Shahid Bahonar University of Kerman
Journal of Advances in Plant Protection
JAPP 2023
Association of Iranian Plant Protection Societies

Identification of reservoir hosts of tomato yellow leaf curl virus in southeastern Iran

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Article Info.

Article type:
Short article

Article history:
Received 03 Jun. 2026
Received in revised form 17 Jun. 2026
Accepted 21 Jun. 2026
Available Online 21 Jun. 2026

Keywords:
Begomovirus coheni,
Reservoir hosts,
Tomato yellow leaf curl virus,
Wild hosts.

Abstract

Tomato yellow leaf curl disease, caused by tomato yellow leaf curl virus (TYLCV; *Begomovirus coheni*), is among the most devastating viral diseases affecting tomato crops as well as numerous cultivated and wild plant species throughout tropical and subtropical regions worldwide. Wild plant hosts play a critical role in the epidemiology and persistence of TYLCV infections in cultivated crops. In the present study, wild hosts of TYLCV in Jiroft, southeastern Iran, were identified, and partial molecular characterization of the recovered viral isolates was conducted. Detection was performed using PCR assays with degenerate primers, followed by amplification of the majority of the viral coat protein gene with specific primers, as well as Sanger sequencing of the PCR products. Based on the results obtained, three symptomatic plant species, namely cornflower (*Centaurea* sp.), castor bean (*Ricinus communis*), and common mallow (*Malva* sp.), were identified to be infected with TYLCV. This study represents the first documented evidence of TYLCV infection in cornflower, common mallow, and castor bean in Iran. To enhance the effectiveness of TYLCV disease management strategies, the elimination of annual and perennial weed species present within and around agricultural fields is recommended.

Cite this article: Besharati, N., Heydarnejad, J., & Esmaeili, M. (2026). Identification of reservoir hosts of tomato yellow leaf curl virus in southeastern Iran. *Journal of Advances in Plant Protection*, *3*(1), 33–40.

Publisher: Shahid Bahonar University of Kerman

Introduction

Tomato yellow leaf curl virus (TYLCV; *B. coheni*) is recognized as one of the most destructive plant viruses infecting tomato and a wide range of vegetable and crop species in tropical and subtropical regions across the world (Rybicki, 2015; Scholthof et al., 2011; Varma & Malathi, 2003). The family *Geminiviridae* comprises 15 genera, among which the genus *Begomovirus* represents the largest group, currently including 464 species and encompassing numerous economically important plant viruses (Maruthi et al., 2026; Roumagnac et al., 2022). Begomoviruses possess genomes composed of either one or two circular single-stranded DNA (ssDNA) molecules ~2.5–5.2 kb in size (Fiallo-Olivé et al., 2021), which are encapsidated within twinned icosahedral particles measuring nearly 22×38 nm (Hesketh et al., 2018). Viruses belonging to this genus are transmitted in a persistent (Fiallo-Olivé et al., 2021) or in the case of TYLCV, propagative manner by several cryptic species of the whitefly *Bemisia tabaci* Genn. (He et al., 2020).

Three categories of circular ssDNA satellites, including alphasatellites, betasatellites, and deltasatellites, are commonly associated with monopartite Old World begomoviruses and, less frequently, with bipartite New World begomoviruses. Alphasatellites are ~1.4 kb in length and encode the alpha-Rep protein, which is involved in self-replication of alphasatellites. Through interactions between the Rep proteins encoded by helper begomoviruses and the alpha-Rep protein encoded by alphasatellites, both symptom severity and viral

accumulation are negatively influenced (Hussain et al., 2026). Betasatellites are similar in size to alphasatellites, and their single or double open reading frames encode the βC1 protein alone or both βC1 and βV1 proteins. These proteins act as pathogenicity determinants, contribute to symptom induction, and enhance viral accumulation within infected hosts (Farooq et al., 2026). Deltasatellites are smaller noncoding molecules of ~0.7 kb associated with helper begomoviruses (Nawaz-ul-Rehman et al., 2021), and are thought to suppress the accumulation of their associated helper viruses (Fiallo-Olivé et al., 2016).

Tomato yellow leaf curl disease (ToLCD) is caused by several phylogenetically related begomoviruses possessing either monopartite or bipartite genomes (Yan et al., 2021). To date, three begomoviruses responsible for ToLCD in Iran have been identified, including TYLCV (Hajimorad et al., 1996), tomato leaf curl Palampur virus (ToLCPalV) (Heydarnejad et al., 2009), and tomato leaf curl New Delhi virus (Yazdani-Khameneh et al., 2016). In periods when cultivated hosts are unavailable, annual and perennial plant species may function as reservoir hosts for TYLCV. Previously, four wild species have been documented as the natural hosts of the virus (Shamshiri et al., 2019) and therefore removal of the wild hosts must be considered in integrated disease management programs (Papayiannis et al., 2011; Prasad et al., 2020).

Due to suitable climatic conditions and intensive agricultural activities, ToLCD is widely distributed throughout southern and southeastern Iran (Fazeli et al., 2009; Hajimorad et al., 1996; Salari et al., 2022). During a field survey conducted to detect begomoviruses associated with ToLCD, three symptomatic wild plant species were collected from Jiroft in southeastern Iran. The principal objective of the present study was to identify the virus associated with the diseased plant samples. In addition, phylogenetic relationships between the detected isolates and related GenBank isolates originating from wild and cultivated hosts worldwide (other than tomato) were investigated.

Material and Methods

Sample collection and amplification of DNA

Three symptomatic wild plant samples were collected from agricultural fields in Jiroft, Kerman Province, southern Iran. These samples included cornflower (*Centaurea* sp., Asteraceae), which exhibited upward leaf rolling along the main veins together with dwarfing symptoms (Fig. 1a); castor bean (*Ricinus communis* L., Euphorbiaceae), showing marginal downward leaf curling accompanied by severe vein swelling on the abaxial leaf surfaces (Fig. 1b); and common mallow (*Malva* sp., Malvaceae), displaying vein clearing and dwarfing symptoms (Fig. 1c). Total DNA was extracted from the collected plant materials using the cetyltrimethylammonium bromide (CTAB) extraction protocol described by Zhang et al. (1998).

Fig. 1. (A) Common mallow (*Malva* sp.) infected with tomato yellow leaf curl virus (TYLCV) exhibiting vein clearing and dwarfing symptoms; (B) Castor bean (*Ricinus communis*) displaying downward marginal leaf curling together with severe vein swelling; and (C) Cornflower (*Centaurea* sp.) showing upward leaf curling symptoms. Samples were collected from Jiroft, Kerman Province, southeastern Iran.

PCR and sequencing

Extracted DNA samples were initially analyzed by PCR using the degenerate begomovirus primer pair 181v/Bc (Deng et al., 1994; Rojas et al., 1993). Subsequently, the specific primer pair TYLCV-526-F/TYLCV-1237-R (Shamshiri et al., 2019) was employed to identify the begomovirus associated with the symptomatic plant samples. This primer pair specifically amplifies the most part of coat protein gene of TYLCV, as well as the 3′ end of the gene encoding replication enhancement protein. The resulting PCR amplicons, ~700 bp in size, were subjected to Sanger sequencing by Microsynth

Company, Switzerland.

Phylogenetic analysis

Coat protein gene sequences obtained from the three PCR-positive samples, designated as C35 (cornflower), M28 (common mallow), and RIC (castor bean), together with related sequences available in the GenBank database, were analyzed using the BLASTn algorithm (Altschul et al., 1990). For this analysis, nucleotide sequences corresponding to 1250 TYLCV isolates were retrieved from the NCBI database on 11 December 2025, considering host species and country of origin as selection criteria and using an E-value of 0.0 together with 100% query coverage. Owing to the large number of TYLCV sequences available in GenBank, isolates originating from tomato were excluded from the analysis. The obtained nucleotide sequences were aligned with the remaining 119 sequences using the ClustalW algorithm implemented in MEGA11 (Tamura et al., 2021) under default settings. Phylogenetic relationships were inferred using the maximum-likelihood method based on the Jukes–Cantor model with gamma distribution and invariant sites (G+I) in MEGA11 with 1000 bootstrap replicates. The resulting phylogenetic tree was rooted using East African cassava mosaic Kenya virus (EACMKV), accession number AJ717575, as the outgroup. Tree visualization was carried out using iTOL v6 (Letunic & Bork, 2024).

Results

PCR, sequencing and phylogenetic analysis

PCR amplification using both the degenerate primer pair 181v/Bc and the TYLCV-specific primer pair TYLCV-526-F/TYLCV-1237-R, together with BLASTn analysis of the obtained nucleotide sequences, confirmed the association of TYLCV with cornflower, common mallow, and castor bean samples. Three TYLCV nucleotide sequences of ~680 nucleotides in length were deposited in the GenBank database under accession numbers PZ451579, PZ451580, and PZ451581 for the cornflower, common mallow, and castor bean isolates, respectively.

Nucleotide sequence analysis of the coat protein (CP) gene demonstrated that the three TYLCV isolates obtained from cornflower, common mallow, and castor bean shared 94.40–96.80% sequence identity among themselves and 91.30–99.90% identity with previously reported GenBank isolates recovered from cultivated hosts (excluding tomato), and wild plant species. The highest and lowest amount of nucleotide identities were detected between M28 (common mallow) and OQ319125 isolates (faba bean, Iran), as well as RIC (castor bean) and KF435136 isolates (hot pepper, Saudi Arabia), respectively.

The three TYLCV isolates obtained in this study grouped together with previously characterized GenBank isolates originating from different cultivated (excluding tomato) and wild host plants in Iran, as well as neighboring countries such as Oman and Pakistan (Fig. 2). Based on the phylogenetic clustering pattern, the cornflower isolate (C35) was positioned alongside basil TYLCV isolates reported from Oman. Likewise, the common mallow isolate (M28) clustered with faba bean, soybean, and sunflower isolates that were recently identified in Iran. In addition, the castor bean isolate (RIC) formed a cluster together with several isolates originating from cultivated plant species in Iran and Oman.

Discussion

TYLCV is widely distributed throughout Iran (Bananej et al., 2004; Behjatnia et al., 2003; Fazeli et al., 2009; Hajimorad et al., 1996; Heydarnejad et al., 2018), and infects a broad range of cultivated and wild plant species, including soybean, faba bean, basil, Moldavian dragonhead, euphorbia (Salari et al., 2022), sunflower, Guar (Salari et al., 2026), and ground cherry (Shamshiri et al., 2019). Complete genome sequences of these isolates are currently available in the GenBank database. In addition, TYLCV has previously been detected in wild plant species such as flower-of-an-hour (*Hibiscus trionum*), bishop's weed (*Ammi majus*), and castor bean through PCR amplification of an ~730 bp fragment of the coat protein (CP) gene (Shamshiri et al., 2019). Consequently, according to the CP gene sequencing results obtained in the present study, this work constitutes the first documented report of TYLCV infecting cornflower, common mallow, and castor bean in Iran.

Tomato leaf curl disease in Iran is also associated with at least two additional begomoviruses (Heydarnejad et al., 2009; Yazdani-Khameneh et al., 2016). Besides TYLCV, several cultivated plants, as well as four wild species namely *Chenopodium* sp. (Chenopodiaceae), *Heliotropium europaeum* (Boraginaceae) (Heydarnejad et al., 2013), *Chrozophora hierosolymitana* (Euphorbiaceae), and *Herniaria* sp. (Caryophyllaceae) (Fazeli et al., 2009), have been identified as hosts of ToLCPalV.

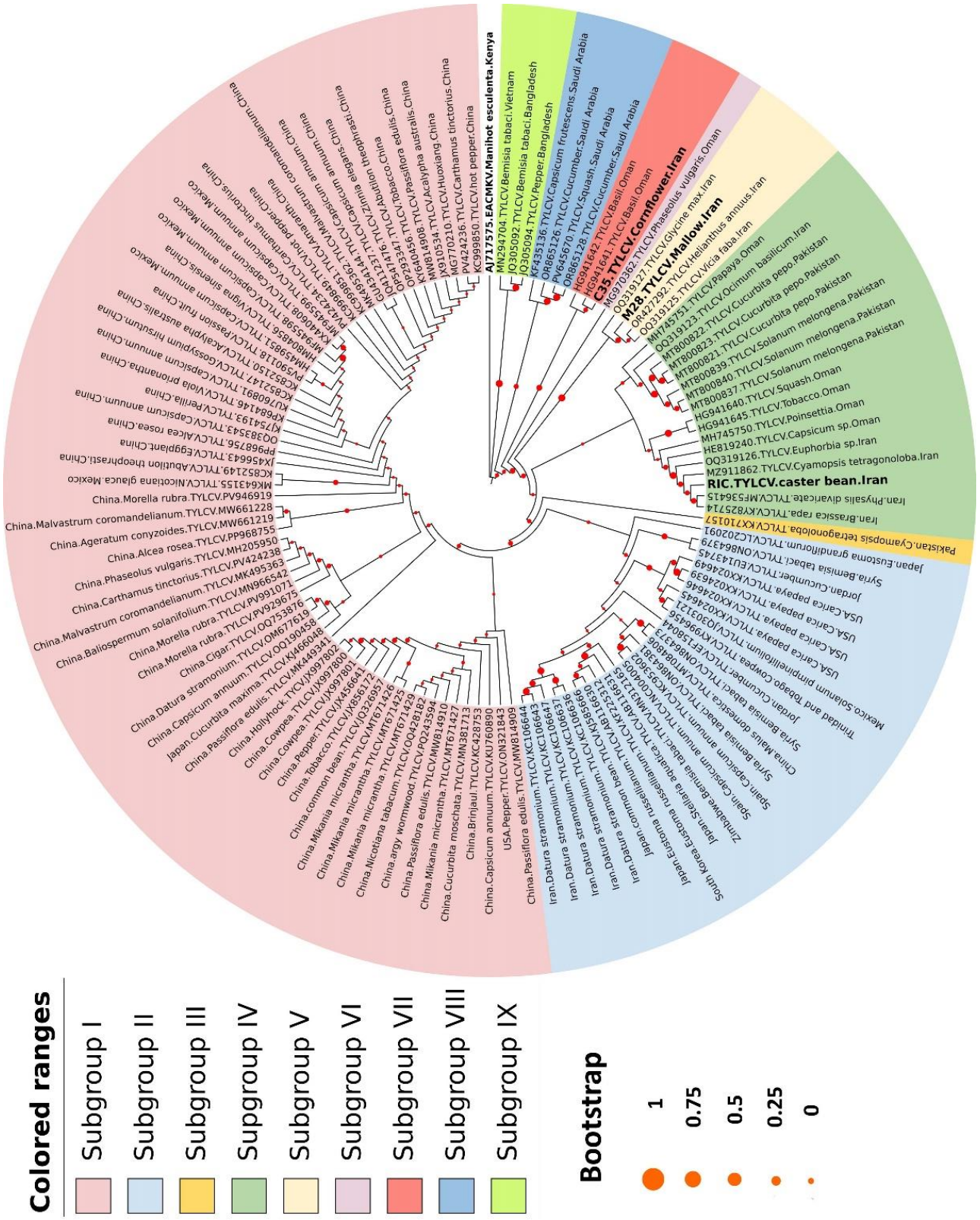

Fig. 2. Maximum-likelihood phylogenetic tree constructed based on alignments of the coat protein gene sequences of tomato yellow leaf curl virus (TYLCV) isolates recovered from cornflower, common mallow, and castor bean (designated as C35, M28, and RIC isolates, respectively; indicated in bold), together with related sequences available in the GenBank database. Numerical values at the nodes indicate bootstrap support percentages calculated from 1000 replicates. The TYLCV phylogenetic tree was rooted using East African cassava mosaic Kenya virus (EACMKV), accession number AJ717575, as the outgroup. Tree visualization was carried out using iTOL v6 (Letunic & Bork, 2024).

Warm and arid climatic conditions prevail across most regions of Iran (UNESCO-EOLSS, n.d.), creating highly favorable environmental conditions for the widespread distribution of TYLCV throughout the country. More broadly, the Middle East, particularly the regions surrounding Iran, is believed to represent both a historical and current center for ongoing TYLCV diversification (Lefeuvre et al., 2010). Under these circumstances, annual and perennial dicotyledonous plant species from diverse taxa are continuously exposed to ToLCD, thereby increasing the probability of susceptible plant genotypes becoming infected. In southern Iran, favorable climatic conditions allow agricultural activities to continue throughout the year. As a result, populations of the whitefly vector, *B. tabaci*, as well as the disease cycle of ToLCD, remain uninterrupted. Consequently, numerous cultivated and wild plant species are persistently subjected to infection pressure.

Generally, detection of plant viruses infecting wild plants can be a challenging task. First of all, many viral infections are asymptomatic in wild species (Hasiów-Jaroszewska et al., 2021), for example, infection of ryegrass by wheat dwarf virus did not induce any typical disease symptoms, which can be attributed likely to a very low level of the virus titer compared to infected wheat (Yazdkhasti et al., 2021). Furthermore, low-titer virus in the plant can potentially reduce the sensitivity of the method used and consequently cause false negatives results (Rubio et al., 2020). However, TYLCV was easily detected by routine PCR in this study using specific primers.

Causal viruses of tomato yellow leaf curl disease possess a broad host range, and among its host plants, species belonging to the families Solanaceae and Malvaceae, such as common mallow (*Malva* sp., Malvaceae) identified in the present study, are regarded as favorable hosts for both disease development and feeding activity of the whitefly vector, *B. tabaci* (reviewed by Morales, 2011). Reservoir host plants may contribute to the maintenance and persistence of the virus during periods when cultivated hosts are unavailable and/or when environmental conditions are unfavorable. Therefore, effective management strategies, including the removal of weeds within and surrounding agricultural fields, especially perennial weed species, may contribute significantly to disease control.

Acknowledgments

The authors express their gratitude to the Shahid Bahonar University of Kerman, Iran.

Ethical Approval and Consent

This article does not contain any studies with human participants or animals performed by any of the authors.

CRediT author statement

N. Besharati: Performed PCR tests and collected the samples. **J. Heydarnejad:** Designed the project, Provided laboratory support, Analysed the sequence data and drafted the manuscript. **M. Esmaeili:** Constructed phylogenetic tree; and all authors read and contributed to the final draft of the manuscript.

Funding

This study was financially supported by Research and Technology Institute of Plant Production (RTIPP), Shahid Bahonar University of Kerman, Kerman 7616913439, Iran (Project number: 1404/6223).

Data Availability

All data generated or analyzed during this study are included in the published article.

Conflict of interest

The authors declare that they have no conflict of interest.

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