



Woody ornamental plants surrounding greenhouses as potential reservoirs of tomato spotted wilt virus (*Orthotospovirus tomatomaculae*)

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Abstract

In 2021, plants exhibiting characteristic virus-like symptoms were observed both inside and close vicinity of a plastic tunnel used for pepper (*Capsicum annuum*) breeding. Inside the plastic tunnel various pepper breeding lines were cultivated, while different perennial woody ornamental plant species were located in the surrounding area. The presence of tomato spotted wilt orthotospovirus (*Orthotospovirus tomatomaculae*, TSWV) was detected by RT-PCR assays from all the collected samples, including samples from *Prunus tenella* (syn. *Amygdalus nana*), *Parthenocissus quinquefolia*, *Hypericum calycinum* and the pepper breeding lines. Nucleotide sequence analysis of the nonstructural protein encoding NSs gene revealed the presence of genetically diverse TSWV isolates both inside and outside of the plastic tunnel. This is the first report of TSWV from these perennial ornamental species labelling them as new hosts of TSWV. This suggests their potential role as reservoirs of the virus and emphasizes the importance of monitoring virus presence in non-crop vegetation to minimize the sanitary risks.

Keywords *Orthotospovirus tomatomaculae* · TSWV · Ornamental plants · Virus reservoir · NSs protein · Pepper

Introduction

Tomato spotted wilt orthotospovirus (*Orthotospovirus tomatomaculae*, TSWV) is still one of the most significant viruses of agronomically important crops, vegetables and ornamental plants (Scholthof et al. 2011). Despite the resistance breeding, it still causes heavy fruit losses in tomato and pepper production (Adkins 2000; Pappu et al. 2009). Although the main pepper and tomato producing area in Europe is located in the Mediterranean, they are also important cultivated plants in Hungary.

Orthotospovirus tomatomaculae within the *Tospoviridae* family (order *Elliovirales* in *Bunyaviricetes* class) is an enveloped single-stranded negative-sense RNA virus

infecting plants and also capable of replicating within its thrips vectors (Abudurexiti et al. 2019).

The genome of TSWV is segmented, consisting of three RNA molecules. The L RNA encodes for the RNA dependent RNA polymerase (RdRp) in negative orientation, while the M and S RNAs are both ambisense. From the M RNA, the precursor of glycoproteins (Gn-Gc) encoding gene is transcribed and translated in negative sense, while the movement protein (NSm) is encoded in positive orientation. The nucleocapsid (N) protein is encoded in negative orientation and the nonstructural (NSs) protein in positive orientation on the S RNA (Adkins 2000; German et al. 1992). The NSm and NSs proteins are multifunctional (De Ronde et al. 2014; Kormelink et al. 2011; Margaria et al. 2007; Oliver and Whitfield 2016; Takeda et al. 2002).

TSWV has an exceptionally wide host range, infecting more than 1000 plant species among both mono- and dicotyledons (Parrella et al. 2003). Effective management of TSWV requires an integrated strategy based on thrips vector control, elimination of virus reservoir plants, strict hygiene requirements and using resistant breeding lines or cultivars (Srinivasan et al. 2017; Batuman et al. 2020). In

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pepper production the majority of the cultivars carry the dominant *Tsw* resistance gene (originating from *Capsicum chinense*), which was the only TSWV resistance gene in pepper cultivars until recently (Boiteux, and Avila, 1994). The widespread use of resistant cultivars has resulted in the emergence of resistance breaking (RB) TSWV strains (Almási et al. 2023; Batuman et al. 2017; Margaria et al. 2004; Roggero et al. 1999, 2002). It was previously demonstrated that RB strains can develop locally from the various TSWV strains present in the region (Almási et al. 2015). The local emergence of new TSWV strains and the worldwide trade of propagating materials have led to the growing heterogeneity of the strains in distinct geographical areas. This process can be further supported by recombination events and the occurrence of reassortants, which are facilitated by the tripartite (segmented) virus genome (Tentchev et al. 2011; Tsompana et al. 2005).

Reservoir plants play a crucial role in the re-emergence and persistence of TSWV. Between the cultivation cycles, vector insects can survive and feed on the infected plant species, thus sustaining the continuous infection of TSWV. Most described reservoir plants are different weed species like *Datura stramonium*, *Solanum nigrum*, *Stellaria media* etc., but woody reservoir plants have not yet been identified (Fidan et al. 2024; Takács et al. 2006; Tiberini et al. 2025).

In a plastic tunnel located in Kecskemét (one of the main pepper-producing regions in Hungary) where several pepper lines were cultivated, despite careful plant protection measures, TSWV infection outburst year by year. Various woody ornamental plants observed around the plastic tunnel showed characteristic virus-like symptoms, therefore samples were collected from these ornamental plants and the symptomatic pepper plants within the plastic tunnel. Nucleotide sequence determination and phylogenetic analysis of the NSs gene revealed the presence of genetically distinct TSWV strains both inside and in the immediate surroundings of the plastic tunnel.

Materials and methods

Plant material

Plant leaf and fruit samples were collected from eight symptomatic and two asymptomatic pepper (*C. annuum*) breeding lines in a plastic tunnel near Kecskemét, Hungary during the 2021–2022 growing seasons. At the same time, symptomatic leaves of ornamental plants (*P. quinquefolia*, *H. calycinum*, *P. tenella*) around this plastic tunnel were also sampled.

Serological assay

Double-antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) was performed (Clark and Adams 1977) using a commercially available ELISA kit for TSWV (Bioreba AG, Switzerland) according to the Manufacturer's instructions. The plant tissue was homogenised in the extraction buffer in 1:10 w/v ratio. Absorbance (optical density, OD) values were detected at 405 nm wavelength in a Clariostar® Plus microplate reader, (BMG LABTECH, Ortenberg, Germany). Samples were considered positive if the OD value was three times of that of the negative control.

Molecular characterization (RT-PCR)

Total nucleic acid was extracted from the samples (100 mg plant tissue was homogenized of each sample) with Spectrum™ Plant Total RNA Kit (Sigma-Aldrich/Merck USA/Germany) according to the supplier's instructions. The extracted RNAs served as templates for cDNA synthesis using random hexamer primer (Thermo Fisher Scientific, USA). First, all the samples were checked for cucumber mosaic virus (*Cucumovirus CMV*, CMV), tobamoviruses and TSWV by multiplex RT-PCR (Nemes and Salánki 2020). Samples positive for TSWV were further investigated using RT-PCR with TSWV NSs forward (5'-GGCT GTAGCAGAGAGCAATTGTGTCATAATTTT-3') and TSWV NSs reverse (5'-GGACATAGCAAGATTATTTTGA TCCTG-3') primer pair. The parameters for the amplification were as follows: 95 °C for 5 min, 30 cycles of 95 °C for 30 s, 55 °C for 30 s, 72 °C for 90 s, and a final extension step at 72 °C for 10 min. The PCR products were separated and visualized on 1% agarose gels (stained with ethidium bromide). The purified PCR products (GeneJet Gel Extraction Kit, Thermo Fisher Scientific, USA) were sent to determine their nucleotide sequences (Eurofins Biomi Ltd. Hungary), and the sequence data were deposited in the NCBI GenBank database (GenBank accession numbers of this study are listed in Table 1).

Phylogenetic analysis

Nucleotide sequences of the TSWV NSs partial gene from this study were blasted and aligned by ClustalW method (v1.6) (Thompson et al. 1994) with sequences retrieved from the NCBI GenBank. Maximum Likelihood phylogenetic tree was constructed using MEGA 12 software (Kumar et al. 2024) and was composed of representatives of different TSWV clades retrieved from the NCBI GenBank database. Groundnut ringspot orthotospovirus (*Orthotospovirus arachianuli*, GRSV) SA 05 isolate (under accession number JN571117) was chosen as an outgroup.

Table 1 TSWV strains or isolates included in the phylogenetic analysis

Strain/isolate	Host plant	Collection date	Location	GenBank Accession number
TS 2	<i>Capsicum annuum</i> Kapitány F1	25/05/2022	Kecskemét, Hungary	PX114138
TS 4	<i>C. a.</i> line F2	19/07/2021	Kecskemét, Hungary	PX114139
TS 5	<i>C. a.</i> line F2	25/05/2022	Kecskemét, Hungary	PX114140
TS 6	<i>C. a.</i> Kapitány F4	19/07/2021	Kecskemét, Hungary	PX114141
TS 7	<i>C. a.</i> line F2	19/07/2021	Kecskemét, Hungary	PX114142
TS 8	<i>C. a.</i> line F2	19/07/2021	Kecskemét, Hungary	PX114143
TS 9	<i>C. a.</i> line F2	19/07/2021	Kecskemét, Hungary	PX114144
TS 10	<i>C. a.</i> line F2	19/07/2021	Kecskemét, Hungary	PX114145
TS 11	<i>Prunus tenella</i>	19/07/2021	Kecskemét, Hungary	PX114146
TS 12	<i>Hypericum calycinum</i>	19/07/2021	Kecskemét, Hungary	PX114147
TS 13	<i>Parthenocissus quinquefolia</i>	19/07/2021	Kecskemét, Hungary	PX114148
HUP4-2012-WT	<i>C. a.</i> Cibere	June 2012	Szentes, Hungary	KJ649611
TSWV-QLD1	<i>C. a.</i> Yolo Wonder	2014	Australia	KT717693
P202/3WT	<i>C. a.</i>	1999	South Italy	HQ830187
CAA19	<i>C. a.</i>	1991	France	FR692822
PepCal_22	<i>C. a.</i>	2014	Italy	MG989675
Pujol1TL3	<i>Solanum lycopersicum</i>	2003	Spain	KP008131
TswvTRPep	<i>C. a.</i>	2016	Turkey	MK692930
LK-1	<i>Amaranthus thunbergii</i>	15/06/2015	South Africa	KY250490
Pepper1 CY-CN	<i>C. a.</i>	2009	South Korea	HM581939
YNta	<i>Nicotiana tabacum</i>	01/09/2013	China	KM657115
BR	<i>C. a.</i>	05/06/2016	South Korea	MF159062
Tarquinia	<i>C. a.</i>	2016	Italy	MG983521
P203	<i>C. a.</i>	2008	Spain	FR692900
VE430	<i>C. a.</i>	-	Spain, Almeria	DQ376184
P1	<i>C. a.</i>	-	South Korea	LC549181
BasC	<i>Ocimum basilicum</i>	2014	USA	KU179515
100/23	<i>Solanum lycopersicum</i>	2023	Montenegro	PP968746
P105	<i>C. a.</i>	-	North Italy	DQ376178
71SET22S	<i>Solanum lycopersicum</i>	May 2022	Croatia	OQ534343
GRSV SA05	<i>Arachis hypogaea</i>	-	South Africa	JN571117

TSWV isolates indicated by TS 2, 4–13 are those collected in this study, while the others were retrieved from the NCBI GenBank collection

The evolutionary history was inferred by using the Maximum Likelihood method and Tamura-model (Tamura 1992). The tree with the highest log likelihood (−4704.02) is shown. The percentage of trees in which the associated taxa clustered together (1000 replicates) is shown next to the branches (Felsenstein 1985). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. This analysis involved 31 nucleotide sequences. There were a total of 1353 positions in the final dataset.

Results

Macroscopic symptoms

All collected plant samples, except two pepper samples, showed leaf symptoms, and in the case of pepper plants symptoms were also observed on the fruits. On the leaves

of *C. annuum* breeding lines, symptoms included mosaic, chlorotic ringspot pattern or necrotic lesions and leaf deformation, while on the fruit typical ringspot or yellow/green/red color pattern and necrotic spots were observed. *P. quinquefolia*, *H. calycinum* and *P. tenella* showed different systemic symptoms like mottling, mosaic, chlorotic ringspot or ring pattern and leaf deformation (Fig. 1).

Serological assay

All symptomatic plant samples were positive for TSWV in DAS-ELISA observation while two samples from symptomless pepper plants gave negative results. The eight positive pepper and three ornamental plant samples were subjected for molecular analysis.



Fig. 1 Macroscopic symptoms of the ornamental plants infected with TSWV around the plastic tunnel used for pepper breeding in Kecskemét. a–b: leaves of *Parthenocissus quinquefolia*; c–d: leaf samples of *Hypericum calycinum*; e: leaves of *Prunus tenella*

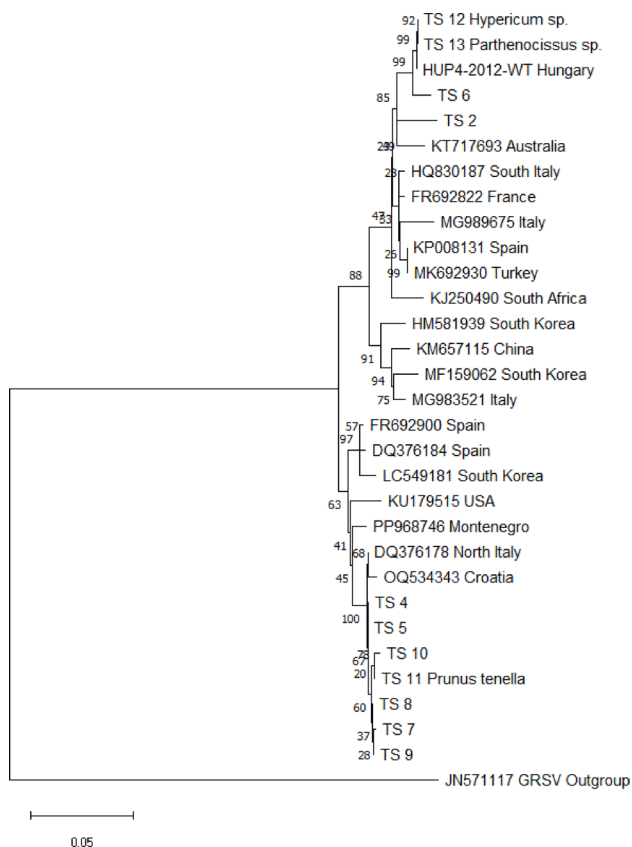


Fig. 2 Maximum likelihood phylogenetic tree based on the partial nucleotide sequences of TSWV NSs gene. Sequences characterized in this study are indicated with the isolate name (TS 2, 4–13) while those retrieved from the NCBI GenBank are indicated with the accession numbers and country of origin

Molecular characterization and phylogenetic analysis

All samples were tested for the most common viral pathogens in pepper growing plastic tunnels in Hungary, such as CMV, tobamoviruses and TSWV, using multiplex RT-PCR. No amplicons were observed for CMV and tobamoviruses, while all symptomatic pepper plants and ornamental species yielded cca. 1400 nucleotide long products using primer pair specific to the NSs segment of the TSWV genome. After the nucleotide sequences of the purified amplicons were determined, they were aligned with different sequences from distinct countries and continents retained from the NCBI GenBank and an ML tree was constructed for phylogenetic analyses, revealing three major clades (Škorić et al. 2025) (Fig. 2). The pepper isolates were genetically diverse, representing two clades. The isolate collected from *H. calycinum* grouped together with the isolate from *P. quinquefolia*, while the isolate collected from *P. tenella* located on the other clade. The nucleotide sequence homology values varied between 93.0 and 100.0% according to the pairwise distance analysis (Supplementary Table S1).

Discussion

In TSWV epidemic cycles under climate conditions in Hungary, reservoir host plants play a crucial role in sustaining the virus source between growing seasons in pepper or tomato cultivation. Since TSWV has an extremely broad host range, a wide variety of plant species can serve as reservoirs for the pathogen. The most studied reservoirs are annual and perennial herbaceous weed plants (Batuman et al. 2017; Fidan et al. 2024; Kil et al. 2020). These plants are common hosts of both TSWV and thrips, with the insect vectors usually feeding and laying eggs on their leaves.

However, perennial woody plant species around the greenhouses or plastic tunnels may serve not only as simple virus reservoirs, but during subsequent years they can assist virus evolution by accumulating distinct strains facilitated by recombination or viral reassortant formation. These processes may lead to locally emerging new RB strains of TSWV. The perennial ornamental species can be infected by feeding thrips specimens repeatedly over multiple growing seasons, thus contributing to the recurrence of the virus serving as an infection source in the beginning of the growing season.

In our experiment, three woody ornamental species were confirmed to be infected by TSWV, and the phylogenetic analysis revealed that the isolate collected from *P. tenella* differed from the two other isolates originated from *H. calycinum* and *P. quinquefolia*. Moreover, the isolates

originated from the pepper breeding lines within the plastic tunnel also displayed genetic diversity.

To our knowledge, these ornamental species (*P. quinquefolia*, *H. calycinum*, *P. tenella*) are not listed among the host plants of TSWV on the EPPO (European and Mediterranean Plant Protection Organization) website, nor are they included in the revised host range compiled by Parrella et al. (2003). These findings highlight the potential role of ornamental and non-crop perennial vegetation in the epidemiology of TSWV, particularly in the surroundings of cultivation facilities. The presence of these plants may contribute to the persistence of the virus and may act as reservoirs for further infection. Our results support the importance of monitoring and managing of the vegetation surrounding the cultivation sites (greenhouses and plastic tunnels) to minimize the risk of TSWV outbreaks and the emerging of new virus strains.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s41348-026-01283-6>.

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Declarations

Conflict of interest We have no conflicts of interest in the published data.

Ethical approval This work is not dealing with humans or animals.

Informed consent All authors declare that they have no conflict of interest.

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References

- Abudurexiti A, Adkins S, Alioto D, Alkhovsky SV, Avšič-Županc T, Ballinger MJ et al (2019) Taxonomy of the order Bunyavirales: update 2019. Arch Virol 164:1949–1965. <https://doi.org/10.1007/s00705-019-04253-6>
- Adkins S (2000) Tomato spotted wilt virus — positive steps towards negative success. Mol Plant Pathol 1:151–157. <https://doi.org/10.1046/j.1364-3703.2000.00022.x>
- Almási A, Csilléry G, Csömör Z, Nemes K, Palkovics L, Salánki K, Tóbiás I (2015) Phylogenetic analysis of Tomato spotted wilt virus (TSWV) NSs protein demonstrates the isolated emergence of resistance-breaking strains in pepper. Virus Genes 50(1):71–78. <https://doi.org/10.1007/s11262-014-1131-3>
- Almási A, Pinczés D, Tímár Z, Sárar R, Palotás G, Salánki K (2023) Identification of a new type of resistance breaking strain of Tomato spotted wilt virus on tomato bearing the *Sw-5b* resistance gene. Eur J Plant Pathol 166:219–225. <https://doi.org/10.1007/s10658-023-02656-5>
- Batuman O, Turini TA, Oliveira PV, Rojas MR, Macedo M, Mellinger HC, Adkins S, Gilbertson RL (2017) First report of a resistance-breaking strain of Tomato spotted wilt virus infecting tomatoes with the *Sw-5* tospovirus-resistance gene in California. Plant Dis 101:637. <https://doi.org/10.1094/PDIS-09-16-1371-PDN>
- Batuman O, Turini TA, Le Strange M, Stoddard S, Miyao G, Aegerter BJ, Chen L-F, Mc Roberts N, Ullman DE, Gilbertson RL (2020) Development of an IPM strategy for thrips and *Tomato spotted wilt virus* in processing tomatoes in the Central Valley of California. Pathogens 9(8):636. <https://doi.org/10.3390/pathogens9080636>
- Boiteux LS, De Avila AC (1994) Inheritance of a resistance specific to Tomato spotted wilt tospovirus in *Capsicum chinense* ‘PI 159236’. Euphytica 75(1):139–142. <https://doi.org/10.1007/BF0024541>
- Clark MF, Adams AN (1977) Characteristics of the microplate method of enzyme-linked immunosorbent assay for the detection of plant viruses. J Gen Virol 34(3):475–483. <https://doi.org/10.1099/0022-1317-34-3-475>
- Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
- Fidan H, Gonbadi A, Kitis YE (2024) Exploring the weed host range of resistance-breaking variants of Tomato spotted wilt orthotospovirus (TSWV) across life cycles in Türkiye. Plant Protect Sci 60:124–138. <https://doi.org/10.17221/118/2023-PPS>
- German TL, Ullman DE, Moyer JW (1992) Tospoviruses: diagnosis, molecular biology, phylogeny, and vector relationships. Annu Rev Phytopathol 30:315–348. <https://doi.org/10.1146/annurev.y.30.090192.001531>
- Kil EJ, Chung YJ, Choi HS, Lee S, Kim CS (2020) Life cycle-based host range analysis for Tomato Spotted Wilt Virus in Korea. Plant Pathol J Seoul 36(1):67–75. <https://doi.org/10.5423/PPJ.FT.12.2019.0290>
- Kormelink R, Garcia ML, Goodin M, Sasaya T, Haenni AL (2011) Negative-strand RNA viruses: the plant-infecting counterparts. Virus Res 162(1–2):184–202. <https://doi.org/10.1016/j.virusres.2011.09.028>
- Kumar S, Stecher G, Suleski M, Sanderford M, Sharma S, Tamura K (2024) Molecular Evolutionary Genetics Analysis Version 12 for adaptive and green computing. Mol Biol Evol 41:1–9. <https://doi.org/10.1093/molbev/msae263>
- Margaría P, Ciuffo M, Turina M (2004) Resistance breaking strain of Tomato spotted wilt virus (Tospovirus; Bunyaviridae) on resistant pepper cultivars in Almería, Spain. Plant Pathol 53:795–795. <https://doi.org/10.1111/j.1365-3059.2004.01082.x>
- Margaría P, Ciuffo M, Pacifico D, Turina M (2007) Evidence that the nonstructural protein of Tomato spotted wilt virus is the avirulence determinant in the interaction with resistant pepper carrying the TSW gene. Mol Plant-Microbe Interact 20(5):547–558. <https://doi.org/10.1094/MPMI-20-5-0547>
- Nemes K, Salánki K (2020) A multiplex RT-PCR assay for the simultaneous detection of prevalent viruses infecting pepper (*Capsicum annuum* L.). J Virol Methods 278:113838. <https://doi.org/10.1016/j.jviromet.2020.113838>

- Oliver JE, Whitfield AE (2016) The genus *Tospovirus*: emerging bunyaviruses that threaten food security. *Ann Rev Virol* 3(1):101–124. <https://doi.org/10.1146/annurev-virology-100114-055036>
- Pappu HR, Jones RA, Jain RK (2009) Global status of tospovirus epidemics in diverse cropping systems: successes achieved and challenges ahead. *Virus Res* 141(2):219–236. <https://doi.org/10.1016/j.virusres.2009.01.009>
- Parrella G, Gognalons P, Gebre-Selassie K, Vovlas C, Marchoux G (2003) An update of the host range of Tomato spotted wilt virus. *J Plant Pathol* : 227–264
- Roggero P, Melani V, Ciuffo M, Tavella L, Tedeschi R, Stravato VM (1999) Two field isolates of Tomato Spotted Wilt Tospovirus overcome the hypersensitive response of a pepper (*Capsicum annuum*) hybrid with resistance introgressed from *C. chinense* PI152225. *Plant Dis* 83:965–965. <https://doi.org/10.1094/PDIS.1999.83.10.965A>
- Roggero P, Masenga V, Tavella L (2002) Field isolates of Tomato spotted wilt virus overcoming resistance in pepper and their spread to other hosts in Italy. *Plant Dis* 86:950–954. <https://doi.org/10.1094/PDIS.2002.86.9.950>
- De Ronde D, Butterbach P, Kormelink R (2014) Dominant resistance against plant viruses. *Front Plant Sci* 5:307. <https://doi.org/10.3389/fpls.2014.00307>
- Scholthof KB, Adkins S, Czosnek H, Palukaitis P, Jacquot E, Hohn T, Hohn B, Saunders K, Candresse T, Ahlquist P, Hemenway C, Foster GD (2011) Top 10 plant viruses in molecular plant pathology. *Mol Plant Pathol* 12(9):938–954. <https://doi.org/10.1111/j.1364-3703.2011.00752.x>
- Škorić D, Zindović J, Grbin D, Pul P, Božović V, Margaria P, Mehle N, Pecman A, Kogej Zwitter Z, Kutnjak D, Vučurović A (2025) Tomato spotted wilt virus in tomato from Croatia, Montenegro and Slovenia: genetic diversity and evolution. *Front Microbiol* 16:1618327. <https://doi.org/10.3389/fmicb.2025.1618327>
- Srinivasan R, Abney MR, Culbreath AK, Kemeraite RC, Tubbs RS, Monfort WS, Pappu HR (2017) Three decades of managing Tomato spotted wilt virus in peanut in southeastern United States. *Virus Res* 241:203–212. <https://doi.org/10.1016/j.virusres.2017.05.016>
- Takács A, Jenser G, Kazinczi G, Horváth J (2006) Natural weed hosts of *Tomato spotted wilt virus* (TSWV) in Hungary. *Cereal Res Commun* 34:685–688. <https://doi.org/10.1556/CRC.34.2006.1.171>
- Takeda A, Sugiyama K, Nagano H (2002) Identification of a novel RNA silencing suppressor, NSs protein of Tomato spotted wilt virus. *FEBS Lett* 532:75–79. [https://doi.org/10.1016/S0014-5793\(02\)03632-3](https://doi.org/10.1016/S0014-5793(02)03632-3)
- Tamura K (1992) Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G+C-content biases. *Mol Biol Evol* 9:678–687. <https://doi.org/10.1093/oxfordjournals.molbev.a040752>
- Tentchev D, Verdin E, Marchal C, Jacquet M, Aguilar JM, Moury B (2011) Evolution and structure of Tomato spotted wilt virus populations: evidence of extensive reassortment and insights into emergence processes. *J Gen Virol* 92:961–973. <https://doi.org/10.1099/vir.0.029082-0>
- Thompson JD, Higgins DG, Gibson TJ (1994) Clustal W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Res* 22:4673–4680. <https://doi.org/10.1093/nar/22.22.4673>
- Tiberini A, Cillo F, Gentili A, Bertin S (2025) Tomato spotted wilt virus (*Orthotospovirus tomatomaculæ*), a cyclically occurring threat to crop production worldwide. *Ann Appl Biol* 186:93–114. <https://doi.org/10.1111/aab.12977>
- Tsompana M, Abad J, Purugganan M, Moyer JW (2005) The molecular population genetics of the Tomato spotted wilt virus (TSWV) genome. *Mol Ecol* 14:53–66. <https://doi.org/10.1111/j.1365-294X.2004.02392.x>

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