



RESEARCH ARTICLE

Identification and genomic characterization of a novel tomato leaf curl virus infecting *Alternanthera ficoidea* in Tamil Nadu, India

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Abstract

Begomoviruses are single-stranded DNA viruses that cause significant yield losses in economically important crops and are transmitted mainly by the whitefly, *Bemisia tabaci*. Weeds frequently serve as alternate reservoirs for viruses when major crop hosts are not available, thereby promoting virus persistence and spread. During a survey in 2024 in tomato-growing regions of Coimbatore, Tamil Nadu, *Alternanthera ficoidea* plants exhibiting yellow-green mosaic and yellow vein mosaic symptoms were observed. PCR amplification using begomovirus specific primers PARIV772/PALIC1960 confirmed the presence of begomoviruses in all symptomatic samples, whereas healthy plants showed no amplification. The remaining sequence of the DNA-A genome was amplified using primer pairs GKToLCV-F/GKToLCV-R and PAL1v1978/PAR1c715. BLASTn analysis of the consensus sequence (2764 bp) revealed a 95.12 % nucleotide identity with tomato leaf curl Kerala virus (ToLCKeV) isolate OQ128343. Subsequent investigation of the ToLCKeV isolate found in this study (GenBank accession no: PQ901324) showed significant genetic variation and recombination, with the potential recombination parents being tomato leaf curl Sri Lanka virus (PP935251) and tomato leaf curl New Delhi virus (MK883715). This study provides the first report of ToLCKeV infecting *A. ficoidea*, suggesting its role as an alternative host and potential reservoir during off seasons, contributing to the persistence and spread of this virus. These findings underscore the importance of weed management in integrated approaches to manage leaf curl diseases caused by begomoviruses.

Keywords: *Alternanthera ficoidea*; alternate weed host; begomovirus; tomato leaf curl Kerala virus; whitefly

Introduction

Alternanthera ficoidea (L.) P. Beauv. (Amaranthaceae: Caryophyllales), is an exotic weed native to tropical regions of South America, Central America and the Caribbean. It predominantly thrives in dry tropical biomes. It has spread to several countries, including Bangladesh, Vietnam, Australia and India (1). Although *A. ficoidea* is considered a weed, it has been extensively used as a food source and in traditional medicine, as various secondary metabolites such as carotenoids, phytochemicals, saponins, tannins and polyphenols have been reported in this species (2). Furthermore, several bioactive compounds have been reported in *A. ficoidea*, including amaranthin, betaine, isoamaranthin, kaempferol, quercetin, vitexin and sterols (3). These compounds contribute to its antipyretic, antiseptic, antidiabetic, antimicrobial, anti-inflammatory, diuretic,

antidiarrheal and immunomodulatory properties. *A. ficoidea* has also been traditionally used to treat asthma, bronchitis and hepatitis (4, 5).

Begomoviruses, the largest group of plant viruses and members of the *Geminiviridae* family, have a significant impact on agricultural production worldwide by severely reducing the yields of several economically important crops (6). They contain single-stranded DNA encapsulated in twinned quasi-isometric particles 18-22 nm in size (7). Majority of begomoviruses have two independently encapsulated genomic components, DNA-A and DNA-B, each measuring 2.7-3.0 kb in size. In contrast, some begomoviruses are monopartite, containing only DNA-A (8). These viruses are exclusively transmitted by the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) (9). *B. tabaci* infects a

wide range of hosts, including farm crops and associated weed flora (10). Weeds frequently serve as reservoirs when primary hosts are unavailable, which is essential for the persistence, evolution and spread of begomoviruses.

Species of *Alternanthera* in India have been shown to be infected by *Alternanthera* yellow vein virus and *Alternanthera* leaf curl virus in earlier research, which underscores the function of weeds in hosting and spreading begomoviruses (11, 12). Given the importance of begomoviruses in agriculture and the possibility that *A. ficoidea* could serve as an alternative host, this study aimed to explore and molecularly describe begomoviruses that infect *A. ficoidea* in Coimbatore, Tamil Nadu, India. Determining the viral diversity of this weed species is crucial for assessing its potential contribution to virus epidemiology and for developing effective management strategies for diseases associated with begomoviruses in economically significant crops.

Materials and Methods

Sample collection and DNA extraction

During November 2023, *Alternanthera ficoidea* plants exhibiting yellow-green and yellow vein mosaic symptoms were observed in a field at Karamadai, Coimbatore (11°15'28"N, 76°57'46"E) (Fig. 1). Leaf samples were collected from six symptomatic *A. ficoidea* plants, along with those from asymptomatic (healthy) plants. Genomic DNA was extracted from the collected samples using a modified cetyltrimethylammonium bromide (CTAB) method (13). Approximately 100 mg of leaf tissue was homogenized in 1 mL of preheated CTAB buffer to release the DNA. The homogenized mixture was transferred to a sterile microcentrifuge tube and incubated at 65 °C in a water bath for 45 min. The sample was then centrifuged at 12000 rpm for 10 min and the supernatant was transferred to a fresh microcentrifuge tube. An equal volume of chloroform: isoamyl alcohol (24:1) was added, vortexed for 2–3 sec and centrifuged again at 12000 rpm for 10 min. The aqueous phase was transferred to a new microcentrifuge tube, followed by the addition of 0.8 volumes of ice-cold isopropanol. The mixture was then gently inverted and incubated overnight at -20 °C for DNA precipitation. The precipitated DNA was pelleted by centrifugation at 12000 rpm for 10 min, washed with 500 µL of 70 % ethanol, air-dried and then dissolved in 30 µL of nuclease-free water. The sample was stored at -20 °C for further use.

PCR amplification and sequencing

The presence of begomoviruses in the samples was detected using polymerase chain reaction (PCR) with universal begomovirus primers PARIV772/PALIC1960 (14). PCR reactions were performed in a 40 µL reaction volume containing 20 µL of Taq DNA Polymerase 2x Master Mix RED (Ampliqon, Denmark), 2 µL of each primer (10 pmol/µL), 10 µL of nuclease-free water and 6 µL of template DNA (100 ng/µL). The PCR conditions were as follows: initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 1 min, annealing at 55 °C for 2 min, extension at 72 °C for 3 min and a final extension at 72 °C for 10 min. The primer pairs PAL1v1978/PAR1c715 and GKToLCVF/ GKToLCVR were used to amplify the remaining genome sequence of begomovirus (15). The PCR conditions for PAL1v1978/PAR1c715 were similar to those described above, while the conditions for GKToLCVF/ GKToLCVR were: initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 sec, annealing at 57 °C for 30 sec, extension at 72 °C for 1.5 min and a final extension at 72 °C for 10 min. Additionally, primers UN101/UN102 and beta01/beta02 were used to detect the presence of alpha and beta satellites in the samples (8). The amplified PCR products were visualized on 1 % agarose gel stained with ethidium bromide. PCR products were purified and sequenced bi-directionally using Sanger sequencing (Ms. Biokart India Pvt. Ltd., Bangalore, India). The forward and reverse sequences obtained were trimmed, aligned into a consensus sequence and submitted to the NCBI GenBank database.

Phylogenetic analysis and sequence analysis

A nucleotide sequence similarity search was conducted using BLASTn (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) against sequences available in the GenBank database. The sequences of begomoviruses infecting *Alternanthera* sp. and related begomoviruses from the BLASTn search were retrieved for phylogenetic and sequence demarcation analysis (Supplementary Table 1). The pairwise nucleotide identity of the selected sequences was calculated using the Sequence Demarcation Tool (SDT v1.3), which employs MUSCLE alignment and the percent pairwise identity was determined (16). A phylogenetic tree was constructed using the Maximum Likelihood (ML) method in MEGA XI, employing the Tamura-Nei model with gamma distribution and invariant sites (TN93+G+I) with 1000 bootstrap replicates (17). Phylogenetic trees were visualized and annotated using the Interactive Tree of Life (iTOL) platform (18).



Fig. 1. Yellow vein mosaic symptoms on *A. ficoidea* leaves infected with begomovirus (a, b), compared to healthy control plants (c).

Table 1. Genome organization of DNA-A of ToLCKeV identified in this study

Virus	ORF positions					
	AV2 (nt/aa)	AV1 (nt/aa)	AC3 (nt/aa)	AC2 (nt/aa)	AC1 (nt/aa)	AC4 (nt/aa)
ToLCKeV (PQ901324)	144-491 (348/115)	304-1074 (771/256)	1077-1481 (405/134)	1222-1626 (405/134)	1529-2614 (1086/361)	2155-2457 (303/100)

Nucleotide diversity analysis and neutrality test analysis

A comprehensive analysis of nucleotide diversity and neutrality tests was conducted using a dataset comprising 25 full-length genome sequences sourced from the NCBI database (Supplementary Table 2) and nucleotide diversity parameters such as the number of segregating sites (S), number of haplotypes (h), haplotype diversity (Hd), average number of nucleotide differences (K), nucleotide diversity (π) and mutation rate (θ) were calculated to assess the genetic structure of these viruses using DnaSP v6.12.03 (19).

Recombinant analysis

Recombinant analysis was performed using Recombination Detection Program (RDP) software, version 4.0, which employs seven algorithms: RDP, GENECONV, BootScan, MaxChi, Chimera, SiScan and 3Seq. The analysis was conducted using default parameters with a Bonferroni-corrected p-value threshold of 0.05 to identify potential recombination events. A recombination event was considered valid if it was detected by at least three algorithms (20).

Results

PCR analysis confirmed the presence of begomoviruses in all six symptomatic *Alternanthera* spp. samples, whereas no PCR amplification was observed in healthy plants. Fragments of approximately 1200, 1200 and 900 bp were amplified using the primer pairs PARiv772/PALic1960, PAL1v1978/PAR1c715 and GKTOLCVF/GKTOLCVR, respectively. No amplification was found for primers UN101/UN102 and beta01/beta02, indicating the absence of alpha and betasatellites. The begomovirus sequences obtained after aligning the raw sequences from both primer pairs were merged to obtain consensus sequences. One sequence, 2764 bp in length, was submitted to NCBI (Accession number: PQ901324). The predicted open reading frames (ORFs) of ToLCKeV (PQ901324) are listed in Table 1.

BLASTn analysis of the consensus sequence (PQ901324) generated in this study revealed that it shared 95.12 % nucleotide identity with the tomato leaf curl Kerala virus (ToLCKeV) isolate (OQ128343), which infects beetroot (*Beta vulgaris*) cultivated in Karnataka, India. Based on the species demarcation threshold of 91 % nucleotide similarity for begomoviruses, the begomovirus identified in our study was classified as tomato leaf curl Kerala virus (21). Pairwise nucleotide identity of the related begomoviruses carried out using the Sequence Demarcation Tool (SDT) is shown in Fig. 2.

Phylogenetic analysis based on multiple sequence alignments of begomoviruses showed that our isolate PQ901324 clustered within the tomato leaf curl Kerala virus (ToLCKeV) clade (Fig. 3). It formed a distinct branch closely related to the ToLCKeV isolates infecting tomatoes (EU910141) and fenugreek (MZ648028) in India. The clustering pattern suggests a strong genetic relationship among these isolates, indicating a possible host range expansion of ToLCKeV to *Alternanthera* species. The phylogenetic tree also highlighted a clear divergence of ToLCKeV isolates from other closely related begomoviruses, such as tomato leaf curl Karnataka virus (ToLCKaV), tomato leaf curl Bangladesh virus (ToLCBV), tomato leaf curl Bangalore virus (ToLCBaV) and tomato leaf curl Gujarat virus (ToLCGuV) further supporting its genetic distinctiveness.

Nucleotide diversity analysis of ToLCKeV sequences from India and Pakistan revealed considerable genetic variation (Table 2). A total of 25 sequences were analyzed, with 593 segregating sites (S), 24 haplotypes (h), 646 mutations (θ) and an overall haplotype diversity (hd) of 0.997, indicating a high degree of genetic differentiation among the isolates. The total nucleotide diversity (π) was 0.05136, with an average nucleotide difference (K) of 138.207, suggesting substantial genetic variation within the virus population. Among the individual country-wise isolates, nucleotide diversity analysis revealed that the Indian ToLCKeV sequences (n = 7) had 386 segregating sites (S), nucleotide diversity (π) of 0.05098 and average nucleotide difference (K) of 137.810. Each sequence represented a unique haplotype (h = 7) with a haplotype diversity (hd) of 1.000, indicating complete genetic differentiation. The Pakistani ToLCKeV sequences (n = 18) exhibited higher variation, with S = 432, π = 0.03574 and K = 98.183. Despite a slightly lower haplotype diversity (hd = 0.993), a greater number of mutations (θ = 462) suggested an increased genetic divergence in the Pakistani isolates. Neutrality tests of the ToLCKeV sequences exhibited a negative Tajima's D value (-0.77239) along with negative Fu and Li's F (-1.00288) and D (-0.88903) values (Table 3).

The recombination events detected in this study are summarized in Table 4. The recombination analysis revealed significant evidence of recombination in the ToLCKeV isolate identified in this study. The ToLCKeV isolate (PQ901324) showed recombination with tomato leaf curl Sri Lanka virus (ToLCLKV) (PP935251) and tomato leaf curl New Delhi virus (ToLCNDV) (MK883715), which infect tomato and cucumber, respectively.

Table 2. Nucleotide diversity of ToLCKeV sequences reported from India and Pakistan

Virus	No. of sequences (M)	No. of Segregation sites (S)	No. of haplotypes (h)	Haplotype diversity (hd)	Average nucleotide difference (K)	Nucleotide diversity (π)	No. of mutations (θ)
India	7	386	7	1.000	137.810	0.05098	398
Pakistan	18	432	17	0.993	98.183	0.03574	462
Total	25	593	24	0.997	138.207	0.05136	646

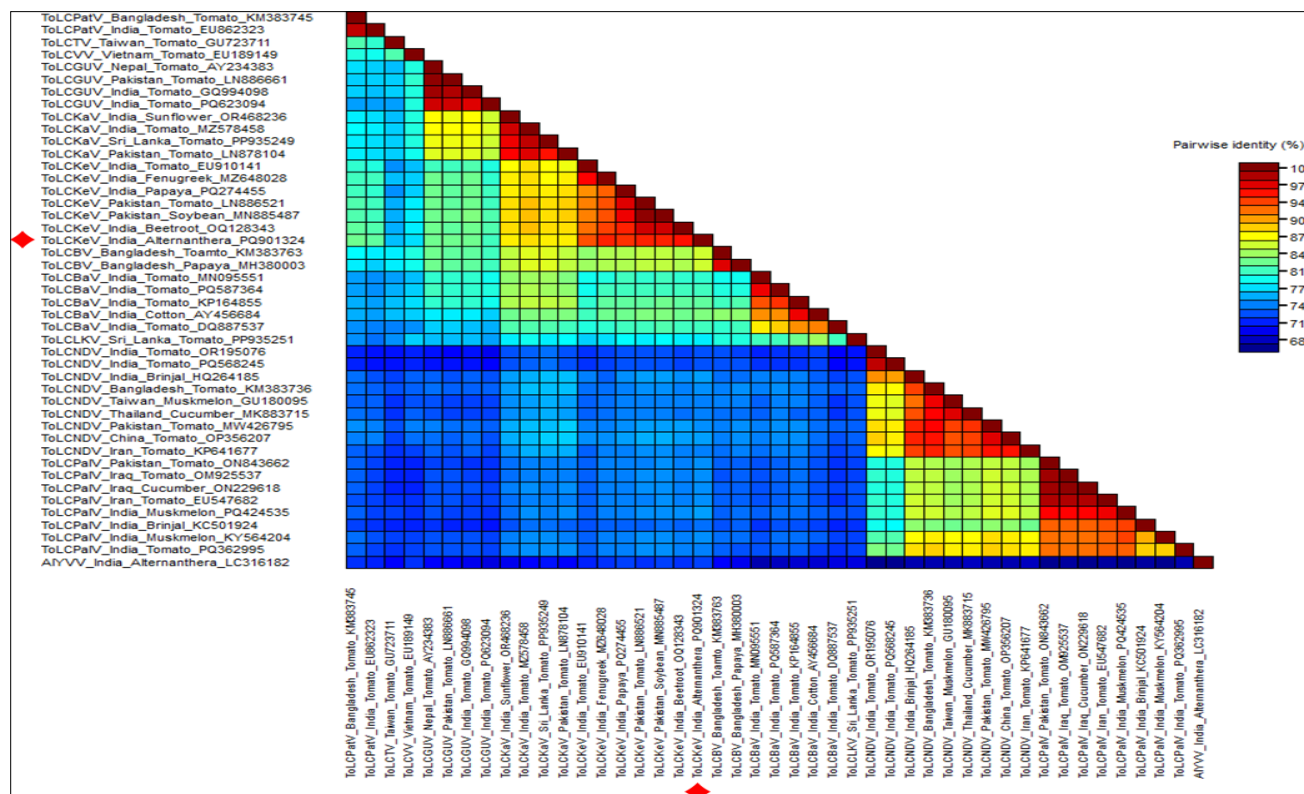


Fig. 2. Pairwise nucleotide identity of the related begomoviruses carried out using the Sequence Demarcation Tool (SDT).

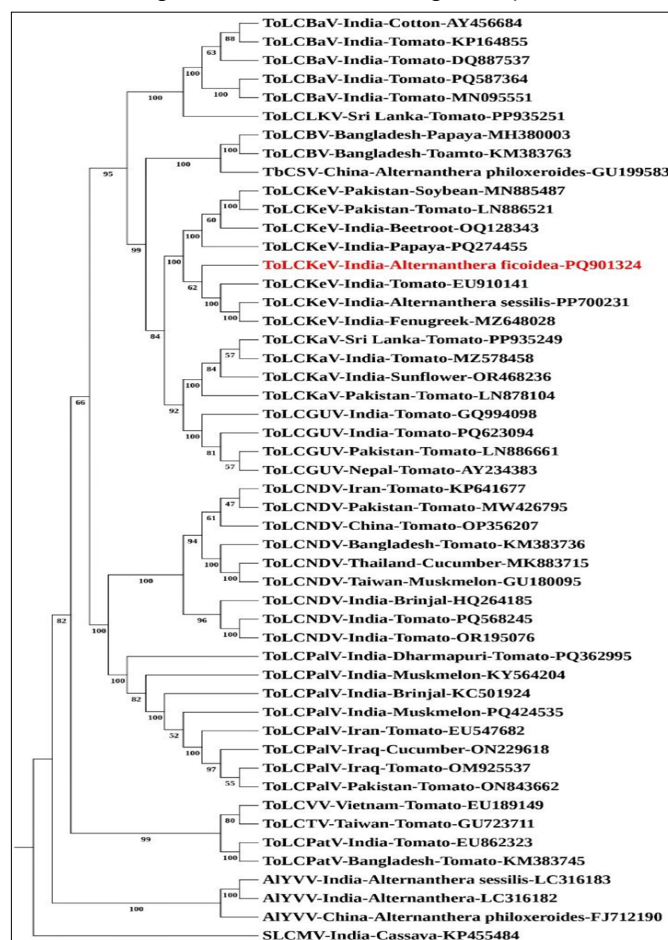


Fig. 3. Phylogenetic tree of nucleotide sequences of ToLCKeV from this study, along with other related tomato leaf curl viruses available in the NCBI/GenBank and International Committee on Taxonomy of Viruses (ICTV) databases as of February 5, 2025. The tree was constructed using the maximum-likelihood (ML) method with MEGA 11 software and 1000 bootstrap replications. The virus species, country, plant host and GenBank accession number are indicated for each isolate included in the analysis. ToLCNDV – Tomato leaf curl New Delhi virus, ToLCPaV – Tomato leaf curl Palampur virus, ToLCLKV – Tomato leaf curl Sri Lanka virus, ToLCBV – Tomato leaf curl Bangladesh virus, ToLCBaV – Tomato leaf curl Bangalore virus, ToLCKaV – Tomato leaf curl Karnataka virus, ToLCKeV – Tomato leaf curl Kerala virus, ToLCGUV – Tomato leaf curl Gujarat virus, ToLCVV – Tomato leaf curl Vietnam virus, ToLCTV – Tomato leaf curl Taiwan virus, ToLCPaV – Tomato leaf curl Patna virus, TbCSV – Tobacco curly shoot virus, AIYVV – Alternanthera yellow vein virus, SLCMV – Sri Lankan cassava mosaic virus (outgroup).

Table 3. Neutrality tests for ToLCKeV sequences reported from India and Pakistan

Virus	Tajima's <i>D</i>	Fu & Li's <i>F</i>	Fu & Li's <i>D</i>
India	-0.89273	-0.90847	-0.79722
Pakistan	-1.14815	-1.10454	-0.86635
Total	-0.77239	-1.00288	-0.88903

Table 4. Recombination analysis of DNA-A of ToLCKeV identified in this study

Virus	Break point	Major parent	Minor parent	RDP	GENECOV	BootScan	Max Chi	Chimera	Si Scan	3seq
PQ901324 ToLCKeV Alternanthera	321-489	PP935251 ToLCLKV Tomato	MK883715 ToLCNDV Cucumber	2.973x10 ⁻⁰²	7.612x10 ⁻⁰³	1.237x10 ⁻⁰²	2.139x10 ⁻⁰²	-	-	1.208x10 ⁻⁰²

Discussion

Begomoviruses are well known for their broad host range and their capacity to evolve through recombination and mutation, enabling them to adapt to new plant species. The detection of ToLCKeV infecting *A. ficoidea* in Tamil Nadu, India, provides critical insights into the role of this weed species as an alternative reservoir host for begomoviruses. The high nucleotide sequence identity (95.12 %) of our ToLCKeV isolate with previously reported isolates infecting fenugreek and tomato suggests possible host range expansion of this virus beyond cultivated crops. This highlights the ability of begomoviruses to infect diverse plant species, including non-cultivated hosts (8, 10).

The role of weeds as reservoir hosts for begomoviruses has been well documented. Several studies from India have reported begomovirus infections in various weed species, emphasizing their role in virus epidemiology. Tomato yellow leaf curl virus (TYLCV) has been shown to use weeds as a “transmission bridge” between cropping and non-cropping seasons, ensuring its survival and spread (22). In China, multiple begomoviruses that infect both cultivated and weed hosts have been identified, including tobacco, papaya, tomato, *Ageratum conyzoides*, *Alternanthera philoxeroides* and *Sida acuta* (23).

In India, natural infections with the tomato leaf curl virus (ToLCV) have been observed in *Parthenium hysterophorus* and *Sonchus asper* in Uttar Pradesh (24). Additionally, Croton yellow vein mosaic virus (CYVMV), which infects croton weeds, has also been found to infect tomatoes, highlighting the cross-host transmission potential of begomoviruses (25). Further evidence of the presence of begomovirus in weed species includes the detection of tomato leaf curl Karnataka virus (ToLCKaV) along with tomato leaf curl Karnataka betasatellite in *Celosia cristata* (26). Additionally tomato leaf curl New Delhi virus (ToLCNDV) has been detected in *Ocimum kilimandscharicum* (27). Similarly, the Chilli leaf curl virus (ChiLCV) has been reported in *Datura innoxia* (28) and ToLCV has been identified in *Parthenium hysterophorus* (29). These findings reinforce the critical role of weeds as reservoirs for viruses, aiding the persistence and transmission of begomoviruses across diverse plant species. Phylogenetic analysis revealed that the ToLCKeV isolate (PQ901324) formed a distinct cluster within the ToLCKeV clade, closely related to isolates from India and Pakistan, suggesting a possible regional evolution or recent cross-border transmission event. This clustering pattern

indicated a shared evolutionary origin among the ToLCKeV isolates infecting different hosts and regions, reinforcing the hypothesis of host range expansion.

The nucleotide diversity values suggested significant genetic variation within the ToLCKeV populations in both India and Pakistan, likely driven by recombination, mutation and host adaptation. The viruses analyzed in this study exhibited relatively high haplotype diversity ($h = 1$), indicating elevated mutation rates or extended evolutionary divergence among the sequences (30). The negative values obtained from Tajima's *D* test indicate an excess of low-frequency polymorphisms, which may result from background selection, genetic hitchhiking, or population expansion, followed by purifying selection (31). Similarly, Fu & Li's *F* and *D* tests predominantly produced negative values, further supporting the presence of purifying selection (32).

The high haplotype diversity observed across both populations implied frequent genetic differentiation, reinforcing the notion of rapid viral evolution. Moreover, the genetic divergence between Indian and Pakistani isolates underscores the role of geographical variation in shaping viral diversity. This may be attributed to geographic isolation limiting gene flow, as well as ecological differences such as variation in host plant species, climate and vector populations influencing viral evolution. Overall, the neutrality test results indicated that ToLCKeV populations in both countries may be under selection pressure that restricts genetic variation at intermediate frequencies, likely due to natural selection eliminating deleterious mutations or the consequences of recent population expansion events. Similar findings have been reported for other begomoviruses, where weeds act as hosts, facilitating the spread of the virus over geographical distances via whitefly transmission (33).

The role of the whitefly (*B. tabaci*) as an exclusive vector of begomoviruses is crucial in the dissemination of ToLCKeV across different hosts (34). Given the polyphagous nature of *B. tabaci* and its ability to transmit multiple begomoviruses, the detection of ToLCKeV in *A. ficoidea* raises concerns regarding its contribution to viral epidemiology. Several species of *Alternanthera* are being cultivated as green vegetables for food purposes and they may serve as potential hosts for the virus. Whiteflies feeding on infected *A. ficoidea* can facilitate cross-infection with adjacent cultivated crops, thereby exacerbating the spread and severity of ToLCKeV-related diseases.

Weeds play a crucial role in the evolution and spread of begomoviruses by serving as alternative hosts, thereby providing a reservoir for these plant viruses even when cultivated crops are absent. This allows begomoviruses to persist in the environment, facilitating their transmission by whitefly vectors. Furthermore, weeds often harbour multiple viral strains, creating opportunities for genetic recombination and the emergence of new, potentially more virulent begomovirus variants. This continuous cycle of infection and evolution in weed hosts significantly contributes to the increased diversity and adaptability of begomoviruses, thereby posing a persistent threat to agricultural crops. Therefore, the results of this study underscore the importance of conducting further surveillance and host range studies to evaluate the role of weed species in begomovirus transmission dynamics in cultivated and non-cultivated hosts. These findings underscore the need for integrated pest and disease management (IPDM) strategies that consider the role of weeds in the transmission cycles of viruses.

Conclusion

This study represents the first report of ToLCKeV infection in *A. ficoidea*. As an alternative host, *A. ficoidea* may enable the virus to survive and spread during off-seasons when primary crop hosts are absent, thereby contributing to its persistence in the ecosystem. Additionally, studies on the vector transmission efficiency of ToLCKeV from *A. ficoidea* to economically important crops will aid in the development of targeted control strategies to mitigate the impact of begomovirus infections. Understanding the interactions between begomoviruses, their plant hosts and vectors is crucial for devising effective strategies for controlling viral diseases that affect major crops. This study emphasizes the importance of weed control and incorporating weed management strategies into IPDM.

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Authors' contributions

PSS, MM and NMB conceptualized the study. MN carried out the experiments and formal analysis. RS and MS supervised and administered the study. PSS, MM, KA and NMB helped in data validation and curation. MN wrote the original draft of the manuscript. PSS, RS, MM and NMB revised the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors do not have any conflict of interest to declare.

Ethical issues: None

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