Population structure of *Phytophthora infestans* collected from potatoes in Guatemala and Honduras

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Abstract

Late blight caused by *Phytophthora infestans* poses a significant global threat to potato and tomato cultivation with profound historical and ongoing impacts on food security. In Central America, particularly in Guatemala and Honduras, the disease has intensified over the last decade, possibly due to favorable climatic conditions and changes in local pathogen populations.

This study identified four distinct clonal lineages of the A2 mating type, US7A2, US8A2, and 13A2, and a newly identified lineage exhibiting genetic variation. Mitochondrial haplotype analysis confirmed that the patterns aligned with those reported in previous studies, thereby reflecting the diverse genetic composition of this pathogen. The genetic variability of *P. infestans*, including its reduced sensitivity to fungicides such as metalaxyl, and its ability to overcome host resistance, underscores the importance of understanding its population dynamics. Approximately 61% of the genetic variation was observed between lineages, likely because of the introduction of genetically distinct propagules into infected seeds.

These findings underscore the urgent need for region-specific disease management strategies guided by local genetic data to effectively mitigate the impact of late blight and suggest the need to strengthen local seed production to minimize the import of new genotypes.

Keywords: *Phytophthora infestans*, genetic structure, late blight, potato

Introduction

Phytophthora infestans (Mont.) de Bary is an oomycete responsible for late blight in potatoes (*Solanum tuberosum* L.), tomatoes (*Solanum lycopersicum* L.), and other Solanaceae species (Perez & Forbes, 2010). The disease is a well-known primary biotic limitation affecting potato cultivation on a global scale and has been the cause of devastating epidemics, such as the one leading to the Irish Potato Famine of 1845, and still poses a significant challenge to global food security (Day & Shattock, 1997; Dong & Zhou, 2022). Management of the disease with fungicides continues to be the most common approach (Abuley & Hansen, 2022), with a limited number of alternatives available to chemical control (Kang & Dobinson, 2004).

P. infestans is a heterothallic species that requires mating types A1 and A2 for sexual reproduction, resulting in oospore formation (Drenth et al., 1995). This pathogen combines the advantages of sexual cycles, which generate genetic diversity, and an expansive population through asexual reproductive cycles (McDonald & Linde, 2002). In sexual populations, both sexual and asexual propagules act as inoculum sources, whereas asexual populations rely entirely on inoculum generated through asexual reproduction (Flier et al., 2002). Monitoring the A1/A2 ratio is crucial to understand the potential for sexual recombination, which supports their evolution (Barton & Charlesworth, 1998). Sexual reproduction allows *P. infestans* to persist in the soil between seasons as thick-walled oospores (Andersson, 2007). In addition, *P. infestans* strains derived from sexual recombination could potentially exhibit a greater capacity to adapt quickly to environmental fluctuations, including the use of fungicides (Goodwin, 1997), resulting in the emergence of fungicide-resistant strains (Bosmans, 2009). Furthermore, in *P. infestans,* genetic diversity is fostered by adaptive evolution, which is driven by the pathogen's unique genomic structure, particularly in regions rich in rapidly evolving effector genes (Leesutthiphonchai et al., 2018; Zhang et al., 2019).

The diversity of *P. infestans* is examined by using a combination of phenotypic and genotypic markers. Microsatellite markers, also referred to as simple sequence repeats (SSRs), are frequently used to determine multilocus genotypes (MLGs) and evaluate genetic diversity within populations (Li et al., 2012; Martin et al., 2019). SSR markers are highly polymorphic, affordable, reproducible, neutral, and co-dominant (Lees et al., 2006), and can differentiate between genotypes, even among clonal lineages (Hansen et al., 2016). Mitochondrial haplotypes are used to trace maternal lineages and provide insights into population structure and migration patterns (Griffith & Shaw, 1998; Widmark et al., 2007; Guo J et al., 2009).

Mexico has been proposed as the geographic region where late blight has originated with several lines of evidence: the historical occurrence of both mating types (A1 and A2) in this region, and the population of *P. infestans* in central Mexico exhibits remarkable diversity in terms of virulence characteristics and molecular markers (Gallegly, 1958; Fry et al., 1993). However, an alternate theory suggests that Peru is the center of origin, supported by the prevalence of the US-1 clonal lineage worldwide, which is notably absent in Mexico (Abad & Abad, 1997; Saville et al., 2016). A recent study conducted by Patarroyo *et al.* (2024) suggested a Peruvian origin of *P. infestans* (probability = 0.631), with an initial migration toward Colombia and Mexico, and a later event from Mexico to the United States and then to Europe and Asia, with no return to northern South America.

The A1 mating type has been dispersed worldwide since the Irish potato famine, and the A2 mating type was first reported in Europe, the Middle East, and South America in 1981 (Spielman et al., 1991; Goodwin,

1995a). In the USA, the US-1 lineage (A1) was the first isolate with a global distribution spread to Europe, Asia, North, Central, and South America (Goodwin, 1994, 1997), between 1992-1993 two new genotypes (US-7 and US-8), A2 mating types, exacerbated disease risk (Goodwin et al., 1998), and were considered to be of Mexican origin (Goodwin, 1995b).

Guatemala produces over 540,000 metric tons of potatoes per year, which are primarily exported to the neighboring El Salvador, and less than 1% of the crop is planted with certified seed potatoes. Late blight is the most important disease because of its cool and wet weather conditions (Joyce, 2020), and there is high genetic variability among isolates (Ruiz-Chutan et al., 2018). The United States is a significant supplier of seed potatoes to Guatemala, and few quantities have been imported from Peru (World Bank, 2023a; b). In contrast, potato cultivation in Honduras was concentrated in Intibucá, Ocotepeque, La Paz, and Francisco Morazán, where 39,633 metric tons of potatoes were produced between 2011 and 2012. The Honduran potato industry also relies on imports; in 2014 and 2015 6,000 tons were used annually for industrial processing, while seed potato imports reached 1,000 tons. Similar to Guatemala, late blight is recognized as the most significant disease affecting potato cultivation in Honduras (Toledo, 2016). According to the USDA, in 2021, the value of potato imports to Honduras grew by 1.9%, increasing from US$7.8 million in 2016 to US$8.4 million in 2020. Most potatoes for fresh consumption were imported from the United States, whereas most seed potatoes were imported from the Netherlands, France (SAG & UPEG, 2021; World Bank, 2023c), Guatemala, and Chile (Sanders et al., 2024).

The aim of this study was to analyze *P. infestans* populations in Central America, given the limited research on this pathogen in the region and the critical role of its geographic location in understanding global pathogen dynamics.

Materials and Methods

Sampling and sample processing

The sampling strategy used in this study was designed to identify dominant pathogen genotypes in Honduras and Guatemala. For this purpose, between 2021-2022, potato leaflet samples exhibiting late blight symptoms were collected from the main potato-growing areas at altitudes ranging from 1700 to 2088 m above sea level (masl) in Honduras and 1750–3633 masl in Guatemala, with approximately 94 fields studied based on latitude and longitude (Table S1).

Samples were collected on FTA cards (Whatman FTA Classic Card, catalog number WB120055; GE Healthcare UK Ltd.), following the manufacturer's instructions (Cooke, 2020). Each sample had its sporulating side facing down, crushed individually in the field, and then FTA cards were stored in zip-lock bags and sent by post for processing in the pathology laboratory at the International Potato Center (CIP), Lima, Peru.

DNA extraction from FTA was performed following the manufacturer's instructions, with some modifications using two discs of 3 mm, and two rinses with modified Tris(hydroxymethyl) aminomethane-ethylenediaminetetraacetic acid (TE^{-1}) buffer (10 mM Tris and 0.1 mM EDTA), and then resuspended in 50

114 µL TE buffer (10mM Tris and 1mM EDTA) and incubated for 5 min at 95 °C as the last step before being
115 stored at -20 °C until use.

116 Mating type determination

117 The mating types were determined using the W16 CAPS assay to determine the A1 and A2 mating types
118 of *P. infestans* isolates using PCR primers W16-1 (5'-AACACGCACAGGCATATAAATGTA-3') and W16-2 (5'-
119 GCGTAATGTAGCGTAACAGCTCTC-3') following the protocol outlined by Judelson et al. (1995). The PCR
120 reaction was carried out in, 20 µL mixture, which included 4 µL of 5x buffer (Gotaq®, Promega), 6 µl $MgCl_2$
121 (25 mM), 0.2 µl dNTPs (100 µM), 0.4 µM of each primer, 1 U of Taq DNA polymerase (Gotaq®, Promega)
122 and 10ng of template DNA. The thermal cycling conditions were as follows: initial denaturation at 94 °C
123 for 5 min, followed by 30 cycles of denaturation at 94 °C for 1 min, primer annealing at 53 °C for 1 min,
124 and primer elongation at 72 °C for 1 min. The PCR process was concluded with a final elongation step at
125 72 °C for 10 minutes. Subsequently, the PCR products were subjected to a three-hour digestion at 37 °C
126 using the restriction enzyme (recognition site 5'-GG/CC-3' from New England Biolabs (NEB)
127 (https://www.neb.com). The digestion mixture for each sample included 7.7 µL of H_2O, 2 µL of CutSmart
128 Buffer 10X, 0.3 µL Hae III (NEB, #R0108) and 10 µl of PCR product (Brylińska et al., 2018).

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130 Mitochondrial haplotype determination

131 Mitochondrial DNA (mtDNA) haplotypes were determined by analyzing DNA profiles and comparing them
132 with reference isolates exhibiting the Ia, Ib, IIa, and Ic mitochondrial genome profiles, as described by
133 Griffith and Shaw (1998). The analysis involved the amplification of specific mitochondrial regions using
134 the P2 primer, followed by digestion of the amplified products with the restriction enzyme MspI. The
135 resulting restriction fragment length polymorphisms (RFLPs) were resolved by gel electrophoresis and
136 compared to the reference profiles to accurately classify the haplotypes.

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139 Microsatellite analysis

140 The genomic DNA of *the P. infestans* isolates was amplified using a predetermined set of microsatellite
141 markers following a modified version of the protocol for the 12-plex method (Table S1, (Li et al., 2013)).
142 The Type-It Microsatellite PCR kit (QIAGEN, https://www.qiagen.com) was used for PCR reactions
143 according to a modified protocol described by Saville *et al.* (2016). The PCR amplicons were then sent to
144 Arizona State University for post-PCR processing in 96-well plates. To prepare the samples for fragment
145 analysis on the 3730 instrument, 3 µL of the LIZ500 size standard ladder was mixed with 1 mL of formamide
146 in a 96-sample plate. Each well of the plate contained 9 µL of the ladder/formamide mixture and 2 µL of
147 1:50 diluted sample. The total sample volume in each well was 11 µL when loaded onto 3730 instrument
148 for fragment analysis. Single sequence repeat (SSR) alleles were sized using GENEMARKER v. 1.9 software
149 developed by SoftGenetics (https://softgenetics.com/), using the allele sizing parameters specified by Li *et*
150 *al. (*2013) in conjunction with a reference dataset comprising European (13A2) and North American
151 (US8A2, US7A2) isolates that were previously genotyped by David Cooke's laboratory
152 (https://thz.lab.mcgill.ca/) at The James Hutton Institute in the UK.

Data Analysis

Statistical analyses were performed using R statistical software version R version 4.3.1 (R Core Team, 2019). The R package poppr was used for locus and population statistics and to calculate the number of multilocus genotypes (MLGs) (Kamvar et al., 2014). The clonality assessment employed the index of association, and statistical significance was determined by conducting 999 permutations on each subset of data using a t-test. Population clustering was determined using principal component analysis (PCA), based on the genetic distance metric of Bruvo *et al.* (2004) and examined in Polysat (Clark & Jasieniuk, 2011). The optimal number of clusters was determined using the within-cluster sum of squared errors (WSS) and The Bayesian model based on the clustering algorithm STRUCTURE V.2.3.4 (Pritchard et al., 2000) to infer population structure, and the optimum value of K was selected using the method of Evanno et al. (2005). An iterative process was employed, considering the genotypic classification of the control isolates and the assumption that these isolates should form distinct groups.

A phylogenetic tree was constructed considering the Bruvo distance and generated using the unweighted pair group method with arithmetic mean (UPGMA) hierarchical clustering. Genotypes were also identified using a minimum spanning network (MSN) which was constructed and visualized using the R package poppr(Kamvar et al., 2014).
Genetic variation for each population was evaluated according to lineage, with clonal diversity measured using Simpson's and Shannon–Wiener diversity indices. Other metrics included genetic richness (R), defined as the number of expected multilocus genotypes (eMLG) adjusted to the smallest sample size, and Hedrick's standardized index (G'ST), used to assess within-population diversity for multiallelic markers (Simpson, 1949; Hedrick, 1999, 2005; Shannon, 2001).

To prevent artificially inflated population differentiation due to repeated sampling of the same genotypes, the population was assessed using clone-corrected data. An analysis of molecular variance (AMOVA) was performed, leading to rejection of the null hypothesis of no genetic differentiation ($p < 0.05$), which suggests that a significant genetic structure exists among the populations.

The analytical scripts and the data are available at https://github.com/myriamiz/Pinf_G_H.

Results

Samples collected

In Honduras, 192 potato samples were collected from four departments (equivalent to the state): Intibucá, Francisco Morazán, Ocotepeque, and Lempira. In Guatemala, 45 potato samples were collected from five departments: Huehuetenango, Quetzaltenango, San Marcos, Chimaltenango, and Sololá (Tables 1 and S2).

Table 1. Number of *Phytophthora infestans* isolates collected from different altitudes in Honduras and Guatemala.

Country	Potato	Departments	Fields	Altitudes (masl)
Honduras	181	Intibucá	48	1170-2088
	5	Ocotepeque	1	1900
	5	Francisco Morazán	1	1558
	1	Lempira	1	1800
Guatemala	16	Quetzaltenango	14	2387-3633
	10	San Marcos	10	2336-2974
	5	Chimaltenango	5	1750-2312
	10	Huehuetenango	9	3010-3411
	4	Sololá	4	1967-2650
Grand Total	237			

Mating type test

The primer set W16–1 and W16–2 generated a 557-bp product. Subsequent digestion with the HaeIII endonuclease revealed two fragments, 557 bp and 457 bp, for A1 mating-type isolates, whereas A2 mating-type isolates of *P. infestans* produced a single fragment of 457 bp. Isolates from Honduras (n = 181) and Guatemala (n = 45) were identified as A2.

Genotypic characterization

Analysis of mitochondrial haplotypes revealed that all 237 *P. infestans* isolates were classified under the Ia haplotype (Figure S1, Table S2).

Among the 12 SSR markers, D13 exhibited the highest number of alleles, indicating its significant contribution to the genetic diversity. This marker was confirmed to have high levels of genetic diversity and variability within populations, as reflected by its high values of 1-D (Simpson's diversity index, which measures the probability that two randomly chosen individuals belong to different alleles) and Hexp (expected heterozygosity, which represents the probability of heterozygosity at a given locus under Hardy-Weinberg equilibrium). In contrast, some markers, including SSR8, Pi04, SSR6, Pi63, SSR3, and Pi4B, demonstrated high evenness and maintained substantial genetic diversity despite having fewer alleles (Table 2).

Table 2. Population statistics for the 12 microsatellite loci in *Phytophthora infestans* populations in Honduras and Guatemala

locus	alleles	1-D	Hexp	Evenness

D13	20	0.8493	0.8506	0.6478
SSR8	6	0.6275	0.6287	0.8642
SSR4	11	0.6303	0.6315	0.6537
Pi04	3	0.5232	0.5243	0.9119
Pi70	2	0.0082	0.0082	0.3053
SSR6	4	0.5747	0.5759	0.842
Pi63	3	0.5683	0.5695	0.872
G11	10	0.6967	0.698	0.7321
SSR3	5	0.4704	0.4714	0.8096
SSR11	6	0.3394	0.34	0.4975
SSR2	2	0.1337	0.1339	0.5223
Pi4B	5	0.531	0.5321	0.8608
mean	6.4167	0.4961	0.497	0.7099

The AMOVA results indicated that the greatest genetic differentiation was found between lineages (61.048%), and that there was a moderate level of genetic diversity within the samples, which was statistically significant (p = 0.001) (Table 3).

Table 3. Analysis of molecular variance (AMOVA) of *P. infestans* isolates from Honduras and Guatemala

				Components of covariance		Monte-Carlo test for significance nrepet=999			
	Df	SumSq	MeanSq	Sigma	%	Obs	Std.Obs	Alter	Pvalue
Within sample	147	93.264	0.634	0.634	38.294	0.634	-17.303	less	0.001
Between sample within lineage	21	14.190	0.676	0.011	0.658	0.011	1.065	greater	0.155
Between lineage	3	67.103	22.368	1.011	61.048	1.011	6.770	greater	0.001
Total	171	174.556	1.021	1.657	100				

Cluster identification from the microsatellite data was performed using PCA, considering the nine departments and three controls, which identified two main groups, with most isolates from Honduras (n=180) and Guatemala (n=14) belonging to the 13A2 clonal lineage (Figure 1). This result was confirmed using Evanno's method with STRUCTURE software, which gave an optimal value of K as 2 (Figure S2); therefore, the samples were best grouped into two separate genetic groups.

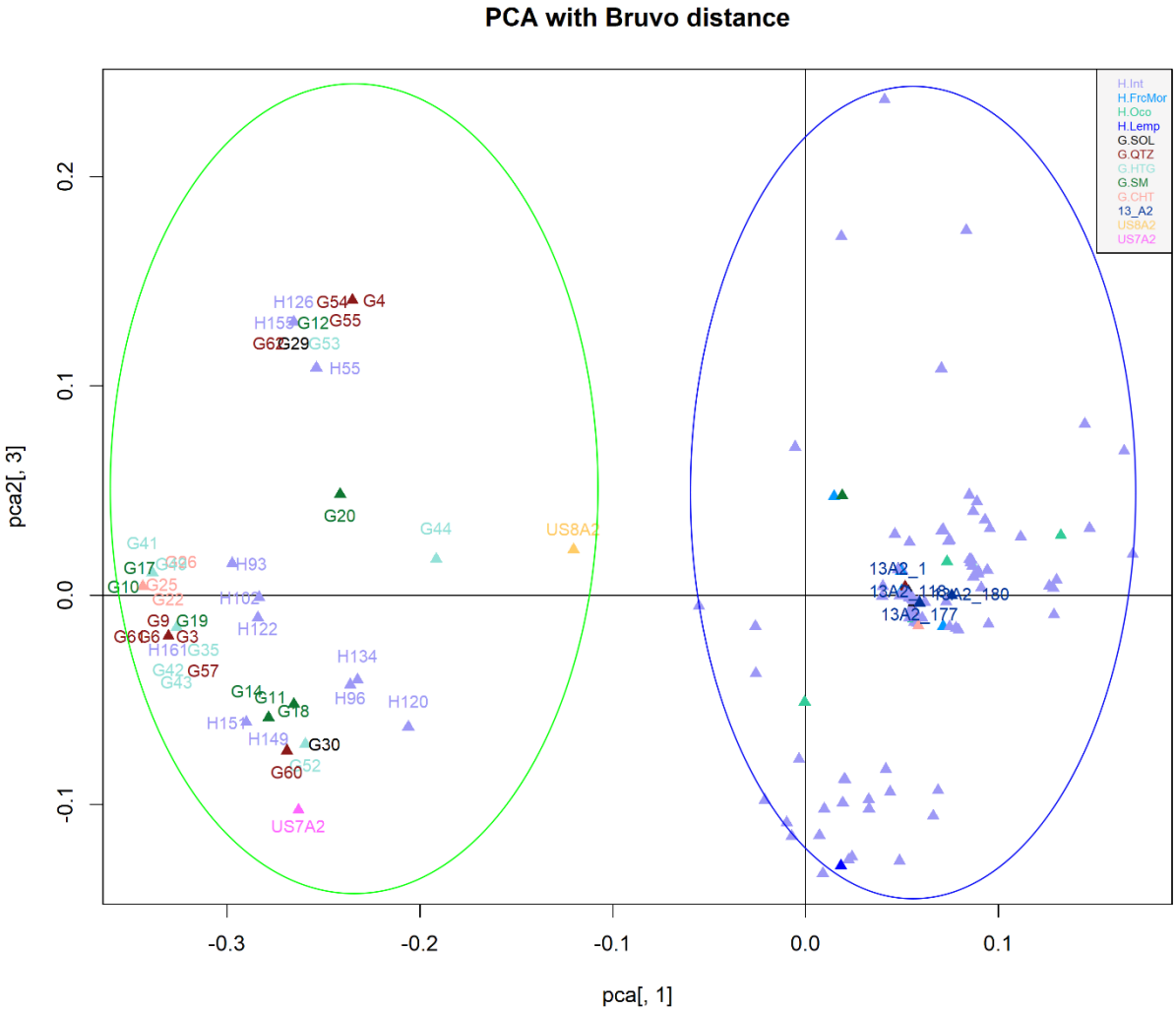

Figure 1. Principal component analysis (PCA) plot of *Phytophthora infestans* isolates from H: Honduras [H.Intibucá (light lilac), H.FranciscoMorazán (Bright Sky Blue), H.Ocotepeque (Aquamarine Green), H.Lempira (Blue)], G: Guatemala [G.Sololá (Black), G. Quetzaltenango (Dark Brick Red), G. Huehuetenango (light turquoise), G.SanMarcos (Olive Green), G. Chimaltenango (Soft melon pink)]. 13A2 (dark navy blue), US8A2 (golden yellow), and US7A2 (bright pink) were used as the clonal lineage controls.

The UPGMA dendrogram separated the subgroups into different branches, resulting in four clusters based on the clonal lineage controls used with a maximum distance of 0.05 (Figure 2). The cluster grouping with 13A2 contained 194 isolates from G.Quetzaltenango (6), G.San Marcos (2), G.Chimaltenango (2), G.Sololá (2), G.Huehuetenango (2), H.Intibucá (169), H.Lempira (1), H.Ocotepeque (5), H.Francisco Morazán (5), another cluster grouping with US7A2 included 33 isolates from G.Quetzaltenango (6), G.San Marcos (6), G.Chimaltenango (3), G.Sololá (1), G.Huehuetenango (6), H.Intibucá (9), a separate cluster (designated CA "Central-America") was identified, which was different from the other clusters identified in this study,

and had 13 isolates from G.Quetzaltenango (4), G.San Marcos (1), G.Sololá (1), G.Huehuetenango (1), H.Intibucá (4), and a cluster grouping with US8A2 had five isolates each from G.San Marcos (1) and G.Huehuetenango (1) (Figure 3).

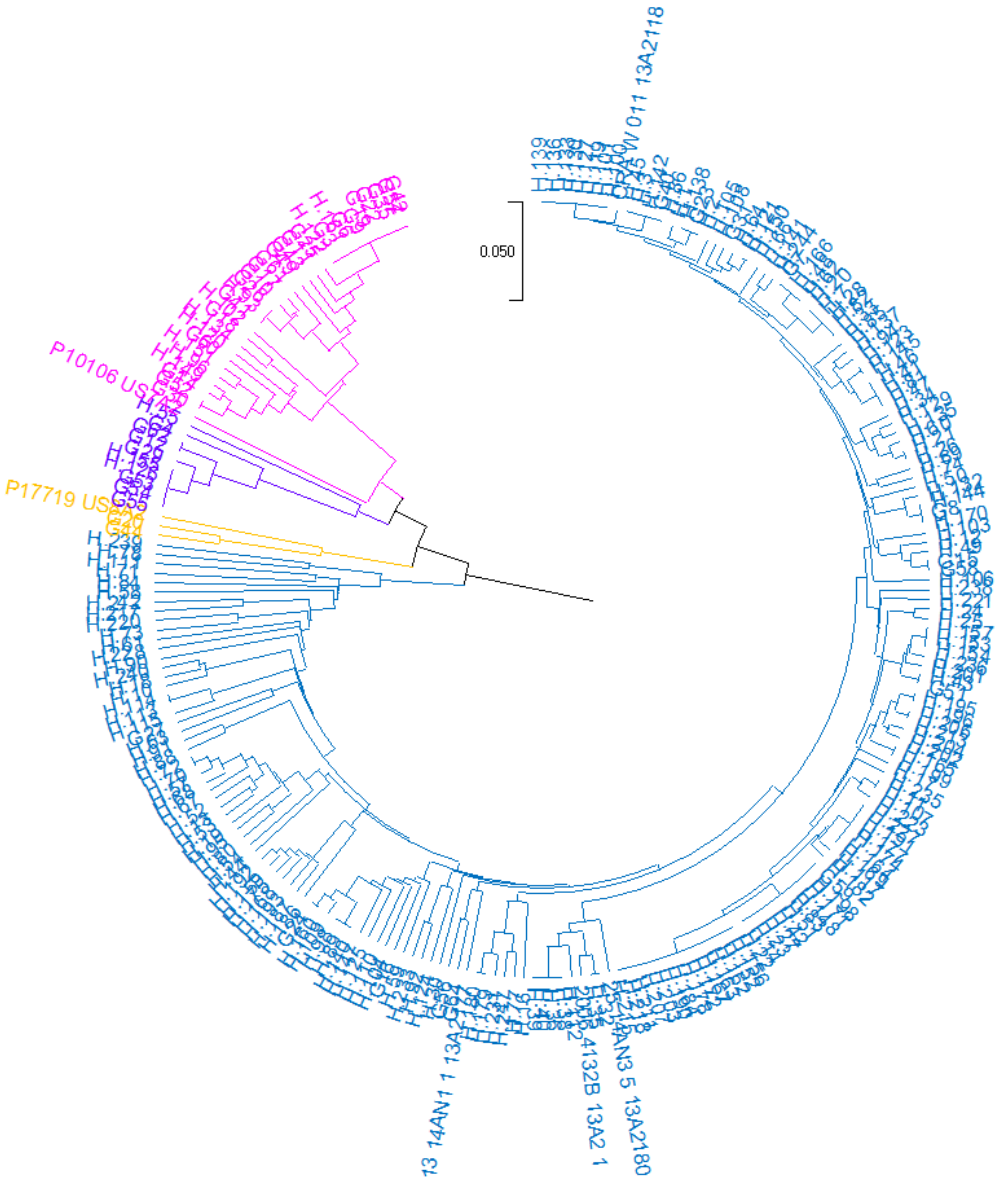

Figure 2. Dendrogram for UPGMA cluster analysis using Bruvo distance in 237 *Phytophthora infestans* strains. Three references were used as clonal lineages: 13A2 (dark blue), US7A2 (pink), US8A2 (yellow). The CA cluster is shown in purple.

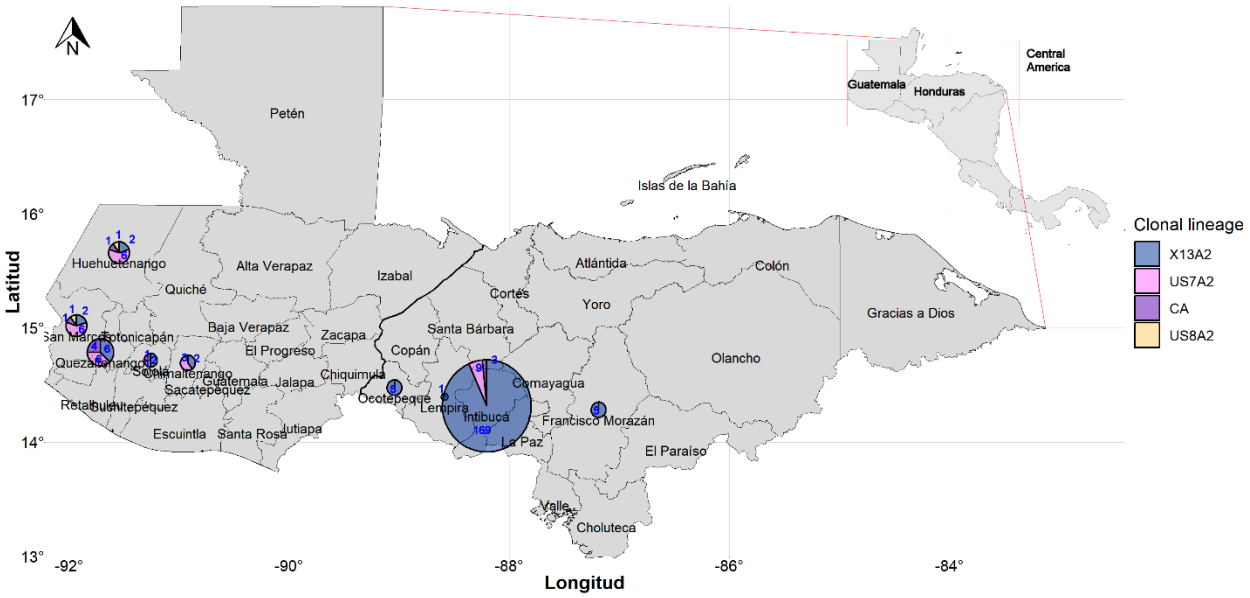

Figure 3. Geographical distribution of clonal lineages 13A2, US7A2, CA, and US8A2 among *Phytophthora infestans* isolates (n = 237) collected in Honduras and Guatemala in 2022. The size of the pie charts is relative to the sample size. A boundary line is shown between the Honduras (right) and Guatemala (left).

When we analyzed the 237 isolates, 154 MLGs were identified. Populations with a high number of isolates, such as Intibucá, comprised 75.3% of the MLGs, with 13A2, CA, and US7A2 clonal lineages identified. Intibucá and San Marcos showed the highest eMLG diversity, indicating a high level of genetic diversity (Table 4). The most frequent MLGs were MLG97 (n=14), MLG122 (n=11), MLG14 (n=9) and all MLG97 belonged to Intibucá. Additionally, 116 MLGs were unique to this isolate. Furthermore, ten MLGs (MLG14, MLG49, MLG85, MLG109, MLG112, MLG122, MLG133, MLG143) shared the same MLGs between Honduras and Guatemala (Figure 4, Table S2).

Table 4. Diversity statistics for microsatellite data across 12 loci in *Phytophthora infestans* populations in Honduras and Guatemala were categorized by location. *H:Honduras, G:Guatemala, Int: Intibucá, Lemp: Lempira, Oco: Ocotepeque, FrMz: Francisco Morazán, Qtz: Quetzaltenango, Sm: San Marcos, Cht: Chimaltenango, Sol: Sololá, Htg: Huehuetenango.

Pop*	N	MLG	eMLG	SE	H	G	lambda	E.5	Hexp	Ia	rbarD
H.Int	181	116	9.45	0.728	4.44	52.76	0.981	0.616	0.454	1.666	0.178
H.FrMz	5	4	4	0	1.33	3.57	0.72	0.922	0.502	1.829	0.346
H.Oco	5	5	5	0	1.61	5	0.8	1	0.484	0.606	0.108
H.Lemp	1	1	1	0	0	1	0	NaN	0.833	NA	NA
G.Sol	4	4	4	0	1.39	4	0.75	1	0.609	1.596	0.207
G.Qtz	16	12	8.12	0.892	2.34	8.53	0.883	0.804	0.569	3.468	0.424
G.Htg	10	9	9	0	2.16	8.33	0.88	0.952	0.569	2.648	0.314
G.Sm	10	10	10	0	2.3	10	0.9	1	0.556	1.884	0.233

G.Cht	5	5	5	0	1.61	5	0.8	1	0.587	4.472	0.684
Total	237	154	9.57	0.646	4.72	69.72	0.986	0.619	0.497	2.823	0.298

N number of individuals, *MLG* number of multilocus genotypes, *eMLG* expected number of MLGs, *SE* Standard error. The subsequent columns are descriptors of MLG diversity: *H* Shannon- Weiner Index, *H Stoddart and Taylor's Index (G), lambda* Simpson's index, *E.5* Evenness, H_{exp} Nei's unbiased gene diversity. *Ia* Index of Association, *rbarD* standardized index of association.

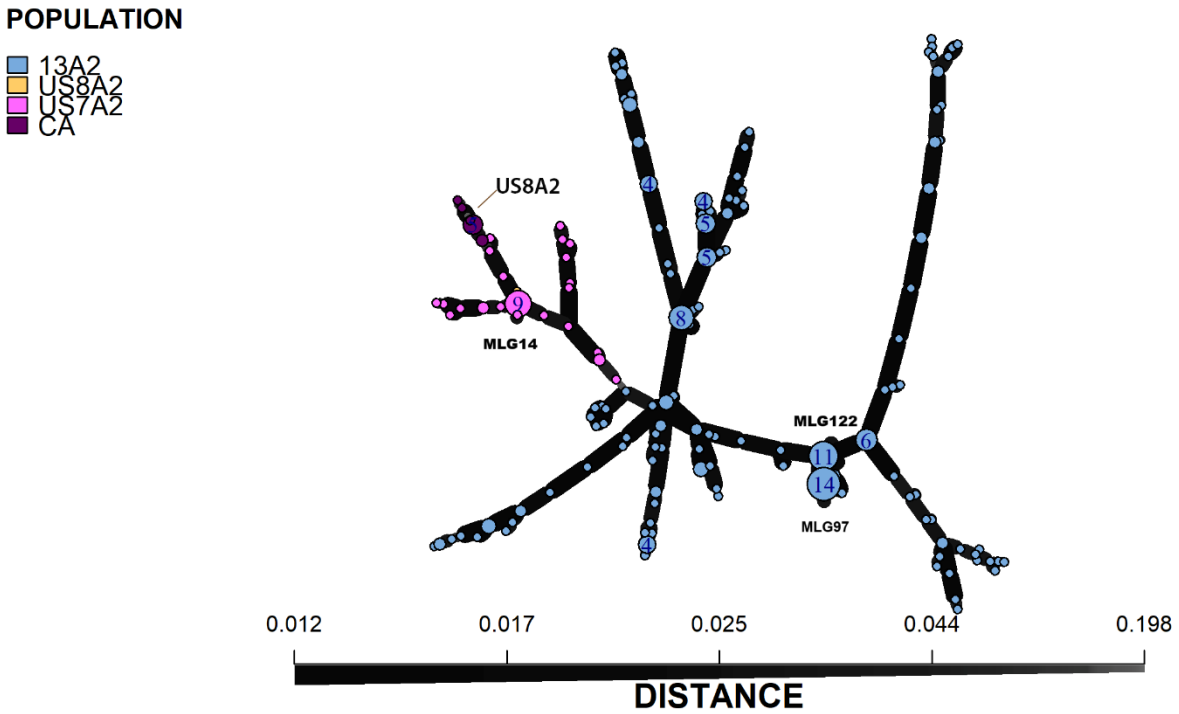

Figure 4. Minimum spanning network (MSN) of multilocus genotypes (MLGs) of *Phytophthora infestans* clusters 13A2, US8A2, US7A2, and CA.

Discussion

The effective management of late blight, a disease caused by *P. infestans*, is essential for the sustainable production of potatoes and tomatoes. In Central American nations like Honduras and Guatemala, understanding the genetic composition, variability, and resistance patterns of local *P. infestans* populations is vital for developing targeted control strategies. Despite the significant impact of this pathogen on agriculture in Central America, there is limited information on its genetic diversity and behavior in these countries. This lack of knowledge presents a substantial obstacle for implementing area-specific management approaches that address the unique challenges encountered in these regions.

In this study, we found four clonal lineages (US7, US8, 13A2, and CA) in the collected samples; US7 was previously identified in Guatemalan tomato samples by Euroblight (2022). Furthermore, US-7 shares a common ancestor with isolates from Costa Rica, where a second genotype associated with wild *Solanum* exhibited multi-locus similarity to US-8, indicating a possible common lineage (Knapova & Gisi, 2002). In Honduras, Forbes (2004) reported only A1, in contrast to our A2 report, which could indicate the introduction of a new mating type through infected seeds (Drenth et al., 1993). However, the presence of both mating types is not always a symbol of sexual reproduction, as reported in Costa Rica by Gomez-Alpizar (2005), in which the population was clonal. With respect to the mitochondrial haplotype, our results showed correspondence with the controls, which were previously genotyped by Martin *et al.* (2019), and confirmed the previous results of Blandón-Díaz *et al.* (2012), who indicated that the Ia mtDNA haplotype replaced IIb in Nicaraguan potato fields, near the border with Honduras.

The composition and genetic variability of *P. infestans* populations can significantly affect disease management. Genetic makeup and clonal lineage structure of these populations play crucial roles in determining effective control measures. For example, certain lineages may show reduced sensitivity to previously effective fungicides such as decreased susceptibility to metalaxyl (Lindqvist-Kreuze et al., 2020). Additionally, some lineages can overcome host resistance, as demonstrated by the ability of the EU_13_A2 lineage to infect previously resistant potato varieties (Stellingwerf et al., 2018). These factors underscore the importance of understanding *P. infestans* population dynamics to develop successful disease management approaches.

Higher diversity is typically found in areas closer to the center of origin of the pathogen (Wang et al., 2017; Shakya et al., 2018). In addition, sexual reproduction can occur in regions where both A1 and A2 mating types coexist, potentially leading to progeny with mixed genotypes that can result in progeny with diverse genetic compositions (Oliva et al., 2002). Examination of the genetic data revealed that a substantial portion of the genetic variation (61.05%) existed between lineages, lending support to the idea of potentially distinct origins for these lineages. This observation echoes the findings of Goodwin (1995), who noted that 63% of the total pathogenic variation in *Phytophthora infestans* across the United States and Canada was attributed to inter-lineage differences, with only 37% variation within lineages. This pattern suggests the introduction of a few genetically distinct lineages, possibly via infected seeds or other propagules, which are subsequently maintained, primarily through asexual reproduction. The use of introduced seeds may have facilitated the dissemination of these genetically distinct lineages across various regions, resulting in genetic differentiation. The introduction of genetically distinct lineages via infected seeds or propagules has been documented in several areas. For instance, in France, cluster analyses identified two differentiated genetic groups of *P. infestans* isolates, indicating multiple introductions either through a mixed population or successive introductions of isolates with diverse genetic backgrounds (Montarry et al., 2010). Similarly, in Algeria, three main lineages (EU_13_A2, EU_2_A1, and EU_23_A1) have been identified, and their distribution was influenced more by seed dispersal than by cropping regions (Beninal et al., 2022). Evidence also suggests an important role for 13A2 in the 2013–14 late blight epidemic in eastern and northeastern India, where it has replaced the existing populations (Dey et al., 2018). This indicates that 13_A2 likely spread from Europe to India, possibly through seed importation.

The 13_A2 lineage has not been previously reported in America. In our study, the allele sizes of the 12 SSR markers corresponded with those documented in our European reference isolates of the 13_A2 clonal lineage, which is in contrast to the results of Blandón-Díaz et al. (2012) for the Nicaraguan isolates. As

potato seeds used in Honduras originate from the Netherlands and France (SAG & UPEG, 2021; World Bank, 2023c), where this clonal lineage has already been reported (Cooke et al., 2012; Mariette et al., 2015), it is plausible that 13_A2 could have been introduced to Central America via imported potato seeds. In the case of clonal lineage CA, which shares the majority of allele sizes with EC-1 but not with its reported mt haplotype (IIa)(Martin et al., 2019), clonal lineage CA is likely the result of new seed introductions from South America (World Bank, 2023b). Therefore, these importation issues pose a significant risk because infected tubers can introduce inoculum early in the growing season, thereby facilitating rapid disease establishment. Even a few infected seed tubers that may go unnoticed can initiate epidemics. Moreover, tubers infected immediately before planting are more likely to produce viable infected shoots, which increases the risk of disease transmission (Johnson, 2010). These factors highlight the importance of quarantine measures to prevent the introduction of new, aggressive clonal lineages through imported potato seeds and the need to strengthen local seed production, starting with the introduction of advanced germplasm to be tested and selected under local conditions or the implementation of a local breeding program. Other actions for strengthening local seed production include the production of early generation seeds, decentralized seed multiplication, and the adaptation of quality assurance mechanisms, among others (Forbes et al., 2020).

In this study, MLG97, which was the most abundant, belonged to 13A2, all in Intibucá, suggesting its recent establishment (Göre et al., 2021). Conversely, MLG122 and MLG14 were found across different localities, suggesting that these MLGs may be older and have more time to spread (Dey et al., 2018). For example, MLG 122 (13A2) and MLG14 (US7) were detected in Intibucá and Quetzaltenango, respectively, with approximately 644 km between them. Therefore, the number of MLGs within a clonal lineage of *P. infestans* may be substantial, reflecting the importance of asexual reproduction and persistence of *P. infestans* populations and the ability of the pathogen to adapt and diversify, possibly through mutations and other mechanisms (Hansen et al., 2016; Göre et al., 2021). This diversity underscores the importance of the continuous monitoring and characterization of *P. infestans* populations to inform effective disease management strategies (Dey et al., 2018).

These results provide important insights into the *P. infestans* population in Central America and important data to support future *P. infestans* migration studies.

Author contributions

MI: coordination, sample processing, molecular laboratory work, marker scoring, analysis, interpretation of data, and drafting of the manuscript.
WP: coordination, interpretation of data, and drafting of the manuscript.
SG: sample processing.
JA: coordination.
EV: sampling.
BF: sampling.
AS: coordination.
GP: sampling.
LM: sampling.
JK: interpretation of data and drafting of the manuscript.

Supplementary Information

Supplementary Table Legend

Table S1. Details of the SSR markers of the 12-plex microsatellite assay utilized for the characterization of *Phytophthora infestans* isolates

Table S2. All data of the *Phytophthora infestans* isolates characterized in this study

Supplementary Figure Legend

Figure S1. Results of Restriction fragments from digestion of the P2 region with enzyme *MspI* with Honduran and Guatemalan isolates (H78, H85, H86, G12, G14, and G15). Ladder 1kbplus.

Figure S2. Structure analysis showing Delta-K values of strains of *P.infestans* population from Honduras and Guatemala.

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Data Availability Statement

The generated data are available on the CIP database website at [https://data.cipotato.org/dataset.xhtml?persistentId=perma:organame/dsVJLRDL]

Footnotes

Conflict of Interest declaration: The authors declare that they have no affiliations with or involvement in any organization or entity with any financial interest in the subject matter or materials discussed in this manuscript.

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