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# Evaluation of genetic diversity of tomato spotted wilt virus (TSWV) NSs gene region isolates at geographical level

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**Abstract:** One of the most significant plant protection problems that adversely affect agricultural production is diseases caused by viruses, as there are no direct and rapid control methods. Tomato spotted wilt virus (TSWV), which is known to cause major losses in vegetable production and is quite common in the Mediterranean basin, is one of these viruses. In reducing the prevalence of the agent, control of vector insects and use of resistant varieties are the primary parameters. In this study, the genetic diversity of the partial Non-Structural NSs gene, which produces a putative silencing suppressor protein of TSWV, was investigated at the level of geographical populations. A total of 325 isolates were clustered from Eastern European, European Mediterranean, Asian, African, and American populations and geographic genetic diversity analyses were performed. Phylogenetic analyses revealed 2 major phylogroups (Clade I and II). Isolates reported from Asia and Africa were clustered only in Clade II, while other isolates were distributed in both groups. Haplotype network analyses revealed that the isolates had genotypes partially related to their geography. In support of these results, molecular variance analyses (AMOVA) showed that there were significant results for both proposals when applied between and within geographic groups. The findings highlight that TSWV has experienced different evolutionary processes in geographical regions, that the virus spreads along different genetic lines in regions, that local genotypes may dominate in regions and potentially adapt more quickly, and that local plant health institutions should increase regional quarantine measures and isolation strategies, and that it is important to take these genetic differences into account in order for the control to be more effective and targeted.

**Keywords:** TSWV, NSs gene, haplotype network, AMOVA

## 1. Introduction

Tospoviruses (Order Bunyavirales, family Tospoviridae) are a serious threat to crop yield, costing more than $1 billion globally (Prins and Goldbach 1998). Among these viruses, tomato spotted wilt virus (TSWV) is a significant pathogen that infects over 1000 plant species across more than 85 families, including important crops such as tomato, lettuce, and pepper (Gupta et al. 2018). However, the emergence of TSWV resistance-breaking strains that overcome the resistance genes in vegetables such as tomatoes and peppers, which are among the most produced and consumed vegetables globally, has become one of the production-limiting factors in the Mediterranean basin (Turina et al. 2012).

The TSWV viral particle, like other members of the Bunyaviridae family, is spherical and membrane-enveloped. Genome is consists of three single-stranded RNAs (ssRNAs) named L (Large ~ 8.9 kb ), M (Medium ~ 4.8 kb), and S (Small ~ 2.9 kb) (Turina et al. 2016). Large RNA that encodes RNA-dependent RNA polymerase (RdRp) needs to be copied onto a complementary strand before it can be read because its polarity is negative (De Haan et al. 1991). The M RNA is a double-stranded, antisense RNA that encodes proteins in the amino and carboxy-terminal regions of glycoprotein precursors (GN and GC proteins, 58 kDa and 95 kDa, respectively). These proteins are crucial for virion assembly, development, and release in the host plant (Nagata et al. 2000; Whitfield et al. 2008). The small S RNA genome is a double-sense and antisense RNA that encodes nucleoprotein (NSM 33.6 kDa) and nonstructural protein (NSs 30 kDa) from complementary RNA, which functions as a viral suppressor of RNA silencing, and both proteins play an important role in the infection cycle (Snippe et al. 2007; Ocampo et al. 2016; Guo et al. 2017).

The global dissemination of TSWV is primarily driven by its efficient insect vector, the western flower thrips (*Frankliniella occidentalis*). This vector exhibits several traits that facilitate the virus's spread, including high fecundity, a short generation time, significant mobility, a preference for concealed environments, and a polyphagous feeding habit (Kamran et al. 2024). Furthermore, the development of resistance to multiple insecticides in *F. occidentalis* has exacerbated the spread of vectored plant viruses such as TSWV (Reitz et al. 2020). Moreover, TSWV has been reported to be present in the seeds of plants such as peppers and tomatoes with different rates of transmission (Jones 1944; Wang et al. 2022). Since TSWV infects a wide range of hosts, the symptoms it induces are quite diverse and generally cause brownish ring spots, yellowing, necrosis of several plant organs, leaf purple and curling, stunting or growth retardation, fruit deformities, necrotic spots, local lesions, and even plant death (Francki and Hatta 1981; Oetting 1991).

Plants typically employ RNA silencing as a defense mechanism against viral infections. However, plant viruses have evolved countermeasures, including the production of RNA silencing suppressors. The NSs protein of TSWV acts as an RNA silencing suppressor, playing a crucial role in facilitating the virus's infection, replication, and transmission. In this study, geographic populations were established using partial NSs gene sequences of TSWV reported from various regions of the world, including Turkey. The aim was to elucidate the genetic diversity and dispersal dynamics of this gene region within the framework of population genetics.

## 2. Materials and Method

### *2.1. Isolates and phylogenetic analyses*

In this study, the nucleotide sequences of the NSs gene of TSWV, comprising 318 global isolates from various hosts and geographical regions available in GenBank (accessed on July 21, 2024), along with 7 tomato isolates obtained as part of project no. 2022-01.BŞEÜ.06-02, were analyzed. The partial nucleotide sequence of the NSs gene covers the nt sequence at position 128-851 in the small S genome (reference isolate: accession no MN854653, South Korea).

Phylogenetic relationships among 325 TSWV isolates were inferred based on partial NSs gene sequences. Nucleotide sequences of the NSs gene were aligned using ClustalW in MEGA 11 software (Tamura et al. 2021). An unrooted phylogenetic tree was constructed using the Neighbour-Joining (NJ) method, with the Tamura-Nei model (Tamura and Nei 1993) applied as the substitution parameter and uniform rates of complete deletion for gaps in the partial NSs gene region. Phylogenetic data obtained using the algorithms and methods of Mega 11 software (Tamura et al. 2021) were transferred to the iTOL (Interactive Tree Of Life) V.6 online software (Letunic and Bork 2024) for re-evaluation and visualization. In addition, 1000 boostrap was applied to increase the reliability values of the branches of the obtained clusters.

### *2.2. Haplotype network analyses*

Haplotype networks were constructed at the geographic level to illustrate the genetic variation in the aligned NSs gene sequences of TSWV. The isolates were classified based on their geographic origins: the Asian population (n=22) (South Korea and China), the American population (n=15) (U.S.A. and Mexico), the Eastern European population (n=41) (Serbia, Croatia, Slovenia, Bulgaria, and Hungary), the Euro-Mediterranean population (n=243) (Türkiye, France, Spain, Italy, U.K., Germany, Netherlands, and Algeria), and the African population (n=3) (South Africa). Haplotype data for the partial NSs gene of TSWV were generated and analyzed using DnaSP v6.12.03 (Rozas et al. 2017). The haplotype networks were constructed using the Median Joining (MJ) algorithm (Bandelt et al. 1999) and visualized using PopART software (http://popart.otago.ac.nz) (Leigh and Bryant 2015).

### *2.3. Analyses of molecular variance (AMOVA)*

Molecular variance analysis (AMOVA) (Excoffier et al. 1992) was performed to estimate the effects of genotype distributions on the total variation of TSWV isolates based on the partial NSs gene. Nucleotide sequence data for the NSs gene region from a total of 325 TSWV isolates were compiled to form the dataset. The analyses were conducted using Arlequin version 3.5.2.2software (Excoffier and Lischer 2010).

## 3. Results

### *3.1. Phylogenetic inferences*

Phylogenetic analyses examining the molecular evolutionary relationships among geographic populations revealed that the 325 TSWV isolates were grouped into two major clades. In our study, these clades were designated as Clade I and Clade II (Figure 1).

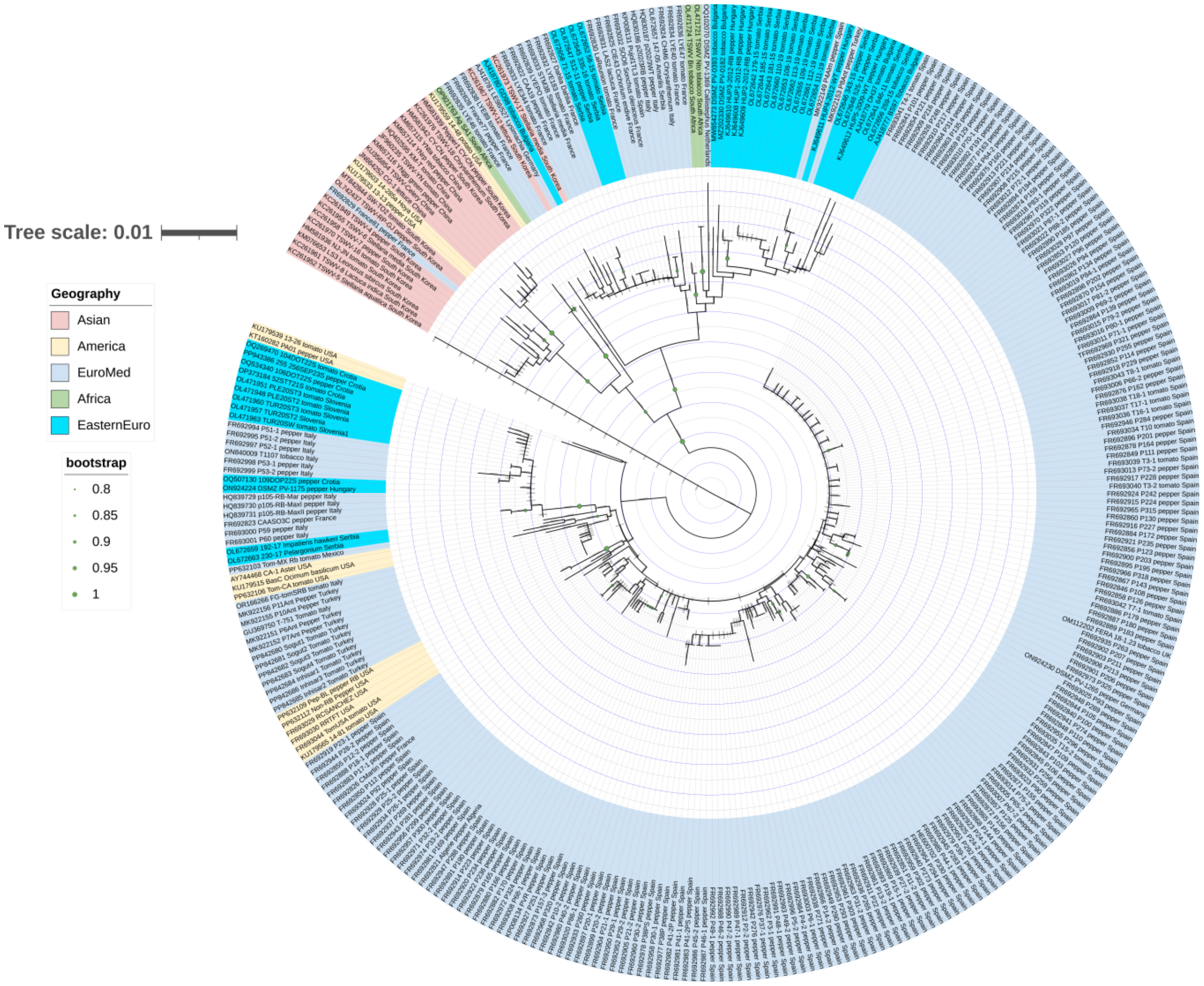

**Fig. 1** Phylogenetic tree based on partial NSs gene of the TSWV (n=325 isolates)

Clade I comprised a total of 255 isolates, including 11 from the America, 13 from Eastern Europe, and 221 from the Europe-Mediterranean region. Notably, no isolates from Asia or Africa were present in Clade I. In contrast, Clade II consisted of 80 TSWV NSs gene isolates, including 22 from Asia, 3 from Africa, 3 from the Americas, 28 from Eastern Europe, and 24 from the Europe-Mediterranean region. Additionally, while the Türkiye isolate P8Ant (GenBank accession number MK922153) clustered within Clade I, the other Türkiye isolates were also found in Clade I. Specifically, the seven TSWV isolates obtained from project no. 2022-01.BŞEÜ.06-02, along with four TSWV isolates from Antalya recorded in GenBank, clustered within the same subclade, showing a close relationship with each other and one isolate from Italy. The phylogenetic tree showed that in general, isolates obtained locally clustered more closely with each other.

### *3.2. Haplotype Network Results*

The haplotype network analysis of the partial NSs gene region from 325 TSWV isolates illustrated distinct clustering patterns based on geographic origins (Figure 2). The 22 Asian isolates had 17 haplotypes, while the 243 Europe-Mediterranean isolates had 123 haplotypes. Additionally, the 15 American isolates corresponded to 15 distinct haplotypes, the 3 African isolates formed 2 haplotypes, and the 41 Eastern European isolates were had 27 haplotypes. However, the most distinct and common haplotypes originated from isolates obtained from Spain. The Europe-Mediterranean isolates (in pink) form the largest and most diverse group, indicating a higher level of genetic diversity within this region. Conversely, isolates from Asia (green) and Africa (light blue) show more distinct and isolated clusters, reflecting limited gene flow between these regions and others. The isolates from the Americas (yellow) and Eastern Europe (blue) are distributed across smaller clusters, suggesting a moderate degree of genetic differentiation.

### *3.3. Results of molecular variance analysis (AMOVA) among geographical populations*

The AMOVA results for the partial NSs gene region of TSWV revealed that 36.49% of the total genetic variation is attributed to differences among populations (ΦST = 0.36491, $p < 0.001$), indicating significant genetic differentiation between the defined geographic populations (Asian, Euro-Med, America, Africa, and Eastern Europe) (Table 1).

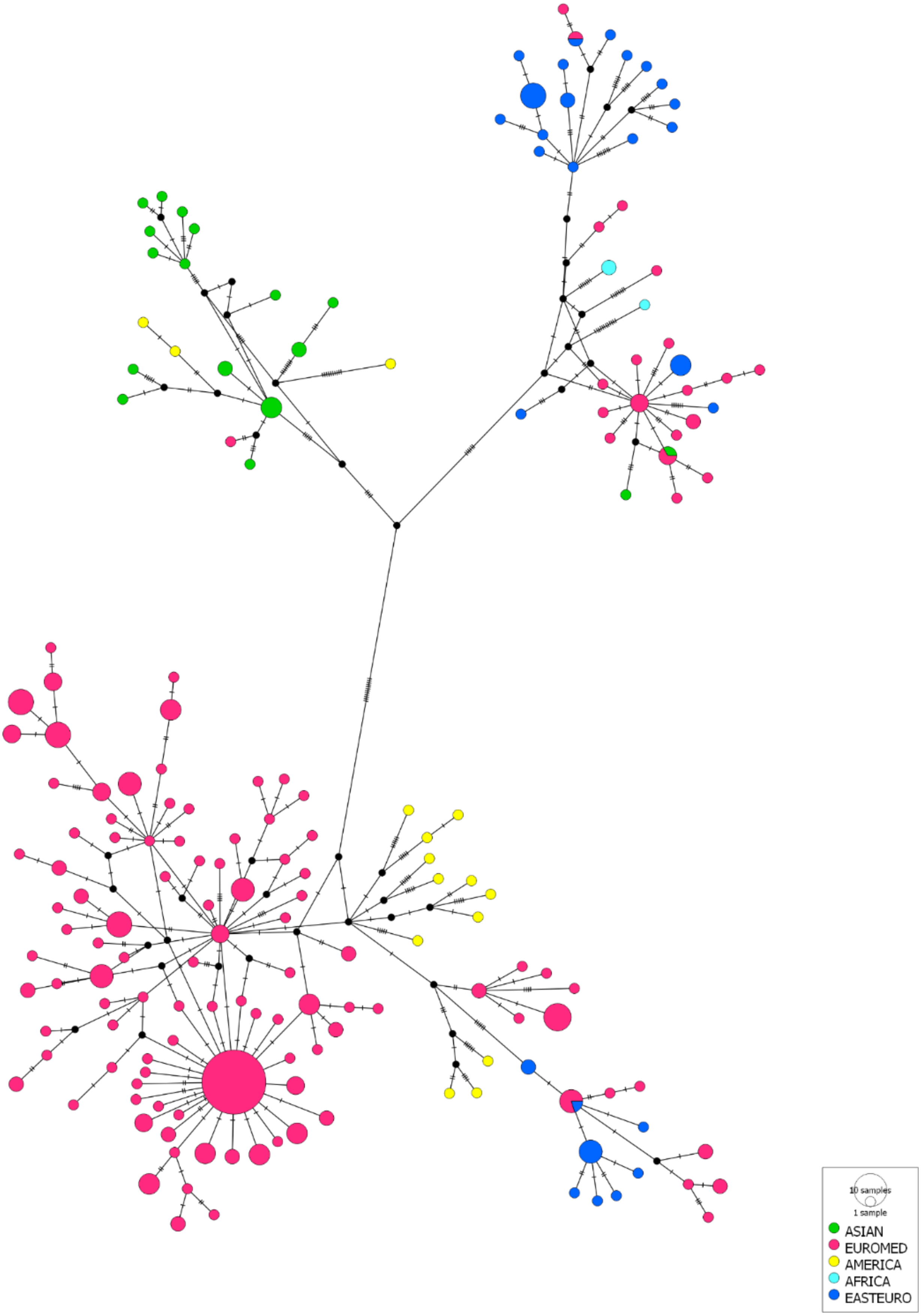

**Fig. 1** Network analysis of TSWV partial NSs haplotypes. The colour of each node represents different geographical populations and allele types. Green: Asian, Pink: Euro-Med, Yellow: American, Light blue: Africa, and Blue: Eastern Europe populations

**Table 1** Molecular variance results obtained among and within five different geographical populations consisting of NSs isolates of TSWV

| Population definition | Source of variation | Sum of squares | Variance components | Percentage variation | ΦST and p-value |
|---|---|---|---|---|---|
| Partial NSs gene region<br>Pop1: Asian<br>Pop2:Euro-Med<br>Pop3: America<br>Pop4: Africa<br>Pop5: Eastern-Euro | Among populations | 421165.597 | 63.952 | 36.49098 | ΦST=0.36491<br>P< 0.001 |
| | Within populations | 31935505.329 | 111.302 | 63.50902 | |
| Total | | 32356670.926 | 175.254 | | |

Significance (1000 permutations): ΦST: Pr(random value > observed ΦST) < 0.001

The remaining 63.51% of the variation was found within populations, highlighting the substantial genetic diversity present within each region. These results demonstrate that both inter-population and intra-population genetic variations contribute to the overall genetic structure of the TSWV NSs gene.

## 4. Discussion

TSWV is one of the most economically destructive plant pathogens globally, with its rapid evolution and adaptation to various hosts and environments presenting major challenges for agriculture and disease management worldwide. Given the virus's extensive genetic diversity and adaptability, the development of resistant cultivars through genetic breeding has become crucial in mitigating crop losses. Breeding efforts that focus on enhancing resistance to TSWV in economically important crops, such as tomatoes, are essential for reducing the virus's spread and ensuring sustainable agricultural production in affected regions. Therefore, in this study, phylogenetic, haplotype network and molecular variance analyses were performed to understand the genetic diversity of the NSs gene of TSWV, which is responsible for breaking plant resistance genes, at the geographical level and to contribute to future studies. Population genetic studies are being conducted to understand the epidemiological cycle, evolutionary processes, host-vector interactions, genetic diversity and many factors related to evolutionary dynamics of plant viruses (Zelyüt and Ertunç 2021; Karanfil et al. 2023; Santosa et al. 2023; Güller et al. 2023). In addition, population dynamics have been reported from some studies for different gene regions of TSWV (Abadkhah et al. 2018; Morca et al. 2022; Usta et al. 2023). Here, NSs gene region isolates of TSWV were clustered in a geographical hierarchy and examined comprehensively.

NSs, identified as the suppressor protein of the host plant’s gene silencing mechanism, plays a pivotal role in overcoming plant resistance as an avirulence (avr) factor (De Ronde et al. 2013). Recent studies have provided detailed insights into how various domains of the NSs protein contribute to its gene silencing suppression function and its role as an avr factor (Du et al. 2020). Margaria et al. (2014) reported that while the NSs protein is not required for TSWV acquisition by thrip larvae, it is essential for its abundant accumulation in adults, which is necessary for successful virus transmission. TSWV resistance isolates are further categorized into resistance-inducing (RI) isolates, which trigger a hypersensitive response in resistant cultivars, and resistance-breaking (RB) isolates, which can overcome host resistance (Peiró et al. 2014; Turina et al. 2016). Thus, analyses conducted in other studies to determine isolates capable of breaking host resistance genes and the phylogenetic relationships of other isolates revealed the existence of 2 phylogroups for the NSs gene (Almási et al. 2015). In this study, the topology of the phylogenetic tree constructed with 325 isolates was similar to the tree topology reported by Almási et al. (2015). Similarly, the data indicating that isolates that breaking-resistance genes did not show a separate clustering showed the same results in our study. However, one of the most important findings regarding the phylogenetic tree is that the clustering of the isolates is mostly due to geographical origin. Almási et al. (2015) reported similar results for pepper TSWV isolates.

Herein, network analyses indicates the presence of geographically structured genetic diversity within TSWV populations. The central positions of certain haplotypes suggest that these may be ancestral or more widespread genotypes, particularly within the Europe-Mediterranean region. Meanwhile, the separation of Asian and African isolates into distinct clusters could indicate localized evolution, potentially driven by region-specific selection pressures or vector dynamics. These results align with the broader geographic distribution of the virus and its vector, *F. occidentalis*, which is known to contribute to the global spread and genetic diversification of TSWV. In addition, the knowledge that TSWV is also transmitted by pepper and tomato seeds, as reported in another study, may contribute significantly to these findings (Jones 1944; Wang et al. 2022).

The AMOVA results for the partial NSs gene region of TSWV indicate that 36.49% of the total genetic variation is explained by differences among the five geographic populations (Asian, EuroMed, America, Africa, and Eastern Europe), with a highly significant ΦST value of 0.36491 ($p < 0.001$) (Table 1). This substantial inter-population variation suggests strong genetic differentiation among these regions, likely driven by limited gene flow and the localized evolution of TSWV in different parts of the world. This geographic structuring could be influenced by factors such as regional differences in host plants, climatic conditions, or the distribution of the primary vector, F. occidentalis. In contrast, 63.51% of the genetic variation occurs within populations, highlighting considerable genetic diversity at the regional level. The high level of intra-population variation suggests that TSWV isolates within each geographic group are still undergoing genetic diversification, possibly due to frequent recombination events, natural selection, or adaptation to local environmental conditions. These findings underscore the complex population structure of TSWV, with both geographic isolation and local evolutionary forces contributing to its genetic diversity. The significant ΦST value further suggests that these regional populations are evolving independently, which has important implications for understanding the spread and management of TSWV on a global scale.

## 5. Conclusion

This study offers important insights into the genetic diversity and population structure of TSWV by analyzing the NSs gene across 325 isolates from around the world. The findings demonstrate significant geographic structuring, with notable differentiation among populations from Asia, Africa, the Americas, Eastern Europe, and the Euro-Mediterranean region. The phylogenetic and haplotype network analyses reveal that this structuring is largely driven by geographic origin rather than resistance-breaking capacity, suggesting localized evolution influenced by regional environmental conditions and vector dynamics. The substantial inter-population variation, as indicated by the AMOVA results, further highlights the independent evolution of TSWV populations across different regions. At the same time, the high level of intra-population genetic diversity emphasizes the ongoing diversification of TSWV within these regions. These results underscore the importance of considering both geographic isolation and local evolutionary pressures in the global management and control of TSWV. Future research should continue to explore the role of genetic recombination, natural selection, and host-vector interactions in shaping the virus's evolution, particularly with regard to the development of resistant cultivars and effective disease management strategies.

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## Conflict of interest disclosure:

The authors state there is no competing interest.

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