


Investigation of Begomovirus Infections in Greenhouse Tomato Production Areas in the Eastern Mediterranean Region

Selin Ceren Balsak¹

¹ Kahramanmaraş, Sütçü İmam University, Agricultural Faculty, Department of Plant Protection, Kahramanmaraş, Turkey

 <https://orcid.org/0000-0002-2326-7520>
✉: cerenbalsak@gmail.com

ABSTRACT

Begomoviruses are the most numerous group of viruses infecting economically important plants. Begomoviruses have a wide host range, high recombination ability, effective transmission by its vector and synergistic interaction with different viruses in the host plant, so they have a high risk of spreading to large areas in a short time and causing epidemics. In this study, the aim was to investigate the presence of begomoviruses, which are among the major threats to tomato (*Solanum lycopersicum* L.) cultivation. The surveys were conducted in the provinces of Adana and Kahramanmaraş, Turkey, where a total of 160 leaf samples were collected from tomato plants exhibiting yellowing, curling, and plant stunting in commercial greenhouses. Total DNAs obtained from the collected leaf samples were tested using multiplex PCR. As a result of the analysis, 10 samples were infected only with TYLCSV-Sic, while 16 were co-infected with TYLCSV-Sic and TYLCV-IL. Additionally, 22 of the samples were co-infected with TYLCV-IL and TYLCV-Mld. Furthermore, PCR testing for the presence of ToLCNDV was conducted, but none of the samples were found to be infected.

Key words: *Begomovirus*, TYLCV, ToLCNDV, tomato, Multiplex PCR.

Doğu Akdeniz Bölgesindeki Örtüaltı Domates Üretim Alanlarındaki Begomovirus Enfeksiyonlarının Araştırılması

ÖZ

Begomovirüsler ekonomik olarak önemli bitkilerde enfeksiyon yapan virüslerin en fazla sayıda bulunan gruptur. Begomovirüslerin geniş konukçu dizinine sahip olması, yüksek rekombinasyon yeteneği, vektörüyle etkili şekilde taşınması ve konukçu bitkide farklı virüsler ile sinerjik etkileşimi nedeniyle üretim alanlarında kısa sürede geniş alanlara yayılmaları ve epidemilere yol açma riskleri oldukça yüksektir. Bu çalışmada, domates (*Solanum lycopersicum* L.) yetiştiriciliğini tehdit eden begomovirüslerin varlığının araştırılması amaçlanmıştır. Adana ve Kahramanmaraş illerinde ticari seralara yapılan sorveylerde sararma, kıvrılma ve bodurlaşma gibi semptom taşıyan domates bitkilerinden toplam 160 yaprak örneği toplanmıştır. Toplanan yaprak örneklerinden elde edilen total DNA'lar multiplex PCR ile testlenmiştir. Analiz sonucunda, 10 örneğin yalnızca TYLCSV ile enfekte olduğu, 16 örneğin ise TYLCSV-Sic ve TYLCV-IL ile enfekteli olduğu belirlenmiştir. Ayrıca, 22 örneğin TYLCV-IL ve TYLCV-Mld ile karışık enfekteli olduğu belirlenmiştir. Bunun yanı sıra, ToLCNDV varlığına yönelik PCR testi yapılmış, ancak hiçbir örnekte enfeksiyon tespit edilmemiştir.

Anahtar Kelimeler: *Begomovirus*, TYLCV, ToLCNDV, domates, Multiplex PCR.

INTRODUCTION

The genus *Begomovirus* belongs to the *Geminiviridae* family and currently contains 424 species (Nigam et al., 2023). Begomoviruses are the most abundant group of viruses infecting economically important plants (Malathi et al., 2017; Rao and Reddy, 2020). They infect important plants from various families, including *Cucurbitaceae*, *Solanaceae*, *Malvaceae*, and *Fabaceae*, in different regions of the world (Seal et al., 2006; Fortes et al., 2016), and are transmitted in a persistent manner by whiteflies in the *Bemisia tabaci* cryptic species (Brown

et al., 2015; He et al., 2020). Begomoviruses have either a monopartite genome (DNA-A) or a bipartite genome (DNA-A and DNA-B) each approximately 2.7-2.8 kb encapsidated in a twinned icosahedral virion (Stanley et al., 2005). Tomato yellow leaf curl disease (TYLCD), is caused by tomato yellow leaf curl virus (TYLCV) and a group of TYLCV-like viruses (ICTV, 2024). TYLCD-causing viruses belong to the genus *Begomovirus* (Stanley et al., 2005). TYLCV, which is a major issue in global tomato production, ranks third among the ten economically important viruses (Scholthof et al., 2011). While TYLCV and most related begomoviruses have a monopartite genome composed of a single-stranded DNA molecule, except for tomato yellow leaf curl Kanchanaburi virus (TYLCKaV) and tomato yellow leaf curl Thailand virus (TYLCTHV) (Yan et al., 2021). TYLCV has been reported to cause up to 100% yield loss in tomato production due to severe infections in tropical and subtropical regions (Glick et al., 2009; Navas-Castillo et al., 2011). Tomato yellow leaf curl virus-Israel (TYLCV-Is) and tomato yellow leaf curl virus-Mild (TYLCV-Mld) strains are globally widespread, while others are found in more limited regions (Navas-Castillo et al., 2011). Infections of both strains (TYLCV-Is and TYLCV-Mld) have been reported in tomato-producing areas, with the TYLCV-Is strain causing severe infections, and it is quite common in pepper (*Capsicum annuum*) and bean (*Phaseolus vulgaris*) plants (Glick et al., 2009). Also, tomato yellow leaf curl Sardinia virus (TYLCSV), along with other closely related species, is responsible for TYLCD, which has been limited to Mediterranean countries (Yan et al., 2021). Some reports have raised concerns about the dramatic increase in the incidence of TYLCD in various regions, where climate changes, particularly warming and drying trends (García-Andre's et al., 2007; Davino et al., 2009).

Tomato leaf curl New Delhi virus (ToLCNDV) is a bipartite begomovirus that infects economically important vegetable and ornamental species, as well as weeds (Zaidi et al., 2017; Lopez et al., 2015). Reports on the presence of ToLCNDV were limited in Asia countries until 2012, but it was first reported in the Western Mediterranean Basin, in southern Spain, where infections were found in squash (*Cucurbita pepo* L.), melon, and cucumber crops (Juárez et al., 2014). However, the spread of this pathogen, along with reports from Iran (Yazdani-Khameneh et al., 2016), indicates that ToLCNDV has rapidly expanded into new geographical regions in recent years. The presence of TYLCV and ToLCNDV in the Mediterranean Basin poses a new threat not only to tomato production but also to other economically important crops. In Turkey, TYLCV and TYLCSV were reported in tomatoes and eggplants grown in greenhouses (Gül-seker et al., 2015; Fidan et al., 2019; Fidan and Sarıkaya, 2020). ToLCNDV was first reported in *Cucurbitaceae* species by Fidan et al. (2023) in Antalya province.

The wide host range of begomoviruses, their high recombination ability, efficient transmission by their vector, and synergistic interactions with different viruses in the host plant, result in a high risk of rapid spread across large areas in production fields and the potential to cause epidemics. In Turkey, since 2019 there has been no further molecular analysis of local TYLCV isolates and concern about the virus and its associated disease in tomato. The objective of this study was to investigate the presence of TYLCV strains and ToLCNDV in tomato plants grown in greenhouses in the provinces of Adana and Kahramanmaraş in Turkey.

MATERIALS AND METHODS

Sampling and DNA Extraction

One-hundred and sixty leaf samples from tomato plants showing yellowing, upward leaf curling, and plant stunting were collected in commercial greenhouses located in the Adana and Kahramanmaraş in Turkey, during 2024. DNA was isolated from about 100 mg of the leaf of the samples using the CTAB DNA extraction method (Doyle and Doyle, 1990) with slight modifications. DNA qualities were checked in agarose gel electrophoresis and quantified using a NanoDrop spectrophotometer.

Detection and differentiation of TYLCD-associated viruses

Total DNA isolated from plants were preliminary screened for the presence of TYLCD-associated viruses by degenerate primer pair TY1 and TY2 (Accotto et al., 2000) (Table 1). Later, two sets of primers were used for multiplex PCR to detect TYLCD-associated viruses: TYLCV-IL (Israel), TYLCV-Mld (Mild), TYLCSV-Sicily and TYLCSV-ES (Spanish). Moreover, in order to detect the presence of ToLCNDV, the total DNAs were subjected to PCR using ToLCNDV-CP1 and ToLCNDV-CP2 primers (Panno et al., 2019).

Table 1. List of the primers that were used in this study

Primers	Sequence (5' to 3')	Product size (bp)	Virus/Strain
TY 1	GCCCATGTAYCGRAAGCC	579	TYLCV
TY 2	GGRTTAGARGCATGMGTAC		
TYv2337	ACGTAGGTCTTGACATCTGTTGAGCTC	634 bp	TYLCV-IL
TYc138	AAGTGGGTCCCACATATTGCAAGAC		
TYAlmv2516	TTTTATTTGTTGGTGTGTTGTTAGTTGAAG	433 bp	TYLCSV-ES
TYAlmc115	ATATTGATGGTTTTTCAAACTTAGAAG		
TYv2664	ATTGACCAAGATTTTACACTTATCCC	316 bp	TYLCV – Mld
TYc138	AAGTGGGTCCCACATATTGCAAGAC		
VP2715	ATACTTGGACACCTAATGGCTATTTGG	543 bp	TYLCV
RVC427	TGCCCTGGACA(A/G)TGGGG(A/G)CAGCAG		
Sa2267	TGGAAAGTACCCCATTCAGAATC	946 bp	TYLCSV-Sic
VP2715	ATACTTGGACACCTAATGGCTATTTGG		
ToLCNDV-CP1	CTCCAAGAGATTGAGAAGTCC	1 kb	ToLCNDV
ToLCNDV-CP2	TCTGGACGGGCTTACGCCCT		

Nucleotide Sequence Comparison and Phylogenetic Analysis

PCR DNAs were purified from agarose gel (QIAGEN). And, PCR products were sequenced directly in both directions. Multiple sequence alignments were made using CLUSTALW (Thompson et al., 1994) and the nucleotide sequences were analyzed with the online software BLASTn (<http://www.ncbi.nlm.nih.gov/BLAST/>). Phylogenetic trees were constructed with MEGA software version 7 (Kumar et al., 2016) in the neighbor-joining algorithm with 1000 bootstrap replicates to assess the robustness of the nodes (Tamura et al., 2013).

RESULTS AND DISCUSSION

A total of 160 leaf samples were collected from commercial greenhouses in Adana and Kahramanmaraş. The most frequently observed symptoms on tomato plants were mosaic, yellowing or chlorosis, leaf rolling, leaf curling, leaf deformation and stunting (Fig.1).



Figure 1. TYLCD symptoms (leaf curling, yellowing, stunting) in tomato plants grown in the greenhouses in Adana and Kahramanmaraş

When the total DNAs were tested using multiplex PCR, the expected sizes for the DNA amplicons were obtained as follows: 634 bp for TYLCV-IL, 316 bp for TYLCV-Mld, 946 bp for TYLCSV-Sic (Fig. 2). In the analysed field samples found that only single or double virus infected. Ten out of 48 infected samples were infected with only TYLCSV-Sic, while 16 were co-infected with TYLCSV-Sic and TYLCV-IL (Table 2). Additionally, 22 of the samples were co-infected with TYLCV-IL and TYLCV-Mld. Moreover, to test for the presence of ToLCNDV, PCR was performed, but none of the samples was found to be infected.

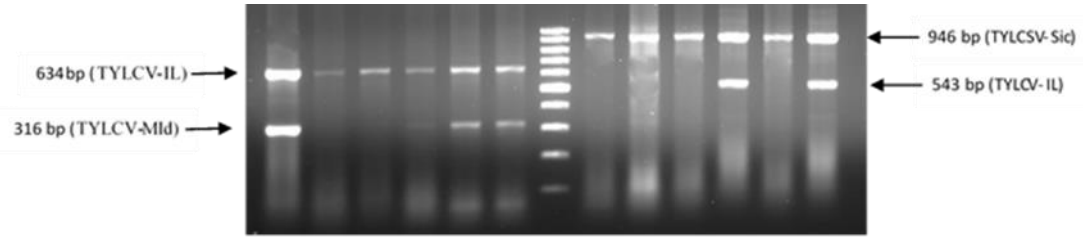


Figure 2. Detecting viruses associated with tomato yellow leaf curl. GeneRuler DNA Ladder Mix (Thermo Fisher Scientific) was used as a marker (100 bp).

Table 2. Number of tomato plants infected with TYLCD-associated viruses in Adana and Kahramanmaraş

Location	TYLCSV-Sic	TYLCSV-Sic+TYLCV-IL	TYLCV-IL+ TYLCV-Mld
Adana	8	12	17
Kahramanmaraş	2	4	5
Total	10	16	22

The analyses of BLASTn and BLASTx were performed using nucleotide sequences of 919 nt from TYLCSV-Sic isolates and 634 nt from TYLCV-IL isolates. The nucleotide sequences of ten randomly selected isolates, including both TYLCV-IL and TYLCSV-Sic, have been submitted to GenBank. The accession numbers for the TYLCSV-Sic isolates are PV067002–PV067011, while the accession numbers for the TYLCV-IL isolates are PV067012–PV067021. The TYLCSV-Sic isolates obtained in this study showed high nucleotide identity, with 97–99% sequence homology to previously reported isolates in GenBank. Phylogenetic analysis of TYLCSV-Sic isolates obtained in this study were divided into two subgroups (Fig. 3). The isolate closest to TYLCSV-Sic-Turkey was from Jordan (EU307940.1), followed by Italy (DQ317778.1, DQ317780.1, DQ317783.1) isolates. Furthermore, the TYLCV-IL isolates obtained in this study showed high nucleotide identity, with 94–97% sequence homology to previously reported isolates in GenBank. Phylogenetic analysis showed that the TYLCV-IL isolates are close to previously reported from Turkey (MK348219.1), Jordan (MF351605.1), Spain (DQ058085.1, DQ317760.1, DQ317746.1) and Iran (JQ928340.1) isolates (Fig.4).

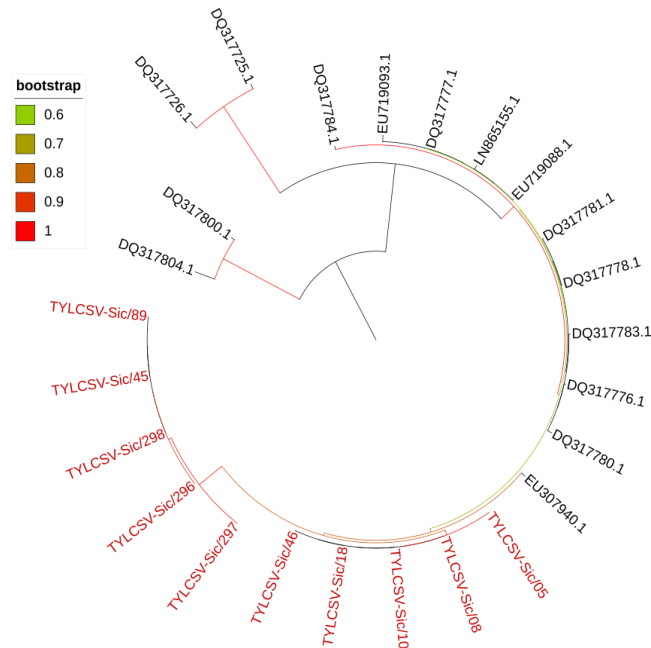


Figure 3. Phylogenetic tree for TYLCSV-Sic isolates. The analyses were performed using MEGA 7 software. The bootstrap consensus of the tree was derived from 1000 replicates.

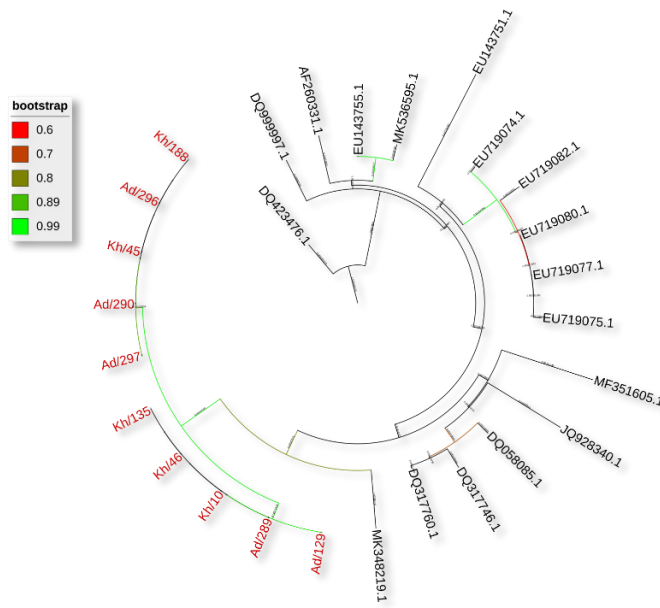


Figure 4. Phylogenetic tree for TYLCV-IL isolates. The analyses were performed using MEGA 7 software. The bootstrap consensus of the tree was derived from 1000 replicates

While TYLCV is widespread globally and causes significant epidemics in tomato, TYLCSV is restricted to Mediterranean countries (Navas-Castillo et al., 2011). Sánchez-Campos et al. (1999) reported that TYLCV had higher transmission rates among *B. tabaci* biotypes than TYLCSV. Other begomovirus species, closely related to TYLCV and responsible for TYLCD, are found in more limited geographical areas. Previous research has indicated that various species within the *B. tabaci* complex can transmit a specific begomovirus with varying levels of efficiency (Jiu et al., 2006; Zhao et al., 2019). TYLCV-like viruses are present throughout the growing seasons, but the high infection was detected in the spring in both provinces, coinciding with a high population of *B. tabaci*. The increasing vector populations driven by global warming have significantly contributed to the rise of viruses infecting economically important crops such as peppers and tomatoes worldwide. During the survey, it was determined that intensive use of insecticides was involved in the discussions with the producers. The intensive use of insecticides by producers contributes to the development of insecticide resistance in whiteflies, reducing their effectiveness. This, in turn, may lead to an increase in disease incidence, as the resistant whiteflies continue to spread viruses to agricultural crops (Horowitz et al., 2007; Patra and Hath, 2022).

Moreover, Kil et al. (2016) reported that TYLCV is transmitted through the seeds of tomato and pepper plants. However, subsequent studies by Pérez-Padilla et al. (2020) and Tabein et al. (2021) showed no evidence of seed transmission for TYLCV-IL or TYLCSV, despite detecting the virus in seeds, indicating that the virus is seed-borne but not transmitted via seeds. These findings suggest that seed transmission is not a common characteristic of TYLCV. The worldwide spread of TYLCD is strongly linked to the international movement of planting material, as well as the global rise in insect vector populations and the rapid evolution of virus strains (Seal et al., 2006; Navas-Castillo et al., 2011). Factors such as host range, population dynamics, and genetic diversity within *B. tabaci* biotypes all play a crucial role in the spread of begomoviruses in agroecosystems. Understanding the dynamics of *Begomovirus* transmission by *B. tabaci* whitefly is essential for the development of appropriate control strategies and sustainable agricultural practices to prevent the spread of these economically important viruses.

CONCLUSION

This study confirms the presence of TYLCV and its strains (TYLCV-IL and TYLCV-Mld) in greenhouse-grown tomatoes in Turkey, with co-infections observed between TYLCV strain and TYLCSV. The prevalence of TYLCV-associated viruses in these regions underscores the importance of monitoring begomovirus infections and controlling their spread, particularly in regions where whitefly vectors are abundant.


Acknowledgement

This work was supported by a grant from the Kahramanmaraş Sütçü İmam University Scientific Research Projects Unit, Project Number: 2023/6-20 M.

Conflict of Interest

The author declares no conflict of interest.

ORCID

Selin Ceren Balsak  <https://orcid.org/0000-0002-2326-7520>

Article History

Submission received: 18.12.2024
Revised: 08.03.2025
Accepted: 11.03.2025

REFERENCES

- Accotto, G. P., Navas-Castillo, J., Noris, E., Moriones, E., Louro, D. 2000. Typing of tomato yellow leaf curl viruses in Europe. *European Journal of Plant Pathology*, 106, 179–186. doi.org/10.1023/A:1008736023293
- Anfoka, G., Abhary, M., Haj Ahmad, F., Hussein, A. F., Rezk, A., Akad, F., Abou-Jawdah, Y., Lapidot, M., Vidavski, F., Nakhla, M.K., Sobh, H., Atamian, H., Cohen, L., Sobol, I., Mazyad, H., Maxwell, D.P., Czosnek, H. 2008. Survey of tomato yellow leaf curl disease-associated viruses. *Journal of Plant Pathology*, 90, 313–322.
- Brown, J. K., Fauquet, C. M., Briddon, R. W., Zerbini, F. M., Moriones, E., Navas-Castillo, J. 2012. “Family geminiviridae,” in *Virus Taxonomy: Classification and Nomenclature of Viruses - Ninth Report of the International Committee on Taxonomy of Viruses*. (London: Elsevier Academic Press).
- Davino, S., Napoli, C., Dellacroce, C., Miozzi, L., Noris, E., Davino, M., Acotto, G. P. 2009. Two new natural begomovirus recombinants associated with the tomato yellow leaf curl disease co-exist with parental viruses in tomato epidemics in Italy. *Virus Res* 143: 15–23.
- Doyle, J. J., Doyle, J. L. 1990. Isolation of plant DNA from fresh tissue. *Focus*, 12: 13-15.
- Fidan, H. and Sarikaya, P. 2020. Virus diseases in eggplant (*Solanum melongena*) cultivation in Antalya province. *Mediterranean Agricultural Sciences*, 33(1): 27-35. DOI: 10.29136/mediterranean.642226
- Fidan, H., Karacaoglu, M., Koç, G., Caglar, B. 2019. Tomato yellow leaf curl virus (TYLCV) strains and epidemiological role of Bemisia tabaci (Hemiptera: Aleyrodidae) biotypes on tomato agroecology in Turkey. *Applied Ecology and Environmental Research*, 17(4).
- Fidan, H., Yildiz, K., Sarikaya, P., Calis, O. 2023. First report of Tomato leaf curl New Delhi virus in Türkiye. *New Disease Reports*, 47, e12180. <https://doi.org/10.1002/ndr2.12180>
- Fortes, I. M., Sánchez-Campos, S., Fiallo-Olivé, E., Díaz-Pendón, J., Navas-Castillo, J., Moriones, E. 2016. A novel strain of tomato leaf curl New Delhi virus has spread to the Mediterranean basin. *Viruses*, 8, 307.
- García-Andrés, S., Accotto, G. P., Navas-Castillo, J., Moriones, E. 2007. Founder effect, plant host, and recombination shape the emergent population of begomoviruses that cause the tomato yellow leaf curl disease in the Mediterranean basin. *Virology* 359: 302–312.
- Glick, E., Levy, Y., Gafni, Y. 2009. The viral etiology of tomato yellow leaf curl disease—a review. *Plant Protection Science*, 45, 81–97.
- Gul-Seker, M., and Elibuyuk, I. O. 2019. Occurrence of Tomato yellow leaf curl virus and Tomato chlorosis virus mixed infections in protected tomato plants, Antalya, Turkey. *Phytoparasitica*, 47, 441-449.
- He, Y. Z., Wang, Y. M., Yin, T. Y., Fiallo-Olivé, E., Liu, Y. Q., Hanley-Bowdoin, L., Wang, X. W. 2020. A plant DNA virus replicates in the salivary glands of its insect vector via recruitment of host DNA synthesis machinery. *Agricultural Sciences*, 117, 16928–16937.
- Horowitz, R., Denholm, I., Morin, S. 2007. Resistance to insecticides in the TYLCV vector, Bemisia tabaci. In H. Czosnek (Ed.) *Tomato yellow leaf curl virus disease: Management, molecular biology, breeding for resistance* (pp. 305-325). Dordrecht: Springer Netherlands
- ICTV (International Committee on Taxonomy of Viruses) (2024). Available online: <https://talk.ictvonline.org/taxonomy>
- Jiu, M., Zhou, X. P., Liu, S. S. 2006. Acquisition and transmission of two begomoviruses by the B and a non-B biotype of Bemisia tabaci from Zhejiang, China. *J Phytopathology*, 154:587–91.

- Juárez, M., Tovar, R., Fiallo-Olivé, E., Aranda, M., Gosálvez, B., Castillo, P., Moriones, E., Navas-Castillo, J. 2014. First detection of Tomato leaf curl New Delhi virus infecting zucchini in Spain. *Plant Disease*, 98, 857.
- Kil, E. J., Kim, S., Lee, Y. J., Byun, H. S., Park, J., Seo, H., Kim, C. S. Shim, J. K., Lee, J. H., Kim, J. K., Lee, K. Y., Choi, H. S., Lee, S. 2016. Tomato yellow leaf curl virus (TYLCV-IL): A seed-transmissible geminivirus in tomatoes. *Scientific Reports*, 6, 19013.
- Kumar, S., Stecher, G., Tamura, K. 2016. MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33, 1870–1874.
- Lopez, C., Ferriol, M., Pico, M. B. 2015. Mechanical transmission of Tomato leaf curl New Delhi virus to cucurbit germplasm: selection of tolerance sources in Cucumis melo. *Euphytica*, 204:679–691. <https://doi.org/10.1007/s10681-015-1371-x>
- Malathi, V. G., Renukadevi, P., Chakraborty, S., Biswas, K. K., Roy, A., Sivalingam, P.N., Venkataravanappa, V., Mandal, B. 2017. Begomoviruses and their satellites occurring in India: distribution, diversity and pathogenesis. In A century of Plant Virology in India (Mandal, B. et al., eds), pp. 75–177, *Springer*
- Navas-Castillo, J., Fiallo-Olivé, E., Sánchez-Campos, S. 2011. Emerging virus diseases transmitted by whiteflies. *Annual Review of Phytopathology*, 49:219-48. doi: 10.1146/annurev-phyto-072910-095235. PMID: 21568700.
- Nigam, D., Muthukrishnan, E., Flores-López, L. F., Nigam, M., Wamaitha, M. J. 2023. Comparative Genome Analysis of Old World and New World TYLCV Reveals a Biasness toward Highly Variable Amino Acids in Coat Protein. *Plants* (Basel). 2023 May 16;12(10):1995. doi: 10.3390/plants12101995. PMID: 37653912; PMCID: PMC10223811.
- Panno, S., Caruso, A. G., Troiano, E., Luigi, M., Mangli, A., Vatrano, T., Lacono, G., Marchione, S., Bertin, S., Tomassoli, L., Parrella, G., Davino, S. 2019. Emergence of tomato leaf curl New Delhi virus in Italy: estimation of incidence and genetic diversity. *Plant Pathology*, 68:601–608. <https://doi.org/10.1111/ppa>.
- Patra, B., Kumar, H.T. 2022. Insecticide Resistance in Whiteflies Bemisia tabaci (Gennadius): Current Global Status. Insecticides-Impact and Benefits of Its Use for Humanity. *IntechOpen*. <http://dx.doi.org/10.5772/intechopen.101954>
- Pérez-Padilla, V., Fortes, I. M., Romero-Rodríguez, B., Arroyo-Mateos, M., Castillo, A. G., Moyano, C., De León, L., Moriones, E. 2020. Revisiting Seed Transmission of the Type Strain of Tomato yellow leaf curl virus in Tomato Plants. *Phytopathology*, 110:121–129. doi: 10.1094/PHYTO-07-19-0232-FI.
- Rao, G. P., Reddy, M. G. 2020. Overview of yield losses due to plant viruses. In *Applied Plant Virology* (Awasthi, L.P., ed.), (pp. 531–562), Academic Press
- Sánchez-Campos, S., Navas-Castillo, J., Camero, R., Soria, C., Díaz, J. A., Moriones, E. 1999. Displacement of tomato yellow leaf curl virus (TYLCV)-Sr by TYLCV-Is in tomato epidemics in Spain. *Phytopathology*, 89:1038–43.
- Scholthof, K. B. G., Adkins, S., Czosnek, H., Palukaitis, P., Jacquot, E., Hohn, T., Hohn, B., Saunders, K., Candresse, T., Ahlquist, P., Hemenway, C., Foster, G. D. 2011. Top 10 plant viruses in molecular plant pathology. *Molecular Plant Pathology*, 12(9): 938–954.
- Seal S., van den Bosch F., Jeger, M. (2006). Factors influencing begomovirus evolution and their increasing global significance: Implications for sustainable control. *Critical Reviews in Plant Sciences*, 25:23–46. doi: 10.1080/07352680500365257.
- Stanley, J., Bisaro, D. M., Briddon, R. W., Brown, J. K., Fauquet, C. M., Harrison, B. D., Rybicki, E. P., Stenger, D. C. 2005. Geminiviridae. In: Fauquet, C.M., Mayo, M.A., Maniloff, J., Desselberger, U. and Ball, L.A., Eds., *Virus Taxonomy*, 8th Report of the International Committee on Taxonomy of Viruses, *Elsevier Academic Press*, London, 301-326.
- Tabein, S., Miozzi, L., Matić, S., Accotto, G. P., Noris, E. 2021. No Evidence for Seed Transmission of Tomato Yellow Leaf Curl Sardinia Virus in Tomato. *Cells* 10(7):1673. doi: 10.3390/cells10071673. PMID: 34359841; PMCID: PMC8306144.
- Thompson, J.D., Higgins, D.G., Gibson, T.J. 1994. CLUSTALW: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight. *Nucleic Acids Research*, 11;22(22):4673-80. doi: 10.1093/nar/22.22.4673. PMID: 7984417; PMCID: PMC308517.
- Yan, Z., Wolters, A. A., Navas-Castillo, J., Bai, Y. 2021. The global dimension of tomato yellow leaf curl disease: current status and breeding perspectives. *Microorganisms*, 9:740.
- Yazdani-Khameneh, S., Aboutorabi, S., Shoori, M., Aghazadeh, A., Jahanshahi, P., Golnaraghi, A., Maleki, M. 2016. Natural occurrence of tomato leaf curl New Delhi virus in Iranian cucurbit crops. *Plant Pathology Journal*, 32, 201.

- Zaidi, S . S. E. A., Martin, D. P., Amin, I., Farooq, M., Mansoor, S. 2017. Tomato leaf curl New Delhi virus: a widespread bipartite begomovirus in the territory of monopartite begomoviruses. *Molecular Plant Pathology*, 18:901–911. doi.org/10.1111/mpp.12481
- Zhao, J., Chi, Y., Zhang, X. J., Teng, Lei, Wang, Xiao-Wei, Liu, S. S. 2019. Comparative proteomic analysis provides new insight into differential transmission of two begomoviruses by a whitefly. *Virology*, 16, 32. doi.org/10.1186/s12985-019-1138-4