdoviruses and partitiviruses reported in coriander. Small RNA sequencing (sRNA-seq) detects virus-derived small RNAs and has been useful for identifying mixed and latent infections in coriander and fennel (Ho and Tzanetakis, 2014; Sidharthan *et al.*, 2023). Metatranscriptomics, already applied successfully to other Apiaceae species, is a promising route for future virome studies in cumin and fennel, though it needs greater sequencing depth and more demanding bioinformatics (Massart *et al.*, 2017; Kang *et al.*, 2025). Table 2 presents a comparative performance matrix of virus detection methods relevant to surveillance and diagnostics in seed spice crops.

Table 2. Comparative performance matrix for virus detection methods applicable to surveillance of seed spice crops

Method	Sensitivity	Specificity	Cost (Per sample)	Field deployable	Novel virus discovery	Validation required	Best use case
Visual/Symptom inspection	Very Low	Very Low	Very Low (~\$0)	Yes	No	No	Initial field screening; triggers further testing
ELISA	Medium (known viruses)	High (with good antisera)	Low (\$2–5)	Possible (portable kits)	No	Antisera required	Routine surveillance of known viruses; seed lot testing
Bioassay (indicator plants)	Medium	Medium–High	Low (\$5–15)	No	Partial (symptom-based)	Biological confirmation	Koch's postulates; detect mechanically transmissible viruses
RT-PCR	High	High	Medium (\$10–25)	Possible (field PCR units)	No	Yes (primers)	Species-specific confirmation; quarantine testing; epidemiological surveys
qPCR / RT-qPCR	Very High	Very High	Medium (\$15–30)	Limited	No	Yes (primers + probes)	Quantitative load estimation; certification testing; seed lot rejection thresholds
dsRNA enrichment + Illumina HTS	Very High (unbiased)	High (with bioinformatics)	High (\$200–500)	No (lab only)	Yes — major tool for virome discovery	Yes (Koch's postulates)	Comprehensive virome surveys; novel virus discovery; regulatory baseline establishment
sRNA-seq (small RNA)	Very High (active + latent)	High	High (\$250–600)	No	Yes — best for cryptic viruses	Yes	Detection of viroids, small RNA-generating viruses; cryptic/latent virome
VirHunter deep-learning	Highest (bioinformatics)	Very High	Low (computational only)	No (cloud/HPC)	Yes — frontier novel detection	Yes (biological confirmation)	AI-powered annotation of HTS contigs; automated virus family classification; unknown sequences

VirHunter and AI-assisted virus discovery

Artificial intelligence has opened new options for virus discovery from HTS data. Tools such as VirHunter use convolutional neural networks to classify assembled contigs as viral or non-viral. They can flag candidates that may represent novel virus taxa in coriander, cumin, fennel and fenugreek datasets (Sukhorukov *et al.*, 2022). These

methods will greatly assist in exploring the largely uncharacterised virome of understudied seed spices. Sequence-based detection alone, however, is not enough for regulatory decisions, and biological validation is still required. Massart *et al.* (2022) proposed a tiered framework that links sequence detection to biological characterisation and phytosanitary risk assessment.

Oxford Nanopore sequencing for decentralised diagnostics

Oxford Nanopore Technologies (ONT), and the portable MinION in particular, offers near-real-time sequencing suited to field diagnostics and seed health testing of coriander, cumin, and other seed spices in cultivating nations such as India, Iran, and Morocco (Badial *et al.*, 2018; Mehetre *et al.*, 2021). Improvements in sequencing chemistry and accuracy have increased its value for rapid genome reconstruction and surveillance. Standardised ONT protocols for seed spice virus detection are not yet available, and its use in these crops is still largely experimental (Maina *et al.*, 2024).

Seed transmission biology

Seed transmission is a major pathway for virus spread in seed spice crops because it lets viruses cross geographic barriers, persist through storage, seeds, and trade, and establish primary infection in newly planted fields (Jones and Naidu, 2019; Maina *et al.*, 2024). Two mechanisms are recognised. In the first mechanism, viruses move systemically from the maternal plant through vascular tissue into the developing ovule and embryo; this route is documented for several RNA viruses, including PSbMV, CMV, and AMV. In the second, virus particles contaminate the seed coat externally, but this route is generally less important because it rarely produces systemic infection of emerging seedlings (Jones and Naidu, 2019). Work in other crops shows that seed transmission rates depend on the stage of crop growth at infection, temperature during seed development, host genotype and virus strain. Infection at earlier stages tends to raise seed transmission. In contrast, high temperatures during seed development often lower it, and rates vary widely among cultivars and strains, from negligible to nearly 100 per cent within a single host species (Massart *et al.*, 2017; Maina *et al.*, 2024). No one has systematically studied these factors in any seed spice crop-virus system. Of the known risks, PSbMV in fenugreek is the clearest unresolved biosecurity concern. Aftab *et al.* (2018) recorded about 20 per cent natural PSbMV incidence in an Australian fenugreek crop, with complete yield loss in infected plots. ELISA testing of harvested seed was negative, but the study was limited by sample size and by the low sensitivity of ELISA for low-titre embryo infections, so the seed transmission question stayed open (Aftab *et al.*, 2018; Jones and Naidu, 2019). Because PSbMV can reach seed transmission rates near 100 per cent in susceptible pea cultivars, even moderate seed transmission in fenugreek could move the virus long distances through international seed trade. This gap points directly to the need for dedicated seed transmission studies, sensitive molecular diagnostics and formal risk assessment for PSbMV and other seed-borne viruses in seed spice crops (Jones and Naidu, 2019; Maina *et al.*, 2024).

Vector ecology and virus epidemiology

The epidemiology of viruses in seed spice crops is shaped by a relatively small group of efficient insect vectors. The ecology, seasonal dynamics and transmission efficiency of these vectors are poorly understood in most major producing regions (Table 3).

Aphid vector guild

Myzus persicae is among the most important and widely distributed aphid vectors, given its broad host range and its ability to transmit many plant viruses. It transmits potyviruses such as CeMV, Beet mosaic virus (BtMV) and CMV non-persistently, and acts as a persistent vector of TuYV in coriander and fennel systems (Latham and Jones, 2004). *Cavariella aegopodii* is another key vector, closely tied to Apiaceae crops and central to the spread of specialist apiaceous viruses. In temperate regions, it overwinters on willow (*Salix* spp.) and migrates to Apiaceae hosts in spring, moving viruses of the CMD-like complex, including FvPV and Pastinaca umbravirus 1 (PasUV1) (Latham and Jones, 2004; Erickson *et al.*, 2024). The seasonal ecology and migration of *Cavariella* species in Indian seed spice regions are largely unknown. Because willow is uncommon in these areas, alternative overwintering hosts and transmission routes may be involved, which is a major gap in current epidemiological knowledge.

Whitefly-mediated begomovirus transmission

The whitefly *Bemisia tabaci* is the principal vector of begomoviruses in fenugreek and transmits all currently reported begomovirus complexes in this crop. Transmission is persistent-circulative, with acquisition and inoculation periods of minutes to a few hours (Navas-Castillo *et al.*, 2011). Different *B. tabaci* cryptic species and biotypes, including MEAM1 (B), MED (Q) and several South Asian lineages, differ in host preference, transmission efficiency, insecticide resistance and invasive potential. The identity and distribution of *B. tabaci* populations associated with fenugreek in Rajasthan, Maharashtra, Uttarakhand and Punjab have not been characterised, and their efficiency in transmitting FeYVRaV, the ToLCKeV-ToLCNDV complex, AEV-AYLCB and the fenugreek strain of PeLCV is unknown (Kumar *et al.*, 2023; Sattar *et al.*, 2023). This limits the development of reliable forecasting models, resistance-management programmes and region-specific vector control (International Seed Federation, 2025).

Weed reservoir networks

Weeds and alternative hosts help harbour virus inoculum and vector populations in seed spice systems. Several wild Apiaceae, including *Anthriscus sylvestris*, *Torilis* spp. and *Daucus carota*, can harbour CeMV, CarVY, PasUV1 and TorCLV. *Salix* species serve as overwintering hosts for the *Cavariella* aphids involved in CMD-like complexes.

Weeds in the Chenopodiaceae and Brassicaceae act as reservoirs for BtMV and TuYV, while solanaceous and malvaceous weeds along field margins can maintain PeLCV and related begomoviruses (Latham and Jones, 2004; Sattar *et al.*, 2023). Despite this importance, systematic weed-reservoir surveys have not been done in the major coriander, cumin, fennel and fenugreek regions

of India, Iran and Morocco. The primary inoculum sources and early-season infection foci therefore remain largely speculative rather than field-verified. Better knowledge of vector ecology and weed-virus networks is needed for disease forecasting, surveillance and integrated virus management in these crops.

Table 3. Vector associations, transmission characteristics, and ecological parameters for viruses in the seed spice crop system.

Virus	Transmission Mode	Primary Vector (s)	Secondary Vector(s)	Weed Reservoirs
CeMV	Non-persistent (Stylet-borne)	<i>Myzus persicae</i> , <i>Cavariella aegopodii</i>	<i>Macrosiphum euphorbiae</i> , <i>Aphis gossypii</i>	Wild Apiaceae: <i>Anthriscus</i> , <i>Torilis spp.</i>
BtMV	Non-persistent	<i>Myzus persicae</i>	Multiple aphids	<i>Beta vulgaris</i> , <i>Chenopodium</i>
TuYV/BWYV	Persistent-circulative	<i>Myzus persicae</i>	<i>Brevicoryne brassicae</i>	Brassica weeds, <i>Chenopodium album</i>
PLRV	Persistent-circulative	<i>Myzus persicae</i>	<i>Macrosiphum euphorbiae</i>	Solanaceae weeds, potato volunteers
AMV	Non-persistent	<i>Myzus persicae</i> , <i>Aphis gossypii</i>	Multiple aphid spp.	Alfalfa, clover, legume weeds
BCTV	Persistent-propagative	<i>Circulifer tenellus</i> (beet leafhopper)	<i>Circulifer opacipennis</i>	Brassica weeds, <i>Atriplex spp.</i> , Amaranthus
CoCRV1 (cytorhabdo virus)	Persistent-propagative (presumed)	Unknown (aphid presumed)	Unknown	Unknown
FvPV (CMD complex)	Persistent-circulative	<i>Cavariella aegopodii</i> (primary)	<i>Myzus persicae</i>	<i>Salix spp.</i> (willow), overwintering host
PasUV1+TorCLV (CMD complex)	Non-persistent (umbravirus)	Requires helper virus (FvPV) for transmission	N/A	Wild Apiaceae, <i>Torilis spp.</i>
FeYVRaV	Phloem-limited (begomo virus)	<i>Bemisia tabaci</i>	None known	Unknown; probably Fabaceae weeds
ToLCKeV+ ToLCNDV complex	Phloem-limited (begomo virus)	<i>Bemisia tabaci</i> (B/MEAM1 biotype)	None	Tomato, Chilli volunteers, Abutilons
PeLCV (fenugreek)	Phloem-limited (begomo virus)	<i>Bemisia tabaci</i> (Q/MED biotype suspected)	None	Solanaceae, malvaceous weeds; 25+ host species
CMV (fenugreek)	Non-persistent	<i>Myzus persicae</i> ; multiple aphid spp.	>60 aphid species reported	Broadest weed reservoir of any plant virus

Virome-informed resistance breeding

Virome-informed resistance breeding aims to develop cultivars resilient not only to individual viruses but to the broader virus communities present in production systems (Massart *et al.*, 2022; Maina *et al.*, 2024). HTS-based virome analyses can identify the viruses associated with a crop, estimate their prevalence and abundance, and detect common mixed-infection patterns. This information can help breeders find resistance sources that hold up in the field, where plants face several viruses at once, rather than

only under single-virus screening (Massart *et al.*, 2022). The approach has already been demonstrated in tomato, where virome profiles combined with resistance mapping identified genotypes with broad-spectrum tolerance under natural field conditions.

In seed spice crops, many economically important viruses belong to the Potyviridae, which makes host-factor-mediated resistance an attractive strategy. The eukaryotic translation initiation factor eIF4E and its isoforms have drawn particular attention because they are essential for the

replication of many potyviruses. Naturally occurring recessive resistance genes, such as *sbm1* in pea and related *eIF4E* variants in pepper and lettuce, give durable resistance by disrupting interactions between the viral VPg and the host translation machinery (Kang *et al.*, 2005; Charron *et al.*, 2008). Within a virome-informed framework, HTS can first identify the dominant potyviruses in coriander, cumin, fennel and fenugreek, including CeMV, CarVY, ApVY, VDMV and PSbMV. Available germplasm can then be screened for natural variation in *eIF4E* and *eIF(iso)4E* and other resistance sources, complemented where transformation systems allow by CRISPR-Cas editing of susceptibility factors (Maina *et al.*, 2024; Massart *et al.*, 2022). Beyond identifying resistance genes, virome data can guide breeding by showing which virus combinations occur most often in the field and are therefore most relevant for gene pyramiding. Virome analyses can also indicate when tolerance, meaning reduced symptoms despite infection, is a more practical objective than complete immunity. Integrating virome information into breeding programmes offers a workable path toward seed spice cultivars with durable, broad-spectrum resistance to the virus communities that HTS now reveals (Massart *et al.*, 2022; Maina *et al.*, 2024).

Research gaps and future priorities

Seed spice virology remains underexplored despite the economic importance of coriander, cumin, fennel, and fenugreek. Gaps persist in virome characterisation, seed transmission, biological validation of newly identified viruses, vector ecology and resistance breeding (Table 4) (Maina *et al.*, 2024).

Research gaps

Virome characterisation is incomplete, especially in cumin and fenugreek. In cumin, only a single RT-PCR-based report exists, and no HTS-based virome survey has been done in any major producing region (Meena *et al.*, 2022). The RNA virome of fenugreek is likewise poorly resolved. Knowledge of seed transmission is limited in all four crops, which creates uncertainty about virus movement through international seed trade (Jones and Naidu, 2019). The seed transmission potential of PSbMV in fenugreek is unresolved despite high reported incidence and substantial yield loss; earlier negative seed tests relied mainly on ELISA and may have missed low-titre embryo infections (Aftab *et al.*, 2018). Seed transmission rates of CsDPV1 and CsDPV2, CeMV, CarVY and ApVY in coriander,

fennel and cumin have not been quantified, which limits reliable risk models and seed certification standards (Sidharthan *et al.*, 2023; Latham and Jones, 2004). Several HTS-detected viruses, including PasUV1, TorCLV, PaPV and tobamovirus-like associated RNAs, have not been biologically validated through infectious clone studies or Koch's postulate-type experiments, so their pathogenic role and regulatory status remain uncertain (Erickson *et al.*, 2024; Massart *et al.*, 2022). Vector ecology is poorly understood, particularly the role of *Bemisia tabaci* in fenugreek-begomovirus interactions and the epidemiological significance of *Myzus persicae* and *Cavariella aegopodii* in Apiaceae-based systems (Navas-Castillo *et al.*, 2011; Latham and Jones, 2004). No virus-resistant cultivar has been developed for any of the four crops, largely because germplasm has not been screened systematically.

Future strategies

Six priorities follow from these gaps. Conduct HTS-based virome surveys in cumin and fenugreek across major producing regions to establish baseline diversity and virus incidence. Determine seed transmission rates of PSbMV, CsDPV1 and CsDPV2, CeMV, CarVY and ApVY through controlled inoculation combined with embryo-focused ELISA and RT-PCR. Screen germplasm at scale in all four crops to identify resistance to economically important viruses such as CeMV, AMV, CMV, TuYV and BCTV. Integrate modern resistance breeding, including CRISPR-based editing of key susceptibility genes. Validate priority HTS-discovered viruses through infectious clone development and Koch's postulate-adapted studies, to separate true pathogens from non-pathogenic virome components. Characterise *Bemisia* cryptic species, aphid population dynamics and weed reservoir networks to support region-specific forecasting and vector management. Finally, fold these advances into risk-based phytosanitary frameworks that treat seed lots as pathways for virus dissemination, and progressively bring HTS into routine seed health testing and certification.

Table 4. Priority research gaps in seed spice crop virology

Gap category	Specific gap	Affected crop(s)	Consequence if unaddressed	Proposed approach
Virome characterization	No HTS virome for cumin and fenugreek from any country	Cumin, fenugreek	Surveillance, risk assessment, breeding targets unknown	sRNA-seq surveys: India (Rajasthan, Gujarat), Iran, Morocco
Koch's postulate validation	VDMV, PasUV1, TorCLV, PaPV, tlaRNAs not validated as pathogens in seed spice hosts	Cumin, coriander and fennel	HTS sequences cannot be regulated without pathogenicity proof	Infectious clone construction; inoculation bioassay; Koch's postulate confirmation
Vector ecology	<i>Bemisia tabaci</i> biotype and begomovirus transmission efficiency on fenugreek entirely uncharacterized	Fenugreek	Cannot model epidemic spread or design vector management; biotype affects host range and insecticide resistance.	Whitefly biotyping from fenugreek fields
Vector Ecology	Weed reservoir community uncharacterized for cumin, coriander, fennel	Cumin, coriander and fennel	Primary inoculum source for annual epidemics unknown	Systematic HTS-based survey of wild plant communities adjacent to spice crop fields in major regions
Resistance breeding	No resistance sources identified against any virus in cumin, coriander, fennel, or fenugreek germplasm	All four crops	No practical tools for growers; entire resistance pipeline dependent on prior germplasm screening	Screen germplasm accessions/ crop from national gene banks
Genomic resources	No reference genome available for cumin	Cumin	QTL mapping, CRISPR design, and MAS for virus resistance impossible without genome	Generate chromosome-scale cumin genome assembly using PacBio HiFi or ONT + Hi-C scaffolding.
.Surveillance	No validated rapid assay (LFA, portable ONT) for any seed spice virus	All four crops	Inability to conduct field-level rapid diagnostics in production regions lacking laboratory infrastructure	Develop and validate LFA kits, validate portable MinION nanopore assay, etc.

Conclusion

Seed spice virology is at an early stage, particularly for cumin and fenugreek, where data on virome composition, seed transmission and key epidemiological parameters remain limited despite the importance of these crops in international trade (Maina *et al.*, 2024). Recent HTS-based studies show that earlier serological surveys underestimated the diversity and complexity of these virus communities. New findings, including CMD-like complexes, deltapartitivirus-enamovirus associations and diverse begomovirus-satellite complexes, have expanded understanding of seed spice viromes (Massart *et al.*, 2022; Sidharthan *et al.*, 2023). Together, they suggest that seed lots may carry partially characterised or unknown virus combinations that move across production regions with limited detection and no resistant cultivars (Maina *et al.*, 2024). The most urgent single question is the seed transmission status of PSbMV in fenugreek; well-designed

studies using controlled inoculation, embryo-targeted ELISA and RT-PCR, and cultivar comparisons could resolve it quickly (Aftab *et al.*, 2018; Jones and Naidu, 2019). Similar work on CeMV, CarVY, ApVY and CsDPV1 and CsDPV2 would give quantitative data for biosecurity and risk assessment (Sidharthan *et al.*, 2023; Latham and Jones, 2004). The tools to address these questions already exist. HTS platforms, AI-assisted pipelines, functional genomics tools such as ALSV-based VIGS, and CRISPR-mediated host-factor modification support virus discovery, functional study and resistance development (Massart *et al.*, 2022). Germplasm resources held by ICARDA, ICAR-NRCSS and related institutions provide a foundation for systematic screening and breeding. By combining virome mapping, seed transmission studies, biological validation, vector ecology research and structured germplasm evaluation, seed spice virology can move from an exploratory field to an

evidence-based one that supports sustainable production, biosecurity and safe seed movement (Maina *et al.*, 2024; Massart *et al.*, 2022).

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Conflict of Interest

The authors declare no conflicts of interest.

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