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Phenotypic and Genotypic Structure of *Phytophthora infestans* Populations Infecting Tomato in Türkiye

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Correspondence: Mehmet Erhan Göre (egore@ibu.edu.tr)**Received:** 7 February 2026 | **Revised:** 11 May 2026 | **Accepted:** 12 May 2026**Keywords:** clonal lineages | clone-corrected analysis | mefenoxam resistance | microsatellites | migration dynamics | virulence

ABSTRACT

Phytophthora infestans, causing late blight, remains a major constraint to tomato production due to its high genetic variability, rapid adaptation and evolving fungicide resistance. We investigated the population structure of *P. infestans* isolates from South Marmara, Türkiye, during the 2020–2022 growing seasons using clone-corrected population genetic analysis. Isolates were characterized by mating type, in vitro mefenoxam sensitivity, 12 polymorphic simple-sequence repeat (SSR) markers, and virulence assays using potato differential lines. Overall, 89% of the isolates were A1 mating type and 11% were A2. Mefenoxam assays showed 56% of isolates were sensitive, 21% intermediate and 23% resistant. SSR genotyping revealed extremely high clonality (93.9% clonal fraction) with five distinct clonal lineages among 82 isolates. The population was dominated by the 1_A1_TR clonal lineage (73.2%, $n = 60$), followed by 13_A2_TR, 23_A1_TR1, 23_A1_TR2 and 39_A1_TR. These lineages are first reported here in association with tomato late blight in Türkiye. Isolates from Çanakkale exhibited the highest genetic diversity with four lineages, while isolates found in Balıkesir had only 1_A1_TR present. Clone-corrected analysis of molecular variance revealed no significant genetic differentiation among provinces. *Solanum demissum* virulence assays revealed common phenotypes overcoming multiple potato-specific R-genes ($R1$ – $R11$), absent in agricultural tomatoes. A minimum spanning network illustrated the central role of the dominant 1_A1_TR lineage and its genetic relationships to minor lineages. Thus, the population structure of *P. infestans* in Türkiye is predominantly clonal, probably influenced by migration from Europe and local clonal expansion, with context-dependent fitness advantages under regional production systems.

1 | Introduction

Phytophthora infestans is a hemibiotrophic, heterothallic oomycete that is the most economically significant pathogen of tomato worldwide (Ivanov et al. 2021). Under favourable environmental conditions, the pathogen has the potential to completely devastate the tomato canopy, leading to significant yield losses. Globally, late blight results in an estimated economic loss of \$6.7 billion annually on both potato and tomato crops (Fry et al. 2015; Nowicki et al. 2012). While historically known for causing the ‘Great Famine’ of the 19th century in Ireland (Fry and Goodwin 1997), *P. infestans* continues to trigger catastrophic epidemics today. Recent

examples include the severe, widespread outbreaks on tomato plants across the eastern United States in 2009 (Fry et al. 2013), massive crop failures in Indian tomato and potato fields driven by the emergence of the aggressive 13_A2 lineage (Chowdappa et al. 2015; Dey et al. 2018), and devastating epidemics across Asian potato-growing regions (Guha Roy et al. 2021). The rapid spread and global persistence of the pathogen have been facilitated by international trade of infected plant material (Cohen 2024; Cooke et al. 2011; Dey et al. 2025; Fry et al. 1993). Consequently, since the 1980s, dynamic alterations in *P. infestans* populations have been documented globally (Cooke et al. 2011; Guha Roy et al. 2021; Sjöholm et al. 2013).

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Phenotypic and genotypic characterization studies have demonstrated rapid replacement of established European *P. infestans* populations by genetically distinct lineages across Western Europe and the Mediterranean basin (Huang et al. 2024). Among the identified clonal lineages across solanaceous production regions, the 13_A2 clonal lineage has emerged as particularly significant because to its widespread mefenoxam resistance, and distinct virulence profile (Cooke et al. 2012; Stellingwerf et al. 2018). Initially identified in the Netherlands and Germany in 2004, this lineage subsequently dominated European populations, though its prevalence is now being challenged by emerging lineages such as 37_A2 (Cooke et al. 2012; Schepers et al. 2018). The 13_A2 lineage has demonstrated remarkable global dispersal capacity, spreading beyond Europe to regions including China (Li et al. 2013, 2025), Algeria, where it has triggered severe tomato epidemics (Rekad et al. 2017), and India where it caused devastating outbreaks on both tomato and potato (Chowdappa et al. 2015; Dey et al. 2018), as well as in other Asian countries (Dey et al. 2024; Guha Roy et al. 2021). Notably, subclones of 13_A2 show differential aggressiveness on tomato and potato hosts, and can be subgrouped accordingly (Dey et al. 2018).

Recent surveys have highlighted the dominance of specific clonal lineages in the Mediterranean basin. For instance, in Italy, the population structure of both potato and tomato *P. infestans* populations was dominated by the 13_A2 lineage, along with 2_A1 and 23_A1, indicating a homogenization of populations across hosts (Saville et al. 2021). Similarly, in Algeria, 13_A2 has been reported as a major lineage causing severe epidemics, often coexisting with 23_A1 and 2_A1 (Beninal et al. 2022). These findings suggest a rapid displacement of local populations by aggressive European lineages across the Mediterranean region, with established European clones being replaced in various regions including Western Europe and the Mediterranean basin (El-Ganainy et al. 2022, 2023).

Recent surveillance data revealed a dynamic shift in European populations, where historically dominant lineages such as 1_A1 and 6_A1 are being displaced by more competitive genotypes (Cooke et al. 2012; Puidet et al. 2023). Comparative studies have demonstrated that emerging lineages such as 36_A2 and 37_A2 exhibit superior competitive fitness and spore density compared to 1_A1, resulting in declining frequencies of older lineages across European populations (Puidet et al. 2023).

In Türkiye, tomato production represents a critical agricultural sector with approximately 13.3 million tonnes harvested annually from 166,000 hectares (TURKSTAT 2023). In particular, the South Marmara region (comprising the provinces of Bursa, Balıkesir and Çanakkale), serves as a key production centre, collectively accounting for 19.6% of the total cultivation area and 19.8% of the national output.

The management of late blight outbreaks in Türkiye has become increasingly difficult in recent years, similar to the situation in Europe (Ludwiczewska et al. 2025), the United States (Saville et al. 2015) and Asia (Dey et al. 2024; Islam et al. 2023; Li et al. 2025), partly because of genotypic changes in pathogen population structure and increasing subclonal diversity of the pathogen (Dey et al. 2024). Late blight disease was first identified in Türkiye in 1948 (Bremer et al. 1948) and continues

to pose a significant threat to tomato production owing to favourable climatic conditions (Mizubuti and Fry 1998; Tosun et al. 2007). Since 2017, a marked increase in disease severity has been observed, particularly in major tomato production regions. Although increased disease pressure has been reported since 2017, the present study was not intended to resolve fine-scale temporal dynamics, but rather to characterize the dominant population structure associated with tomato production between 2020 and 2022. Frequent chemical treatments have become necessary to avoid yield losses of up to 100% owing to severe and intense epidemics (Fry et al. 2015; Nowicki et al. 2012). This escalation coincides with documented population structure changes, as shown by analysis of 367 potato isolates revealing 92.1% dominance of the 13_A2 lineage alongside emerging genotypes 34_A1 and 37_A2 (Göre et al. 2021).

The recent detection of 37_A2 in Türkiye raises particular concern given its association with reduced fluazinam sensitivity in Europe—a fungicide crucial for phenylamide-resistant populations (Puidet et al. 2023). The potential establishment of such multiresistant lineages in tomato production systems would significantly compromise current control strategies, further underscoring the need to determine whether these high-risk genotypes have spread from potato to tomato. While some lineages like 13_A2 demonstrate cross-host virulence, population studies indicate host-specific preferences can influence genotype frequencies, as observed in Italian systems where certain lineages showed differential distribution between potato and tomato (Saville et al. 2021). Furthermore, research has demonstrated that even subclones of the 13_A2 lineage can exhibit differential aggressiveness on tomato and potato hosts, allowing them to be subgrouped accordingly (Dey et al. 2018). This underscores the necessity of characterizing populations specifically from tomato crops, as potato-derived data may not fully reflect pathogen dynamics in tomato production systems.

The first comprehensive survey in 2002 analysed 160 isolates from Marmara region tomato fields, revealing 63% A2 mating-type frequency and identifying US-1 and US-8 clonal lineages (Tosun et al. 2002, 2007). Despite extensive population studies on potato, contemporary data on *P. infestans* populations infecting tomato in Türkiye are lacking. Given increasing disease pressure, frequent fungicide applications, and the emergence of aggressive European clonal lineages, there is a critical need to characterize tomato-associated populations independently of potato-derived data.

Therefore, this study aimed to (i) determine mating-type distribution, (ii) assess mefenoxam sensitivity, (iii) evaluate virulence diversity and (iv) resolve population structure using simple-sequence repeat (SSR) markers in *P. infestans* isolates collected from major tomato-growing areas of the South Marmara region between 2020 and 2022.

2 | Materials and Methods

2.1 | Collection and Maintenance of Isolates

Phytophthora infestans isolates were collected from naturally infected tomato leaves across the South Marmara region (Bursa, Balıkesir and Çanakkale) of Türkiye during the 2020–2022



FIGURE 1 | (A) Sampling provinces of *Phytophthora infestans* isolates collected from tomato production areas in the South Marmara region of Türkiye. (B) Representative view of a commercial tomato field during sampling. (C) Typical fruit lesion associated with tomato late blight. (D) Necrotic leaf symptoms characteristic of *P. infestans* infection.

growing seasons (Figure 1A). Sampling was conducted in commercial tomato fields showing typical late blight symptoms (Figure 1B–D). Single-lesion samples were selected to minimize within-isolate genetic heterogeneity. Leaves were rinsed with sterile water, air-dried on sterile filter paper, and incubated individually on 1.5% water agar at 18°C for 18 h to induce sporulation. Individual sporangia were transferred to rye A agar supplemented with 100 mg L⁻¹ rifamycin and 200 mg L⁻¹ ampicillin and incubated in the dark at 18°C (Caten and Jinks 1968). Mycelial colonies were identified under a stereomicroscope and subsequently transferred to fresh rye A medium for further growth. Isolates were maintained on rye A agar at 16°C in the dark. For long-term preservation, cultures were cryopreserved in 15% dimethyl sulfoxide (DMSO) and stored at -152°C following standard protocols.

Although the number of isolates per year was limited, sampling across three consecutive growing seasons and multiple provinces was sufficient to capture dominant clonal lineages and major phenotypic traits of the tomato-associated population.

2.2 | Mating Type Determination

Mycelial plugs (10 mm diameter) were excised from 2-week-old cultures and were paired with reference isolates of known A1 (US-17, US970001) or A2 (US-8, US040009) mating types on pea agar medium. Plates were incubated in the dark at 18°C for 2–3 weeks and investigated under a microscope (Primo Star 3; Zeiss) at 125× magnification for oospore formation at the hyphal junctions of the paired colonies over a span of 10 days. Mating type was assigned based on the reference isolate inducing oospore production. All assays were performed in duplicate with appropriate controls to ensure reliability.

2.3 | Mefenoxam Sensitivity Assessment

Mefenoxam sensitivity was assessed using standardized methodology with thresholds originally described by Therrien et al. (1993) and later applied by Saville et al. (2015). Prior to testing, isolates were cultivated on rye A agar at 16°C in darkness for 10 days to ensure consistent physiological state.

Evaluation was conducted using pea agar fortified with mefenoxam (Ridomil Gold EC, 49% active ingredient; Syngenta) at concentrations of 0, 5 and 100 mg L⁻¹. Mycelial discs from each isolate were positioned on three Petri dishes, each containing medium supplemented with mefenoxam at various concentrations. Plates were stored in darkness at 16°C for 2 weeks. For each replicate dish, colony diameters were measured in two perpendicular directions and mean colony diameter calculated. All sensitivity assays were performed with two biological replicates per isolate to account for physiological variation. Controls included the sensitive reference isolates US-1 (2162 TW97-Pi-42) and US-23 (BL2009P4), and the resistant reference isolates US-8 (US040009) and US-11 (US050007). Isolates were classified as sensitive if colony growth on 5 mg L⁻¹ mefenoxam was <40% relative to control growth, intermediate when growth was 40%–60% of control on 5 mg L⁻¹ but <40% on 100 mg L⁻¹, and resistant when growth exceeded 40% of control on both concentrations.

2.4 | SSR-Based Genotyping

Approximately 100 mg of mycelial material was carefully collected from 7-day-old actively growing colonies cultured on pea agar. Subsequently, it was dried using filter paper and transferred into 1.5 mL microfuge tubes for DNA extraction. Genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen), strictly adhering to the manufacturer's protocol, and DNA was subsequently dissolved in 200 µL of sterile ultrapure water. DNA concentration was quantified using a DS-11 FX series spectrophotometer (Denovix Inc.), adjusted to 50 ng µL⁻¹, and subsequently stored at –20°C for further analysis.

At Bolu Abant Izzet Baysal University, 12 polymorphic SSR markers (D13, G11, Pi02, Pi04, Pi4B, Pi63, Pi70, PinfSSR2, PinfSSR4, PinfSSR6, PinfSSR8 and PinfSSR11) were used in three multiplex reactions. This involved three sets of primers as described by Knapova and Gisi (2002), Lees et al. (2006) and Li et al. (2010). According to the Applied Biosystems (ABI) protocol, one primer from each locus was labelled with fluorescent dye: 6FAM (D13, Pi04, SSR11), VIC (G11, Pi4B, SSR4), NED (Pi02, Pi70, SSR6) or PET (Pi63, SSR2, SSR8). The loci were organized such that markers with the same dye had distinct allele size ranges, allowing for automated fragment analysis and multiplexed detection.

The PCR was performed in a total volume of 10 µL, comprising 1× buffer, 0.2 mM of each dNTP, 1.5 mM MgCl₂, 10 pmol of each primer, and 1 U of AmpliTaq DNA polymerase (Applied Biosystems). PCR was executed using a T100 thermal cycler (Bio-Rad) under the following conditions: initial 95°C for 10 min; followed by 30 cycles of 95°C for 20 s, 58°C for 60 s, and 72°C for 60 s; with a final 72°C for 20 min.

To analyse the length of PCR fragments, a mixture was prepared consisting of 0.05 µL of GeneScan 500 LIZ Size Standard (Applied Biosystems), 9.45 µL of Hi-Di formamide (ABI, PN 4311320), and 0.5 µL of each PCR product from the three multiplex reactions. The PCR products were placed in 96-well ABI 3730xl plates and examined using an ABI 3730xl capillary electrophoresis system equipped with Polymer POP-7 (ABI, PN 4335615). To ensure accurate and standardized allele sizing across runs, DNA from well-characterized US reference strains (US-1, US-8, US-11,

US-17 and US-23) was included in every PCR and capillary electrophoresis run as both positive controls and internal sizing standards. Allele calling was performed using GeneMapper software (Applied Biosystems), where peak heights were filtered at a 200 RFU threshold and fragment sizes were binned according to the EuroBlight protocol (Li et al. 2012). The complete multilocus genotypes and specific allele sizes for all 82 *P. infestans* isolates, along with reference standards, are detailed in Table S1.

2.5 | Virulence Phenotyping

Virulence was assessed in 82 isolates using the detached-leaf technique with a combination of the Mastenbroek and Black differential sets for *Solanum demissum* R-genes (*R1–R11*) supplied by the Scottish Agricultural Science Agency. The differential genotypes used were *R1* (Mastenbroek-43,154-5), *R2* (Black-1512c), *R3* (Mastenbroek-4642-1), *R4* (Mastenbroek-4431-5), *R5* (Black-3053-18), *R6* (Black-XD2-21), *R7* (Black-2182ef(7)), *R8* (Black-2424a(5)), *R9* (Black-2573), *R10* (Black-3618ad(1)) and *R11* (Black-5008ab(6)), in addition to cv. Bintje, which is devoid of resistance genes (*R0*) (Malcolmson and Black 1966).

Although the isolates in this study were exclusively collected from tomato, the standardized *S. demissum* differential set was used to assess the overall virulence complexity and effector diversity of the population. Because dominant clonal lineages (e.g., 1_A1_TR, 13_A2_TR) frequently exhibit cross-host infectivity, using this universal framework enables direct epidemiological comparisons with global *P. infestans* databases (e.g., EuroBlight) and previously characterized potato-derived populations in the region.

Leaflets were obtained from *Solanum* plants aged 6–8 weeks, which were cultivated under controlled environmental conditions. Inoculation was performed in 150 mm Petri dishes containing five leaflets, positioned abaxial side up, and arranged to prevent contact. Each *P. infestans* isolate, cultured on rye B agar for 2 weeks, was prepared as a sporangial suspension (4 × 10⁴ sporangia mL⁻¹), and 20 µL droplets were applied to both sides of the primary vein on each leaflet. Following inoculation, the Petri dishes were sealed with three layers of Parafilm and maintained at 16°C under a photoperiod of 16 h light/8 h darkness. To ensure dependable virulence profiles for each isolate, virulence assays were performed twice with independent biological replicates. Seven days after inoculation, disease severity was evaluated visually using a scale from 0 to 5: 0 indicated no symptoms, 1 represented a small necrotic lesion, 2 signified that less than 10% of the leaflet was affected, 3 denoted that 10%–50% was affected, 4 indicated that 50%–75% was affected, and 5 signified that more than 75% was affected. An isolate was deemed virulent if sporulation occurred on at least 6 out of 10 leaflets, and the total score reached or exceeded 15, signifying a compatible interaction (Runno-Paurson et al. 2009).

2.6 | Data Analysis

Population genetic analysis was conducted using clone-corrected methods specifically designed for clonal and partially clonal organisms, using the *poppr* package v. 2.9.8 (Kamvar et al. 2014) in

R v. 4.3.3 (R Core Team 2023). SSR data from 82 *P. infestans* isolates were converted to genind objects using the *adegenet* package v. 2.1.11 (Jombart 2008). Clonal lineage identification was performed using genetic distance-based clustering with Jaccard similarity coefficients. Isolates were assigned to discrete clonal lineages using hierarchical clustering with complete linkage method, and an appropriate distance threshold was determined through dendrogram examination to balance resolution with biological relevance.

Clone correction was applied using the clone correct function to remove genetic redundancy and focus analysis on unique genotypic diversity, which is essential for appropriate statistical inference in clonal populations (Grünwald et al. 2003). Genetic diversity indices including Shannon diversity (H'), and evenness (E_s) were calculated for both clone-corrected and uncorrected datasets. Clonal fraction was calculated as $(1 - \text{unique genotypes}/\text{total isolates}) \times 100$.

Analysis of molecular variance (AMOVA) was performed on clone-corrected data using the *poppr.amova* function with the *pegas* method and 999 permutations to test for population differentiation among provinces. Pairwise F_{ST} values were calculated using Weir and Cockerham's (1984) estimator implemented in the *hierfstat* package to quantify genetic differentiation between population pairs. Population structure was visualized using a minimum spanning network (MSN) constructed with Bruvo's distance (Bruvo et al. 2004), which accounts for stepwise mutations typical of SSR loci and is particularly appropriate for polyploid organisms. During the calculation of Bruvo's distance and MSN construction, any missing SSR data were handled using the default pairwise deletion method in the *poppr* package, ensuring that genetic distances were calculated only across shared loci. The MSN was created using the *poppr.msn* function and visualized to illustrate genetic relationships among clonal lineages and their geographic distribution patterns. Population genetic parameters, diversity statistics and significance tests were computed following standard procedures for clone-corrected datasets to avoid bias associated with over-representation of dominant clonal lineages.

3 | Results

3.1 | Isolate Acquisition

Between 2020 and 2022, a total of 82 *P. infestans* isolates were collected from tomato fields in three provinces of the South Marmara region of Türkiye (Table 1). Most isolates were collected in 2020 and 2021, with an additional 17 isolates collected in 2022. The number of isolates per province ranged from 15 to 49.

3.2 | Mating Type

Both A1 and A2 mating types were detected in all 3 years of sampling. Of the 82 isolates examined, 73 (89%) were identified as the A1 mating type, while 9 (11%) were categorized as the A2 mating type (Table 1). No self-fertile isolates were identified in this study. In 2020, both mating types were occasionally detected within the same field in Çanakkale province. Among the

64 isolates collected from Balıkesir and Bursa (78% of the total collection), only the A1 mating type was detected.

3.3 | Mefenoxam Sensitivity

Among the 82 *P. infestans* isolates, 56% ($n=46$) were sensitive, 23% ($n=19$) were resistant and 21% ($n=17$) showed an intermediate phenotype (Table 1). Phenotypes exhibiting full sensitivity were commonly observed across all years and sampling locations. Among the isolates collected from Balıkesir ($n=15$), the proportion of sensitive isolates was less than 50%. When analysed by clonal lineage, the 1_A1_TR group comprised 52% sensitive, 25% resistant and 23% intermediate isolates. Conversely, 39_A1, 13_A2 and 23_A1 groups had sensitive isolate proportions of 100% ($n=2$), 89% ($n=8$) and 63% ($n=5$), respectively. Mefenoxam sensitivity assays were performed with two independent biological replicates per isolate. Colony diameter measurements showed high consistency between replicates, with a mean coefficient of variation (CV) of 8.4% across all isolates. Reference sensitive controls (US-1 and US-23) consistently showed <5% relative growth on 5 mg L^{-1} mefenoxam, while resistant standards (US-8 and US-11) exceeded 60% growth in both experimental runs.

3.4 | Clone-Corrected Population Genetic Structure

In an analysis of the 12 SSR loci, a total of 38 alleles were detected across the 82 *P. infestans* isolates (Table 2). The number of alleles per locus ranged from 1 to 7, with an average of 3.16 alleles per locus. The Pi70 locus was monomorphic, producing a single 192bp allele, whereas the remaining 11 loci exhibited polymorphism among isolates from all three provinces. Several alleles were shared across all populations, including alleles 173 (PinfSSR2), 192 (Pi70), 244 (PinfSSR6), 260 (PinfSSR8), 266 and 268 (Pi02), 279 (Pi63) and 341 (PinfSSR11). No null alleles were detected. Rare alleles occurred at low frequencies, appearing only once among the analysed isolates.

Clone-corrected analysis of 12 SSR loci revealed that all isolates grouped into only five distinct clonal lineages (Table S1), demonstrating an extremely high clonal fraction of 93.9%. Lineage frequency varied dramatically among populations, with 1_A1_TR dominating at 73.2% of all isolates ($n=60$), followed by 13_A2_TR (11.0%, $n=9$), 23_A1_TR1 (9.8%, $n=8$), 23_A1_TR2 (3.7%, $n=3$) and 39_A1_TR (2.4%, $n=2$) (Table 3).

Clone-corrected genetic diversity analysis revealed striking differences among provinces (Table 4). Çanakkale exhibited the highest genetic diversity (Shannon index $H'=1.224$), containing four of the five lineages, with the highest genetic diversity among sampled provinces. In contrast, Balıkesir was completely monoclonal ($H'=0.000$) with only 1_A1_TR present across all 15 isolates. Bursa showed intermediate diversity ($H'=0.283$) with 2 lineages, predominantly 1_A1_TR ($n=45$) with minor occurrence of 23_A1_TR1 ($n=4$). The geographic distribution pattern indicated that genetic diversity decreased with distance from Çanakkale, suggesting this province as a potential point of introduction for multiple lineages.

TABLE 1 | Analysis of molecular and phenotypic characteristics of *Phytophthora infestans* isolates collected in the South Marmara region of Türkiye from 2020 to 2022.

Province	Mating type		Clonal lineage	Races	Mefenoxam response ^a	Number of isolates	Total isolates
	A1	A2					
Balıkesir	15	—	1_A1_TR	1.2.3.4.6.7.8.9.10.11	R(1), I(1)	2	15
				1.2.3.4.5.6.7.9.10.11	R(1), S(1)	2	
				1.2.3.4.6.7.8.9.10	I(2)	2	
				1.2.3.4.5.6.7.8.9.10	S(2)	2	
				1.2.3.4.6.7.8.9.11	R(2)	2	
				1.2.3.5.6.7.8.9.10.11	S(1)	1	
				1.2.3.4.6.7.8.10.11	R(1)	1	
				1.2.3.4.5.6.7.8.10	S(1)	1	
				1.2.3.4.5.6.7.8.9.11	S(1)	1	
				1.2.3.4.5.6.7.10	S(1)	1	
Bursa	45	—	1_A1_TR	1.2.3.4.6.7.8.9.10.11	R(1), I(1), S(3)	5	49
				1.2.3.4.5.6.7.9.10.11	S(4)	4	
				1.2.3.4.6.7.9.10.11	I(2), S(3)	5	
				1.2.3.4.6.7.8.9.10	I(2)	2	
				1.2.3.4.6.7.8.10.11	R(3)	3	
				1.2.3.4.5.6.7.8.9.10.11	R(3), S(1)	4	
				1.2.3.5.6.7.8.9.10.11	S(3)	3	
				1.2.3.4.5.6.7.8.9.10	I(2)	2	
				1.2.3.4.5.6.7.8.10	I(2), S(1)	3	
				1.2.3.4.6.7.8.9.11	R(1), S(1)	2	
				1.2.3.4.6.7.9	S(3)	3	
				1.2.3.4.6.7.8.10	S(2)	2	
				1.2.3.4.5.6.7.8.9.11	I(2)	2	
				1.2.3.5.6.7.8.9.11	R(2)	2	
				1.2.3.5.6.7.9.10	S(1)	1	
				1.2.3.4.5.6.7.8	S(1)	1	
				1.2.3.6.7.8.10	S(1)	1	
	4	—	23_A1_TR1	1.2.3.4.5.6.7.9.10	R(1)	1	
				1.2.3.6.7.9.10.11	R(1)	1	
				1.2.3.4.6.7.8.9	R(1)	1	
				1.2.3.6.7.8.9	S(1)	1	

(Continues)

TABLE 1 | (Continued)

Province	Mating type		Clonal lineage	Races	Mefenoxam response ^a	Number of isolates	Total isolates
	A1	A2					
Çanakkale	—	9	13_A2_TR	1.2.3.4.6.7.8.10.11	R(1), S(3)	4	18
				1.2.3.4.6.7.10.11	S(2)	2	
				1.3.4.5.6.7.8.9.10.11	S(1)	1	
				1.2.3.4.6.7.9.10.11	S(1)	1	
				1.2.3.4.6.9.10.11	S(1)	1	
	4	—	23_A1_TR1	1.2.3.4.5.6.7.9.10.11	S(1)	1	
				1.2.3.4.5.6.7.9.11	S(1)	1	
				1.2.3.5.6.7.9.10.11	S(1)	1	
				1.2.3.4.6.7.9	S(1)	1	
	3		23_A1_TR2	1.2.3.4.6.7.8.10.11	I(1)	1	
				1.2.3.4.6.7.8.9	I(1)	1	
				1.2.3.4.6.7.8	I(1)	1	
	2		39_A1_TR	1.2.3.4.6.7.8.10.11	S(2)	2	

Note: Mefenoxam sensitivity assays were performed in two independent biological replicates. The inter-replicate variation was minimal, with a mean standard deviation (SD) of $\pm 4.2\%$ across all growth measurements.

^aResponse to mefenoxam; R, resistant; I, intermediate resistant; S, sensitive. Numbers in parentheses indicate the number of isolates in each category.

The MSN revealed clear genetic relationships among clonal lineages and their geographic distribution (Figure 2). The network exhibited a star-like topology with 1_A1_TR forming the central hub, connected to other genotypes through relatively short genetic distances. This pattern reflected the demographic dominance of the 1_A1_TR lineage and suggested that minor lineages may have evolved from or share recent common ancestry with the dominant lineage. The network clearly illustrated the extreme clonality of the population, with the majority of isolates clustering in the central node representing 1_A1_TR. Minor lineages (23_A1_TR1, 23_A1_TR2, 13_A2 and 39_A1) are connected through short genetic distances, reflecting recent evolutionary relationships. The star-like topology demonstrates the predominantly clonal structure of Turkish *P. infestans* populations.

Pairwise F_{ST} analysis using Weir and Cockerham's method indicated moderate genetic differentiation between Çanakkale and the other provinces ($F_{ST}=0.148$ vs. Balıkesir; $F_{ST}=0.142$ vs. Bursa), whereas Balıkesir and Bursa showed minimal differentiation ($F_{ST}=0.004$). These values suggest relative genetic distinctiveness of the Çanakkale population, while confirming the high similarity between Balıkesir and Bursa populations dominated by the same lineage (1_A1_TR).

Clone-corrected AMOVA revealed no significant genetic differentiation among the three provinces ($\Phi_{PT}=-0.176$, $p=0.685$, 999 permutations), with genetic variation distributed within populations rather than among them (Table 5). The negative Φ_{PT} value indicated that genetic variation among provinces was actually lower than expected by chance alone, indicating no significant genetic differentiation among provinces. This result, combined with the F_{ST} analysis, reflects the widespread

distribution of the dominant 1_A1_TR lineage across Balıkesir and Bursa provinces, and the sharing of some lineages between Bursa and Çanakkale.

3.5 | Virulence Tests

The 29 identified virulence phenotypes remained stable across two independent biological replicates, with no significant differences observed in race assignments or disease severity scores between experimental runs. Virulence assays revealed substantial phenotypic diversity among the 82 *P. infestans* isolates evaluated on the *S. demissum* differential set. Based on reactions on *R1–R11* resistance genes, a total of 29 distinct virulence phenotypes (races) were identified (Table 6). The four most frequent virulence patterns accounted for the majority of isolates, indicating a limited number of dominant race combinations despite overall phenotypic variability. Virulence assays were conducted twice with independent biological replicates. Disease severity scores demonstrated high repeatability between replicates (Spearman's rank correlation $\rho=0.92$, $p<0.001$), confirming the stability of the identified physiological races.

The number of virulence factors per isolate ranged from 7 to 11, indicating a generally high level of virulence complexity within the population. Several races were detected repeatedly across sampling sites, with the most frequent phenotype being R1.2.3.4.6.7.8.10.11. This race was identified in isolates from multiple provinces, suggesting a broad distribution within the South Marmara region. Virulence against individual R genes was unevenly distributed among isolates. High frequencies of virulence were observed against *R1*, *R2*, *R3*, *R4*, *R6*, *R7*, *R8*, *R10*

TABLE 2 | Simple-sequence repeat (SSR)-based analysis to examine allele frequencies within Turkish populations of *Phytophthora infestans*, highlighting both predominant and minor allele occurrences across 12 microsatellite loci.

SSR locus	No. of alleles	Alleles detected (allele frequencies, %)
Pi02	3	266 (47.9); 268 (50.3); 270 (1.8)
D13	5	136 (86.6); 154 (1.2); 156 (5.5); 210 (4.9); 212 (1.8)
Pi04	3	171 (42.1); 173 (2.4); 175 (55.5)
Pi4B	3	205 (6.7); 213 (51.8); 217 (41.5)
G11	7	142 (43.7); 154 (5.4); 156 (6.6); 160 (5.4); 162 (35.9); 204 (1.8); 206 (1.2)
Pi63	3	270 (43.3); 273 (5.5); 279 (51.2)
Pi70	1	192 (100)
SSR11	3	331 (6.7); 341 (56.7); 356 (36.6)
SSR2	2	173 (55.5); 175 (44.5)
SSR4	4	284 (46.1); 288 (3.0); 294 (49.1); 298 (1.8)
SSR6	2	240 (6.7); 244 (93.3)
SSR8	2	260 (51.2); 266 (48.8)
Total	38	

and *R11*, whereas virulence to certain resistance genes occurred less consistently across the population. No isolate exhibited avirulence to all tested resistance genes.

When virulence profiles were examined in relation to clonal lineage, most phenotypes were associated with the dominant 1_A1_TR lineage. Isolates belonging to this lineage displayed a wide range of virulence combinations, reflecting considerable phenotypic variability despite their genetic relatedness. No clear geographic structuring of virulence phenotypes was detected among provinces. Identical or closely related races were observed in multiple locations, indicating that virulence variation was not strongly associated with sampling origin. Overall, virulence phenotyping demonstrated extensive race diversity within a predominantly clonal *P. infestans* population.

4 | Discussion

This study presents the first clone-corrected population genetic analysis of *P. infestans* causing tomato late blight in Türkiye. The clonal fraction of 93.9%, with only five lineages among 82 isolates, indicates a highly clonal population structure, suggesting that the population is driven primarily by asexual reproduction and clonal expansion (Cooke et al. 2012). The dominance of the 1_A1_TR (73.2%) across Balıkesir and Bursa contrasts markedly with the near-complete dominance of the 13_A2 lineage previously reported on potato in the same region (Göre et al. 2019, 2021).

TABLE 3 | Clonal lineage identification, frequency distribution and lineage assignments among *Phytophthora infestans* isolates from the South Marmara region of Türkiye.

Isolates (n)	Frequency (%)	Distribution by province	Clonal lineage	Mating type
60	73.2	Balıkesir (15), Bursa (45)	1_A1_TR	A1
9	11.0	Çanakkale (9)	13_A2_TR	A2
8	9.8	Bursa (4), Çanakkale (4)	23_A1_TR1	A1
3	3.7	Çanakkale (3)	23_A1_TR2	A1
2	2.4	Çanakkale (2)	39_A1_TR	A1
82	100.0	3 provinces	5 lineages	A1 (89%)

TABLE 4 | Clone-corrected genetic diversity indices for *Phytophthora infestans* populations from three provinces in the South Marmara region of Türkiye.

Province	N	Lineages	eLineage	H'	G	E _s
Balıkesir	15	1	1	0.000	1	NaN
Bursa	49	2	1.78	0.283	1.18	0.540
Çanakkale	18	4	3.98	1.224	2.95	0.811
Total	82	5	3.46	0.910	1.79	0.532

Abbreviations: E_s, evenness index; eLineage, expected clonal lineages at smallest sample size; G, Stoddart and Taylor's index; H', Shannon diversity index; Lineages, number of clonal lineages; N, number of isolates.

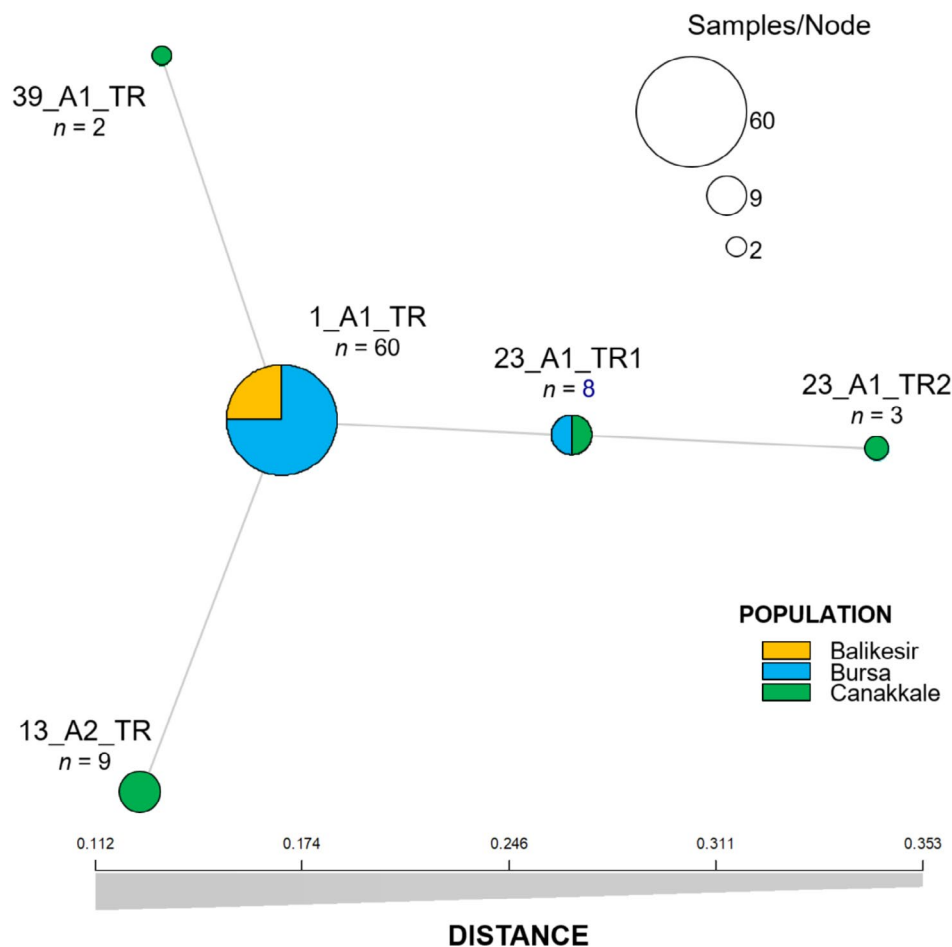


FIGURE 2 | Minimum spanning network (MSN) showing genetic relationships among clonal lineages of *Phytophthora infestans* isolates from the South Marmara region of Türkiye. Node sizes are proportional to the number of isolates within each lineage. Colours represent different provinces: orange (Balıkesir), blue (Bursa), green (Çanakkale). The network was constructed using Bruvo's distance to account for stepwise mutations in SSR loci.

TABLE 5 | Clone-corrected analysis of molecular variance (AMOVA) for *Phytophthora infestans* populations from three provinces in the South Marmara region of Türkiye.

Source of variation	df	Sum Sq	Mean Sq	σ	% Variation	Φ
Among populations	2	4.571	2.285	−0.426	−17.6	$\Phi_{PT} = -0.176$
Within populations	4	17.000	4.250	2.844	117.6	$p = 0.685$
Total	6	21.571	3.595	2.418	100.0	999 perm.

Abbreviations: df, degrees of freedom; Mean Sq, mean square; Source of variation, hierarchical level at which genetic variation is partitioned; Sum Sq, sum of squares; σ , variance component; % Variation, percentage of total genetic variation explained by each source; Φ , PHI statistic measuring genetic differentiation among groups.

While aggressive lineages such as 13_A2 infect both hosts in other Mediterranean regions (Saville et al. 2021), the persistence of the historically dominant 1_A1_TR lineage on Turkish tomatoes suggests distinct host-associated structuring. This pattern may reflect local host adaptation or limited introduction of fitter invasive genotypes into tomato production systems, and contrasts with Western Europe, where 1_A1_TR is considered a declining lineage relative to emerging clones such as 37_A2 (Puidet et al. 2023).

Despite the dominance of 1_A1, the detection of 23_A1 (13.4%) and 13_A2 (11.0%) lineages indicates ongoing population transitions. The presence of 23_A1, a widely recognized

tomato-adapted genotype, is consistent with reports from Algeria (Beninal et al. 2022) and Italy (Saville et al. 2021), suggesting regional connectivity facilitated by movement of infected plant material (Cohen 2024). Similarly, the 39_A1 lineage, detected at low frequency only in Çanakkale, aligns with European surveillance records associating this genotype with tomato hosts (EuroBlight 2026), supporting multiple independent introductions rather than local expansion.

SSR analyses confirmed that Turkish isolates cluster with well-characterized European clonal lineages (Table S1) while exhibiting lineage-specific local variants (e.g., 23_A1_TR1 and TR2).

TABLE 6 | Origin, virulence phenotypes and mefenoxam sensitivity of *Phytophthora infestans* isolates from the South Marmara region of Turkey.

Race	Locations	Virulence factors ^a	N ^b	RM ^c	Clonal lineage
R1.2.3.4.6.7.8.10.11	Balıkesir, Bursa, Çanakkale	9	11	R(1)	1_A1_TR
				R(3)	1_A1_TR
				R(1), S(3)	13_A2_TR
				I(1)	23_A1_TR2
				S(2)	39_A1_TR
R1.2.3.4.6.7.8.9.10.11	Balıkesir, Bursa	10	7	R(1), I(1)	1_A1_TR
				R(1), I(1), S(3)	1_A1_TR
R1.2.3.4.5.6.7.9.10.11	Balıkesir, Bursa, Çanakkale	10	7	R(1), S(1)	1_A1_TR
				S(4)	1_A1_TR
				S(1)	23_A1_TR1
R1.2.3.4.6.7.9.10.11	Bursa, Çanakkale	9	6	I(2), S(3)	1_A1_TR
				S(1)	13_A2_TR
R1.2.3.4.6.7.8.9.10	Balıkesir, Bursa	9	4	I(2)	1_A1_TR
				I(2)	1_A1_TR
R1.2.3.4.5.6.7.8.9.10	Balıkesir, Bursa	10	4	S(2)	1_A1_TR
				I(2)	1_A1_TR
R1.2.3.4.6.7.8.9.11	Balıkesir, Bursa	9	4	R(2)	1_A1_TR
				R(1), S(1)	1_A1_TR
R1.2.3.5.6.7.8.9.10.11	Balıkesir, Bursa	10	4	S(1)	1_A1_TR
				S(3)	1_A1_TR
R1.2.3.4.5.6.7.8.10	Balıkesir, Bursa	9	4	S(1)	1_A1_TR
				I(2), S(1)	1_A1_TR
R1.2.3.4.5.6.7.8.9.10.11	Bursa	11	4	R(3), S(1)	1_A1_TR
R1.2.3.4.6.7.9	Bursa, Çanakkale	7	4	S(3)	1_A1_TR
				S(1)	23_A1_TR1
R1.2.3.4.5.6.7.8.9.11	Balıkesir, Bursa	10	3	S(1)	1_A1_TR
				I(2)	1_A1_TR
R1.2.3.4.6.7.8.10	Bursa	8	2	S(2)	1_A1_TR
R1.2.3.5.6.7.8.9.11	Bursa	9	2	R(2)	1_A1_TR
R1.2.3.4.6.7.8.9	Bursa, Çanakkale	8	2	R(1)	23_A1_TR1
				I(1)	23_A1_TR2
R1.2.3.4.6.7.10.11	Çanakkale	8	2	S(2)	13_A2_TR
R1.2.3.4.5.6.7.10	Balıkesir	8	1	S(1)	1_A1_TR
R1.2.3.5.6.7.9.10	Bursa	8	1	S(1)	1_A1_TR
R1.2.3.4.5.6.7.8	Bursa	8	1	S(1)	1_A1_TR
R1.2.3.6.7.8.10	Bursa	7	1	S(1)	1_A1_TR
R1.2.3.4.5.6.7.9.10	Bursa	9	1	R(1)	23_A1_TR1
R1.2.3.6.7.9.10.11	Bursa	8	1	R(1)	23_A1_TR1

(Continues)

TABLE 6 | (Continued)

Race	Locations	Virulence factors ^a	N ^b	RM ^c	Clonal lineage
R1.2.3.6.7.8.9	Bursa	7	1	S(1)	23_A1_TR1
R1.3.4.5.6.7.8.9.10.11	Çanakkale	10	1	S(1)	13_A2_TR
R1.2.3.4.6.9.10.11	Çanakkale	8	1	S(1)	13_A2_TR
R1.2.3.4.5.6.7.9.11	Çanakkale	9	1	S(1)	23_A1_TR1
R1.2.3.5.6.7.9.10.11	Çanakkale	9	1	S(1)	23_A1_TR1
R1.2.3.4.6.7.8	Çanakkale	7	1	I(1)	23_A1_TR2
Total	3	7–11	85		7

^aVirulence factors of an isolate are given as a series of numbers, representing the R-gene potato genotypes that produce compatible interaction with that isolate.

^bN, number of potato isolates employed in fungicide sensitivity tests and virulence testing using the potato differential set of resistance (R) genes (*R1–R11*).

^cRM, response to mefenoxam; R, resistant; I, intermediate resistant. Numbers in parentheses indicate the number of isolates in each category.

The monomorphic nature of Pi70 and overall low gene diversity reflect the highly clonal structure of the population and the overwhelming demographic dominance of a single lineage (1_A1_TR). The emergence of locally differentiated TR variants suggests that once introduced, *P. infestans* lineages undergo gradual genetic divergence through mutation and selection under local host-driven pressures.

The presence of 13_A2 exclusively in Çanakkale is noteworthy, as this lineage is associated with severe epidemics globally (Cooke et al. 2012; Dey et al. 2018, 2024; Saville et al. 2021). Its restricted distribution suggests recent introduction and limited dispersal. The mefenoxam resistance observed in Çanakkale isolates is consistent with phenotypic characteristics of modern European lineages and underscores the challenges facing chemical control strategies in the region.

Clone-corrected AMOVA revealed no significant genetic differentiation among provinces, indicating a lack of strong population structuring at the regional scale. This pattern is consistent with a predominantly clonal population structure and suggests that the distribution of genotypes is not strongly partitioned by geography. In contrast, pairwise F_{ST} estimates indicated moderate differentiation between Çanakkale and the other provinces, whereas Balıkesir and Bursa showed minimal differentiation. These differences likely reflect the higher genotypic diversity observed in Çanakkale, where four lineages were detected, compared with the near-monoclonal populations in Balıkesir and Bursa dominated by a single lineage (1_A1_TR). The apparent discrepancy between AMOVA and pairwise F_{ST} results can be explained by the strong influence of clonal expansion and unequal genotype frequencies across locations. In such populations, dominant clonal lineages may mask overall population structure in AMOVA, while pairwise comparisons can still capture localized differences associated with the presence of additional lineages. Overall, these findings support a scenario of limited but detectable regional differentiation within an otherwise highly clonal population, with patterns consistent with clonal spread and local diversification rather than strong geographic isolation.

Mefenoxam sensitivity patterns differentiated tomato-associated populations from those on potato in Türkiye (Göre et al. 2019, 2021). Whereas potato populations dominated by 13_A2 are largely phenylamide-resistant, more than half of tomato isolates

remained sensitive, consistent with the prevalence of 1_A1. Similar sensitivity profiles have been documented in South Korea, Poland and the United States (Choi et al. 2020; Hu et al. 2012; Janiszewska et al. 2021; Saville et al. 2015). These data suggest that phenylamide fungicides may still contribute to tomato late blight management within an anti-resistance framework. The observation that 89% of the 13_A2_TR isolates in this study were sensitive to mefenoxam contrasts sharply with the widespread phenylamide resistance typically associated with the 13_A2 lineage globally and on potato crops in Türkiye. This unexpectedly high frequency of sensitive phenotypes in tomato fields could be driven by several interacting factors. Firstly, regional fungicide application programmes in tomato often rely heavily on alternative multisite or non-phenylamide chemistries, leading to a relaxation of selection pressure. In the absence of continuous mefenoxam exposure, a potential fitness cost associated with the resistance trait may allow sensitive subclones to outcompete resistant ones. Furthermore, considering the increasing subclonal diversity within the 13_A2 lineage (Dey et al. 2024), it is plausible that the founder population introduced to these specific tomato niches exhibited an atypical, sensitive phenotypic profile. However, resistant isolates detected among 13_A2 samples from Çanakkale highlight the risk of rapid selection under sustained phenylamide pressure (Gisi and Cohen 1996), underscoring the need for fungicide rotation and resistance monitoring.

Virulence profiling revealed 29 physiological races, with most isolates carrying multiple virulence factors. Although virulence against several major R genes was widespread, *R5* and *R11* remained comparatively effective (Janiszewska et al. 2021; Runno-Paurson et al. 2009), highlighting the limitations of relying solely on vertical resistance (Guo et al. 2009). Virulence patterns evaluated on the standard *S. demissum* differential set were closely associated with clonal lineage. Although these specific potato R genes are absent in tomato, such standardized profiling highlights the intrinsic phenotypic complexity of the isolates. The dominant 1_A1 lineage displayed a narrower virulence spectrum compared with 13_A2 (Puidet et al. 2023), indicating that the current population probably relies on overall aggressiveness rather than specific effector-driven adaptations to infect susceptible tomato cultivars.

In summary, these findings provide essential baseline data for developing targeted, region-specific management strategies

and highlight the critical importance of employing appropriate clone-corrected analytical frameworks for population genetic studies of clonal plant pathogens. Future research should focus on monitoring temporal changes in lineage frequencies and establishing surveillance programmes for early detection of newly introduced aggressive genotypes.

Author Contributions

Mehmet Erhan Göre: conceptualization, methodology, investigation, formal analysis, writing – original draft, writing – review and editing, validation, data curation. **Göksele Özer:** conceptualization, investigation, methodology, visualization, writing – original draft, writing – review and editing, validation, software.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Allele sizes (bp) and multilocus genotypes (MLGs) of *Phytophthora infestans* isolates amplified with each of the 12 SSR markers.