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Distribution of major clonal lineages EU_13_A2, EU_2_A1 and EU_23_A1 of *Phytophthora infestans* associated with potato late blight across crop seasons and regions in Algeria.

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ABSTRACT

Potato is one of the most important agricultural crops in Algeria and worldwide. Each year, potato late blight, caused by *Phytophthora infestans*, is responsible for significant damage that leads to large production losses, and is thus a direct threat to food security in Algeria. In this study, 131 isolates of *P. infestans* and 92 DNA fingerprints captured on FTA cards were sampled from commercial and seed production fields in three major potato production regions (western, eastern and central) during the main-season and late-season in Algeria over six seasons of cropping (2010-2016). Genotypes of *P. infestans* and population genetic diversity were analyzed using a 17-plex simple sequence repeat (SSR) marker assay, and the mating type of all isolates was characterized. Both mating types (A1 and A2) were found, and often occurred in the same field. Differences in mating type proportion were observed between regions and between sampling periods. Analysis with SSR markers showed the prevalence of the EU_13_A2 lineage (70%) over EU_2_A1 (16%), EU_23_A1 (10%) and 4% were of unknown MLL. The EU_13_A2 showed differentiation within the group. EU_23_A1 was found mainly in late-season crops. However, the cropping region did not influence the distribution of lineages due to the dispersal of the pathogen in Algeria by seeds. Genetic structure did not reveal a clear variation in distribution of the three lineages throughout the sampling regions. These data provide important new information on the

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composition and change over time of *P. infestans* populations in Algeria and open the way for a better understanding of the local epidemiology of this important pathogen.

Key words: Potato late blight, mating types, simple sequence repeat (SSR) markers, genotypes, genetic structure.

INTRODUCTION

Potato (*Solanum tuberosum* L.) is a major food crop that provides important nutrients around the world, being the first non-cereal crop globally in terms of production after wheat, rice, and corn (FAOSTAT, 2016) (<http://faostat.fao.org/>). It is the first agricultural, in terms of acreage and production, in Algeria after cereals and vegetables. Potatoes are grown in almost all agricultural regions across the country. However, the most important areas are those where the soil-water potential is favorable such as in the regions of AinDefla, Bouira, Chlef, Mascara, Mostaganem, Relizane, Guelma and Skikda, all located in the north of Algeria. The total potato growing area exceeds 165 000 ha for both the main and late-seasons, with an annual production of 4.6 million tons (FAOSTAT, 2016) (<http://faostat.fao.org/>). Recently, potato production has started in the El Oued region, in the south-east of the country in the Sahara desert.

Late blight caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, is a major threat to potato crops worldwide and is the most devastating potato disease in Algeria. Since 2007, late blight has been responsible for significant yield losses in each growing season. Potato yield losses are greater in the northern regions under the Mediterranean climate due to more favorable conditions for late blight development, compared to areas with semi-arid climates (Beninal et al., 2009).

While the main control method for this disease is currently the repeated application of fungicides, alternative disease control strategies are effective in reducing both the yield losses and the negative side effects of chemicals on the environment and human health (Flier et al., 2003).

Phytophthora infestans is a near-obligate hemibiotrophic pathogen with two known mating types: A1 and A2 (Fry, 2008) which enable the pathogen to reproduce both asexually and sexually, generating zoospores and oospores respectively (Fry & Goodwin, 1997). The presence of both mating types A1 and A2 enables sexual reproduction of the pathogen, which may generate a higher genetic diversity within *P. infestans* populations and lead to increased adaptability of the pathogen to environmental conditions, in particular to wider moisture and temperature ranges (Mariette et al., 2016; Runno-Paurson et al., 2019). These changes could make potato late blight

control even more challenging (Yuen & Andersson, 2013). This is why the detailed knowledge of population genetic structures is critical for sustainable control strategies.

Before 1980, the global *P. infestans* population (except in central Mexico) was asexual and consisted of A1 mating type genotypes only. In the late 1980s, the A2 mating type was introduced into Europe as a result of successive potato imports from Mexico to fill the crop shortage caused by the 1976 drought (Fry *et al.*, 1997).

In Europe, the A2 mating type was first reported in Switzerland in 1981 by Hohl and Iselin (1984) and has subsequently been identified in all European populations (Cooke *et al.*, 2011). In Algeria, the first report of the A2 mating type was in isolates collected in 2008, which showed a complex virulence profile and resistance to the fungicide metalaxyl (Beninal *et al.*, 2009). In neighbouring countries, the A2 mating type was first reported in Morocco in 1999 (Hafidi *et al.*, 2002) and in Tunisia in 2005 (Jmour & Hamada, 2006).

The genotyping of *P. infestans* populations progressed when microsatellite markers (also known as Simple Sequence Repeat (SSR)) were developed (Lees *et al.*, 2006). In Europe, new clonal lineages have spread very quickly and have replaced the old ones (Cooke *et al.*, 2012). EU_13_A2, which is one of the most common genotypes in Europe currently, was first detected in 2004 (Cooke *et al.*, 2012; Chmielarz *et al.*, 2014; Mariette *et al.*, 2016). *Phytophthora infestans* populations have recently undergone rapid genetic changes due to cross-breeding between genotypes and their subsequent appearance through the potato growth areas all over the world (Cooke *et al.*, 2012; Mariette *et al.*, 2016; Dey *et al.*, 2018).

Initial surveys of the composition of Algerian *P. infestans* populations collected from tomato and potato fields have been undertaken in recent years. These studies showed that the clonal lineage EU_13_A2 was present in Algerian *P. infestans* populations along with two other clonal lineages, EU_2_A1 and EU_23_A1, between 2007 and 2014 (Corbière *et al.*, 2015; Rekad *et al.*, 2017). However, these data remain insufficient, because they do not cover all potato production areas in Algeria and more recent epidemics.

Thus, in this study, a larger number of isolates from the main potato producing areas of the three main regions (west, east, central) were collected and genotypically characterized with 17-plex SSR markers set, and also characterized for mating type. More specifically, we were interested in answering the following questions: Is there variation in the genotype and phenotype of *P. infestans* isolates collected in Algeria during the period 2010 to 2016 according to region and cropping season and, if so, does it affect the pathogen's sexual reproductive potential and late

blight management advice? Thus, knowledge of the genetic structure of this pathogen and its geographical distribution in Algeria is a key element in establishing effective control strategies.

MATERIALS AND METHODS

Sampling

Leaves with late blight lesions and stems of several cultivars of potatoes (mainly ‘Spunta’) were sampled to obtain either living isolates for in vitro culture or DNA on Whatman Flinders Technology Associates (FTA) cards. These samples were collected from potato fields in western, central and eastern regions during seven consecutive cropping years, from 2010 to 2016, and from the two main potato crops grown in a calendar year/ The first crop (main season) is planted from November to April, with harvest in May to July, while the second crop (late-season) is planted in August / September and harvested in December / January. A total of 223 isolates were collected from the eleven main potato-growing areas in Algeria: Mostaganem and Mascara in the northwestern; AinDefla, Algiers, Tipaza, Medea, Tizi Ouzou, Boumerdes and Bouira in the Central region; and Guelma and Skikda in the east. Over all years, the number of samples collected from each region was 202 (central), 10 (east) and 11 (west) (Table 1 and Fig. 1). We also scouted crops in the eastern Sahara production area (El oued), but, due to unfavorable climatic conditions for late blight development, *P. infestans* was not found there.

Isolation, purification and conservation of isolates of *P. infestans*

Small pieces of infected tissue (leaves and stems) were cut from the sporulating margin of the lesion and placed on slices of a susceptible potato cultivar (Spunta), making sure that the sporulating side of the lesion was in contact with the tuber surface.

Tuber slices were then placed in closed plastic boxes on a moistened sponge pad, and thereafter incubated at 15 °C for 5 days. The mycelium with sporangiophores and sporangia forming on the tuber slice surface was collected and transferred to pea agar containing antibiotics (30 mg^l⁻¹ rifamycin and 200 mg^l⁻¹ ampicillin) (Corbière & Andrivon, 2003) (<http://www.eucablight.org/EucaBlight.asp>). Petri dishes with pure cultures were incubated in the dark at 15-18 °C.

From the 223 total isolates, 131 were obtained as live cultures. The remaining 92 were obtained as mixed potato and pathogen DNA on FTA cards. These cards were used to collect DNA

fingerprints from remote late blight outbreaks and of different genotypes from closely spaced lesions on the same leaf probably derived from sexual recombination (samples were taken from the same location, from basal leaves very close to the ground and repeated only in the experimental trials) (Table 1).

Mating type determination

The mating type of each live isolate was determined by individual pairing on pea agar with known A1 and A2 tester isolates. After 10-14 days of incubation in darkness at 15°C, Petri dish cultures were examined under a microscope for the presence or absence of oospores in the zone of mycelial interaction between paired isolates. Isolates forming oospores on Petri dishes with the A1 mating type tester were rated as A2; isolates that formed oospores with the A2 mating type were registered as A1.

DNA extraction

Mycelial discs of *P. infestans* were grown in liquid pea broth previously autoclaved at 120 °C for 20 minutes. After three weeks of incubation at 15 °C, mycelium was washed three times in sterilized distilled water and lyophilized. In addition, well-marked prints of late blight were kept on FTA cards, onto which DNA is quickly fixed (<http://www.euroblight.net/>). DNA of the live isolates and FTA cards was extracted using NucleoSpin Tissue kit and according to the manufacturer's instructions. A2 mm disk punched from each card. The manufacturer's protocol was used to purify the DNA from FTA cards.

SSR genotyping

Each isolate was genotyped at seventeen microsatellite loci, namely PiG11, Pi4B, Pi4G (Knapova & Gisi, 2002), D13, Pi04, Pi33, Pi16, Pi56, Pi63, Pi70 (Lees et al., 2006), PinfSSR2, PinfSSR3, PinfSSR4, PinfSSR6a, PinfSSR7, PinfSSR8, PinfSSR11 (Li et al., 2010). For each locus, one of four fluorescent markers (6FAM, NED, VIC, PET) was assigned.

PCRs were performed using Type-it Microsatellite PCR kit (QIAGEN). The PCR reaction volume of 5 µl consisted in 2 µl DNA (5 ng/µl), 2.5 µl of PCR master mix (Qiagen), 0.5 µl of primers and 3nm of MgCl₂.

Amplification was carried out in a Bio-Rad C1000 thermal cycler under the following conditions: initial denaturation step at 94 °C for 5 min; 30 cycles of 20 s at 94 °C; 25 s at 58 °C and 30 s at 72 °C; and a final elongation step of 5 min at 72 °C.

Amplification products were divided into two batches, based on expected allele sizes: 6FAM (D13, PinfSSR8), VIC (Pi04, Pi70), NED (G11, PinfSSR3, and PinfSSR11), PET (PinfSSR2, Pi4B) in batch 1 and 6FAM (Pi63), VIC (Pi16, PinfSSR6), NED (Pi4G, PnfSSR4), PET (Pi33, Pi56) in batch 2. A volume of 8 µl samples, comprising a loading buffer containing a mixture of 5µl Hi-Di deionized formamide, 500 LIZ size marker, and 3 µl of 150-fold dilutions of the multiplexed PCR products, were sequenced in an ABI prism 3130xl DNA sequencer, according to the manufacturer's instructions (Applied Biosystems). Allele size and assignation were read using GeneMapper v 3.5 (Applied Biosystems) software.

Data analysis

Mating type frequency across regions was calculated and the proportions of each type calculated according to each potato growing season (main and late-seasons).

SSR genotypes were grouped according to their geographical location. Parameters were studied such as: total number of alleles (A_r), effective number of alleles (A_e) at each locus and at each population and the number of private alleles (P_a). Genetic diversity, such as expected heterozygosity in the dataset (H_t) and that calculated from expected heterozygosity (H_s) at each locus and in each population, were estimated using Genodive2.0 (Meirmans & VanTienderen, 2004). A kinship covariance matrix constructed in Genodive2.0 was loaded into Primer 7. A two-way analysis of variance (permanova+), (factor1 = regions; factors2 = MLLs), was conducted with 10000 unrestricted permutations of raw data and type III sums of squares. The significance is based on pseudo-F value (Clarke & Warwick, 2001).

Genotype 1.2 login was used to calculate the distance matrix using the Infinite Allele Model with a three's hold set to 0. Two levels of analysis were considered: 1) individuals were grouped according to their geographical location, 2) MLL was assigned to each individual and therefore, the total number of genotypes (MLGt), the effective number of genotypes (MLGe), genotypic diversity (Div) and the Shanon-Weiner's corrected index (Shc) was calculated in Genodive2.0. The constructed genetic matrix, based on the neighbor-joining clustering algorithm using 1000 bootstraps, was used to construct a polar in FigTree 1.4.2. Multilocus lineage (MLLs) for each isolate. Multilocus genotypes (MLGs) were determined using GENALEX software v. 6.5.0.3

(Peakall & Smouse, 2012). The population genetic structure was analyzed using Structure 2.3.4, with the optimal number of clusters (K) determined with the Delta K method (Evanno et al., 2005), implemented in Structure Harvester (Earl & VonHoldt, 2012). The number of genetic groups (K) was tested from k = 1 to k = 10, with 20 replicates for each k to check for the MCMC convergence. For each run, 20000 burn-in period steps followed by 100000 iterations were performed. The posterior probability of the data [lnP(D)] for each k-value was checked to confirm the optimal number of clusters (k) chosen. A complementary principal component analysis (PCA) was performed using Genodive2.0 in order to validate the genetic structure. The pairwise population differentiation F stats and the level of significance were calculated using Genodive2.0.

Analysis of molecular variance (AMOVA) was performed twice (Excoffier et al., 1992). First, the individuals were grouped according to their geographical location (west, central and east). These analyses helped determine how the genetic diversity is partitioned within and among populations; AMOVA was performed using Genodive2.0. The ploidy Independent Infinite Allele Model (*Rho-st*) algorithm (Ronfort et al., 1998) was selected as it is the only measure of population differentiation that is independent of the ploidy level and appears unbiased by the type of inheritance (Meirmans & VanTienderen, 2013).

RESULTS

Mating types

Both A1 and A2 mating types were found among *P. infestans* isolates collected in Algeria. Out of the 131 live isolates characterized, 60% (78 isolates) belonged to the A2 mating type and 40% (53 isolates) to the A1 mating type. No isolate formed oospores with both testers (Table 1).

The A2 mating type prevailed throughout the years of study and in all regions except Boumerdes and Mostaganem. However, it should be noted that in these areas only one isolate (A1 mating type) was collected in 2015 (Fig. 1). Both mating types (A1 and A2) are found in the same disease outbreak, especially in the central and western regions. Differences between the proportion of both mating types and the growing season were observed, with prevalence of the A1 mating type in late-season and of the A2 mating type in main-season isolates (Fig. 2).

SSR polymorphism

The total number of alleles per locus ranged from 2 to 20 according to the populations. When populations were pooled according to regions, the total number of alleles was 45 (East), 47 (West)

and 78 (Central). The D13 locus was most polymorphic, with a large number of alleles ($n = 20$) and a high allele frequency (0.253). By contrast, Pi16, Pi33, Pi56, Pi70, Pinf SSR2 and Pinf SSR7 markers showed a small number of alleles ($n = 2$) and a lower allele frequency of 0.025 (Table 2).

The average number of informative alleles per locus was 2.083, and varied from 1.046 to 3.785 depending on populations (Table 2). The overall mean number of informative alleles was similar in all regions, rating at 2.011 (east), 2.061 (west) and 2.205 (central).

The central population of *P. infestans* exhibited a high number of private alleles (27), while only one private allele was found in the eastern population and none was revealed in the west.

Heterozygosity levels were significantly different for both *Ht* (0.046-0.754) and *Hs* (0.047-0.758) with a mean *Ht* of 0.464 and *Hs* of 0.462 (Table 2). Values of *Ht* and *Hs* were similar for each regional group, with a mean of 0.464 and varying slightly between 0.456 (east), 0.467 (west) and 0.469 (center) (Table 3).

Multilocus lineages

Out of 223 individuals, 213 were genotyped successfully. Number from each region was 192 (Central), 10 (east) and 11 (west). They could be grouped into three major MLLs, namely EU_13_A2 ($N = 152$), EU_2_A1 ($N = 36$) and EU_23_A1 ($N = 18$). Seven individuals exhibited an as yet unrecorded MLL and were excluded from all further analyses. Mating type results supported the assigned genotypes.

The EU_13_A2 lineage was present in all sampling years from 2010 to 2016 and in all Algerian potato growing areas, while EU_2_A1 was not detected in the 2015 collection and was replaced by EU_23_A1. Unclassified MLLs were also found in the central region between 2011 and 2016 (Fig. 1).

F_{st} showed no significance in levels of differentiation between pairs of populations, with F_{st} values of 0.002 (center-east; $p = 0.235$), 0.003 (west-center; $p = 0.086$) and 0.004 (west-east; $p = 0.179$). A different pattern was observed for the same parameter between pairs of MLLs; differences were small but statistically significant between EU_13_A2 and EU_23_A1 (0.068; $p < 0.001$), EU_13_A2 and EU_2_A1 (0.076; $p < 0.001$) and between EU_23_A1 and EU_2_A1 (0.089; $p < 0.001$).

The 2-way permanova showed that the effect of the MLL is very highly significant on the kinship coefficient and is sufficient to explain most of the variance (Pseudo- $F_{3,197} = 13.95$; $p < 0.001$). The region variable explains a small part of the total variance, with no statistical significance (Pseudo- $F_{2,197} = 1.07$; $p = 0.286$) (Table 4). The MLGt and MLGe found by region

varied from 5 to 4.17 in west, from 6 to 3.33 in east and from 32 to 2.6 in center. The genotypic diversity value in the west population was the highest (0.836) followed by the east population (0.778) and the center population (0.618). Shc values were high, ranging from 0.756 in west, 0.89 in center and 0.97 in east. When individuals were grouped according to their MLL, results for MLGt varied from 6 (EU_2_A1), 12 (EU_23_A1) and 18 (EU_13_A2). The MLGe values varied from 1.342; 1.618 and 9.529 respectively for the 3 MLLs. Div values were significantly different between EU_2_A1 (0.262), EU_13_A2 (0.384) and EU_23_A1 (0.948). Also, Shc values varied between EU_2_A1 (0.430), EU_13_A2 (0.574) and EU_23_A1 (1.315) (Table 5).

AMOVA analysis showed a low and insignificant percentage of variance (1.8%; $p = 0.06$), which is explained by the regions that increased significantly for clustering based on MLLs (59.1%; $p = 0.02$) (Fig. 3) (Table 6).

Genetic structure

The genetic structure for the whole data set revealed that individuals were distributed into three main groups, matching the three major lineages described above (Fig. 4). One group contained all individuals belonging to the A1 mating type. EU_13_A2 MLL divided into two groups. No introgression was found except for only one individual from EU_23_A1 MLL that showed a mixed assignment to group 3 (Fig. 5) and might be a recombinant. The EU_13_A2 is the most prevalent lineage, representing 70% of all isolates collected from 2010 to 2016, and was present in all Algerian potato production regions. The EU_2_A1 clonal lineage, representing 16% of the *P. infestans* population collected from 2010 to 2015, was found mainly in the center of Algeria (Algiers, AinDefla and Tizi Ouzou). EU_23_A1, which represented 10%, was detected in 2015 and 2016 in central regions such as Algiers, Boumerdes, Bouira, Tipaza and Tizi Ouzou, but also in the west (Mascara and Mostaganem) and in the east (Guelma). Other, unclassified isolates were detected between 2011 and 2016 in low numbers, and represented only 4% of the collection. Overall, the distribution of MLGs showed multiple occurrences of the same genotypes within each region. In total, 98 MLGs found during the sampling period (2010-2016) with the 218 replicates. The highest frequency of occurrence (0.179) was noticed for MLG_17 with 40 replicates found in four localities. The major MLGs, with a number of replicates above 10, were mainly distributed in Algiers (MLG_17, MLG_22, MLG_11 and MLG_23), Tipaza (MLG_17 and MLG_11), Tizi Ouzou (MLG_17 and MLG_22) and AinDefla (MLG_11 and MLG_23) (Table 7).

DISCUSSION

Several investigations on *P. infestans* populations in Algeria have been carried out over the past decade, such as the studies of Rekad et al. (2017) in the west of Algeria over the period of 2008-2014 and Belkhiter et al. (2019) about host adaptation in *P. infestans* populations. This paper supplements these earlier reports with more comprehensive data on the population structure of *P. infestans*, and opens three major conclusions: 1) in Algeria, *P. infestans* populations are dominated by three major clones (EU_13_A2, EU_2_A1 and EU_23_A1), but also contain some minor lineages which are possibly recombinants; 2) these populations are not geographically differentiated; and 3) temporal variations between seasons and years suggest carry-over of primary inoculum between hosts.

Our data confirm the presence in Algeria of three major clonal lineages (EU_13_A2, EU_2_A1 and EU_23_A1) of *P. infestans*, alongside other unclassified isolates possibly resulting from sexual reproduction.

They highlight the prevalence of *P. infestans* EU_13_A2 genotype across Algerian potato crops, and the regional distribution of EU_2_A1 and EU_23_A1. The rise of EU_13_A2 explains the recent increase of the frequency of the A2 mating type (Rekad et al., 2017), and mirrors findings in neighboring Maghreb countries, Morocco (Sedegui et al., 2000) and Tunisia (Jmour & Hamada, 2006; Harbaoui et al., 2013). The study period (2010 to 2016) was characterized by an important increase in late blight prevalence and severity nationwide, and closely follows the first detection of A2 genotypes in the country in 2007 (Beninal et al., 2009; Rekad et al., 2017). Many reports mention the current dominance of EU_13_A2 on potato since 2004 / 2006 in Europe (Cooke et al., 2012; Mariette et al., 2016), and more recently outside Europe (Dey et al., 2018). This dominance was often attributed to increased virulence and aggressiveness (Cooke et al., 2012; Chmielarz et al., 2014), although recent work showed that other factors, such as overseasoning ability, are probably involved (Mariette et al., 2016). The EU_2_A1 clonal lineage was previously reported on potato and tomato in Algeria (Rekad et al., 2017). However, this genotype was found at low frequencies in recent years, relative to EU_13_A2. It was identified only from potato in high frequency, which strongly suggests its specialization to the potato crop. In France, the EU_2_A1 lineage was dominant on potato before 2006 (Mariette et al., 2016), but is now infrequent. The low frequency of EU_2_A1 isolates in Algerian populations could be explained by a better inclusive fitness or particular adaptive capabilities of EU_13_A2, compared to EU_2_A1 (Corbière et al., 2015). However, EU_2_A1 recently emerged as an invasive clone in

Eastern Africa, where it caused severe epidemics (Njoroge et al., 2019). There is evidence that EU_2_A1 was introduced in Eastern Africa through seed imports from Europe, a situation that may also have occurred in Algeria, where average yearly seed tuber importations are important (100 000 tons) and originate mainly from the Netherlands (58%), France (16%) and Denmark (13%). EU_2_A1 was probably introduced several years ago, and then became established in Algeria. However, it is noteworthy that some clones prevalent in western Europe, such as EU_6_A1 or EU_8_A1 at the same time as EU_2_A1, were not found within the Algerian populations surveyed. In Europe these clones are mainly restricted to oceanic climates prevalent in northwestern Europe, and might not be able to thrive under Mediterranean conditions.

By contrast, EU_23_A1 was detected in one sample collected from potato in Mostaganem in 2013 and in a further 5 samples from the same area the following year (Rekad et al., 2017). We found this lineage in 2015 and 2016 in the centre and east of Algeria. While it is primarily adapted to tomato in Europe (Mariette et al., 2016), it was present at a higher frequency on potato in Egypt (El-Ganainy et al., 2013). EU_23_A1 is genetically identical to the US_23 genotype, which caused severe epidemics on both potato and tomato in the USA in recent years (Danies et al., 2013). It is quite possible that EU_23_A1 may be of local origin, and persists thanks to its ability to bridge hosts grown year-round in the Mediterranean area. This hypothesis is reinforced by the observation that the A2 mating type was rare from late-season samples, unlike the A1 mating type. It is thus likely that the inoculum infecting the late-season crops is mainly born on tomato, to which the EU_23_A1 is best adapted. This inoculum transfer between crops is made easier than in many other areas, since potato and tomato crops are grown year-round in Algeria, often in close proximity under the same environmental conditions (Belkhiter et al., 2019).

While A1 genotypes were well genetically structured, with few MLL variants, the EU_13_A2 lineage seems to be undergoing genetic differentiation. The phylogenetic tree shows a clustering of individuals according to geographical sites, indicating the emergence of local variants of this lineage. This confirms the results obtained in the AMOVA, and mirrors the report of sub-clonal variation noticed by Rekad et al. (2017). Interestingly, four MLGs were missing in the central region (the most intensely sampled). This might be due to restrictive conditions for their development in this area, in response to continuous climate variation. However, this subclonal variation and regional distribution of some of the minor genotypes were not sufficient to generate a strong geographic differentiation within population genetic structures. Indeed, and unlike the situation reported in some other Maghreb countries, such as Morocco (Hafidi et al., 2002), no

clear regional structure emerged from our surveys. The low variance part explained by the variable 'region' for the kinship coefficient indicates that individuals are different not because they belong to different geographical regions, but rather because they are not a clear pattern of MLGs distribution.

This lack of regional differentiation may be due to the national seed production strategy, according to which seeds are produced in defined areas and sold all over the country, favouring the dispersal of the same pathogen genotypes in Algeria. It might also reflect the fact that the hosts themselves are not geographically structured: 'Spunta' is the dominant potato cultivar in all production regions sampled, and all these regions grow both potato and tomato. The relatively low values of MLGs indicate that the pathogen is well adapted within its range of expansion. Often *P. infestans* populations have the capacity to adapt locally and let local variants emerge (e.g. Mariette et al., 2016), but this adaptation is negated when populations are strongly subjected to largely uniform selection pressures by a single host (Montarry et al., 2008).

The geographical and temporal overlaps in the distribution of both crops possibly also favours the presence of both mating types (A1 and A2) in the same field outbreak, that we have been able to observe in several fields in Algiers, Boumerdes or Mascara. This co-occurrence increases the likelihood of sexual reproduction of *P. infestans* in Algerian potato fields. While we have no direct evidence of recombination among genotypes, it is hypothesized that sexual reproduction would generate greater genetic diversity resulting in genotypes that are more aggressive and difficult to control. This sexual population also means increasing the risk of oospores derived late blight attacks very early in the season, as reported in northern populations (Kiiker et al., 2019). However the genetic diversity revealed in this study was quite low within sites with little heterozygosity, which is consistent with a clonal structure of local populations. This result does not match observations by Rekad et al. (2017) for the western region. This discrepancy might be explained by the relatively low number of SSR markers used in their study. It is therefore important to continue tracking both recombinants and oospore formation during future surveys.

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CONFLICT OF INTEREST

The authors declare no conflict 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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Figure legends

Figure 1: Number of isolates per year and sampling map used in this study. (a): each line represents a clonal lineage (blue dash with dot (EU_13_A2 (n=152)), green dotted line (EU_23_A1 (n=18)), red dashed line (EU_2_A1 (n=36)) and purple solid line (Unknown MLL (n=7))). (b): Map of northern Algeria showing sampling sites by clonal lineage, *WR*: Western region, *ER*: Eastern region, *CR*: Central region.

Figure 2: Proportion of both mating type A1 (dark) and A2 (white) by crop season.

Figure 3: Individuals neighbor-joining clustering based on Bruvo's distance for the Algerian *Phytophthora infestans* population by region (Central individuals marked in black, west individuals marked in purple and east individuals marked in brown) and per MLLs (light blue dot : EU_13_A2, red dot: EU_2_A1, green dot: EU_23_A1 and black dot : Unknown MLL).

Figure 4: Principal component analysis results for the whole dataset (N=206) grouped according to MLL on the two factorial that explain 81.195 % of the total variance. Blue dotted (EU_13_A2), red dotted (EU_2_A1) and green dotted (EU_23_A1). EU_23_A1 and EU_2_A1 were negatively correlated to axis 1 while EU_13_A2 was positively correlated with it.

Figure 5: Bar plot indicating the probability of microsatellite assignment based on Structure analysis for the whole dataset grouped by MLLs. (a) $K=3$. (b) $K=4$. (c) $K=5$.

Table 1: Number of isolates collected and frequency for mating types (A1 and A2) per sampling site between 2010 and 2016 on potato fields.

| Region | Locality | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | | 2016 | | Overall | Frequency of mating type (%) (n=131) | |
|------------------------|------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|-------------|--------------------|-------------|------------|---|----------------|
| | | Number of isolates | Number of isolates | Number of isolates | Number of isolates | Number of isolates | Number of isolates | FTA Samples | Number of isolates | FTA Samples | | Mating type A2 | Mating type A1 |
| Central | Algiers | 1 | 8 | 1 | 8 | 31 | 18 | 35 | 1 | 17 | 120 | 58,46 | 41,53 |
| | AinDefla | - | 1 | 3 | 1 | 2 | 2 | 3 | - | - | 12 | 90,00 | 10,00 |
| | Bouira | 1 | - | - | - | - | 8 | 4 | 2 | - | 15 | 83,33 | 16,66 |
| | Boumerdes | - | - | 1 | - | - | 2 | 6 | 2 | 1 | 12 | 11,11 | 88,88 |
| | Médea | - | - | - | 2 | 3 | 5 | 3 | - | - | 13 | 100 | - |
| | Tipaza | - | 2 | - | - | - | 2 | 8 | - | - | 12 | 80,00 | 20,00 |
| | Tizi Ouzou | - | 1 | - | 2 | 2 | 4 | 7 | 2 | - | 18 | 92,11 | 7,69 |
| Overall central region | | | | | | | | | | | 202 | 71,30 | 29,70 |
| East | Guelma | - | - | - | 3 | 1 | - | - | - | 2 | 6 | 75,00 | 25,00 |
| | Skikda | - | - | - | - | 3 | - | - | - | 1 | 4 | 100 | - |
| Overall east region | | | | | | | | | | | 10 | 70,00 | 30,00 |
| West | Mascara | - | - | - | - | - | 5 | 5 | - | - | 10 | 75,00 | 25,00 |
| | Mostaganem | - | - | - | - | - | - | 1 | - | - | 1 | - | 100 |
| Overall west region | | | | | | | | | | | 11 | 70,00 | 30,00 |

| | | | |
|---------|-----|-------|-------|
| Overall | 223 | 60,00 | 40,00 |
|---------|-----|-------|-------|

FTA samples * FTA cards, on which the DNA of *P. infestans* is fixed.

Table 2: Allelic richness, allelic frequency, effective number of alleles, average expected heterozygosity and the overall heterozygosity per locus

| Locus ID | Size range | Ar (Af) | Ae | <i>Hs</i> | <i>Ht</i> |
|------------|------------|------------|-------|-----------|-----------|
| D13 | 132-222 | 20 (0.253) | 3.447 | 0.746 | 0.730 |
| G11 | 140-208 | 10 (0.127) | 3.182 | 0.700 | 0.707 |
| Pi04 | 166-170 | 3 (0.038) | 1.876 | 0.478 | 0.484 |
| Pi16 | 176-178 | 2 (0.025) | 1.818 | 0.462 | 0.466 |
| Pi33 | 203-206 | 2 (0.025) | 1.145 | 0.130 | 0.131 |
| Pi4B | 205-217 | 3 (0.038) | 2.440 | 0.606 | 0.610 |
| Pi4G | 157-161 | 3 (0.038) | 1.897 | 0.500 | 0.490 |
| Pi56 | 174-176 | 2 (0.025) | 2.000 | 0.506 | 0.517 |
| Pi63 | 148-157 | 3 (0.038) | 2.347 | 0.591 | 0.593 |
| Pi70 | 192-195 | 2 (0.025) | 1.046 | 0.047 | 0.046 |
| Pinf SSR11 | 329-356 | 4 (0.051) | 1.276 | 0.224 | 0.224 |
| Pinf SSR2 | 173-175 | 2 (0.025) | 1.088 | 0.085 | 0.084 |
| Pinf SSR3 | 258-272 | 5 (0.063) | 2.308 | 0.577 | 0.584 |
| Pinf SSR4 | 284-300 | 8 (0.101) | 3.785 | 0.758 | 0.754 |
| Pinf SSR6a | 240-246 | 4 (0.051) | 1.811 | 0.464 | 0.464 |
| Pinf SSR7 | 196-198 | 2 (0.025) | 1.786 | 0.447 | 0.456 |
| Pinf SSR8 | 260-268 | 4 (0.051) | 2.153 | 0.543 | 0.554 |
| Overall | | 79(4.647) | 2.083 | 0.462 | 0.464 |

Total number of alleles (Ar), allelic frequency (Af), effective number of alleles (Ae), average expected heterozygosity (*Hs*) and the overall heterozygosity (*Ht*).

Table 3: Number of individuals, allelic richness, allelic frequency, effective number of alleles, number of private alleles, average expected heterozygosity and the overall heterozygosity per geographical region

| Population | N | Ar (Af) | Ae | Pa | <i>Hs</i> | <i>Ht</i> |
|------------|-----|------------|-------|----|-----------|-----------|
| West | 11 | 47 (0.595) | 2.061 | 0 | 0.467 | 0.467 |
| Central | 192 | 78 (0.987) | 2.205 | 27 | 0.469 | 0.469 |
| East | 10 | 45 (0.57) | 2.011 | 1 | 0.456 | 0.456 |
| Overall | | 56.67 | 2.092 | | 0.464 | 0.464 |

Number of individuals (N), allelic richness (Ar), allelic frequency (Af), effective number of alleles (Ae), number of private alleles (Pa), average expected heterozygosity (*Hs*) and the overall heterozygosity (*Ht*).

Table 4: Permanova for the pair of variables Var1=MLL and Var2=Region for the whole dataset (N=206)

| Source | df | Sum of Squares | Mean Squares | Pseudo- <i>F</i> | <i>P</i> |
|--------------|-----|----------------|--------------|------------------|-----------------|
| MLL | 3 | 15.173 | 5.058 | 13.95 | $p < 0.001$ *** |
| Region | 2 | 0.775 | 0.387 | 1.069 | 0.286 |
| MLL x Region | 3 | 1.074 | 0.358 | 0.988 | 0.462 |
| Residual | 204 | 73.96 | 0.362 | | |
| Total | 212 | 90.98 | | | |

*** Very highly significant statistical difference

Multilocus lineage (MLL), degrees of freedom (df), F value by permutation (Pseudo-*F*) and *P*-value from 10000 unrestricted permutations of raw data and type III sums of squares.

Table 5: Number of individuals, total number and effective of genotypes, genotypic diversity and the Shanon-Weiner's corrected index by geographical region (west, central and east) and per multi locus lineage (EU_13_A2, EU_2_A1 and EU_23_A1).

| Population | N | MLGt | MLGe | Div | Shc |
|------------|-----|------|--------|--------|--------|
| EU_13_A2 | 152 | 18 | 1,6182 | 0,3845 | 0,5744 |
| EU_2_A1 | 36 | 6 | 1,3416 | 0,2619 | 0,4296 |
| EU_23_A1 | 18 | 12 | 9,5294 | 0,9477 | 1,3154 |
| West | 11 | 5 | 4,1724 | 0,8364 | 0,7561 |
| Central | 192 | 32 | 2,5968 | 0,6181 | 0,8903 |
| East | 10 | 6 | 3,3333 | 0,7778 | 0,9701 |

N: Number of individuals, MLGt: total number of genotypes, MLGe: effective number of genotypes, Div: genotypic diversity and Shc: Shanon-Weiner's corrected index.

Table6: Results of AMOVA tests for the whole dataset (N=206) divided according to geography and MLL

| Source of Variation | Nested in | Sum of Squared Deviation | d.f. | Mean Squares | Percentage of variance (%) |
|---------------------|-------------------|--------------------------|------|--------------|----------------------------|
| Region | Within Population | 1662.39 | 210 | 7.916 | 98.2 |
| | Among Population | 21.39 | 2 | 10.70 | 1.8 |
| MLL | Within Population | 953.5 | 203 | 4.697 | 40.9 |
| | Among Population | 593.6 | 2 | 296.8 | 59.1* |

*statistical significance with $p < 0.05$

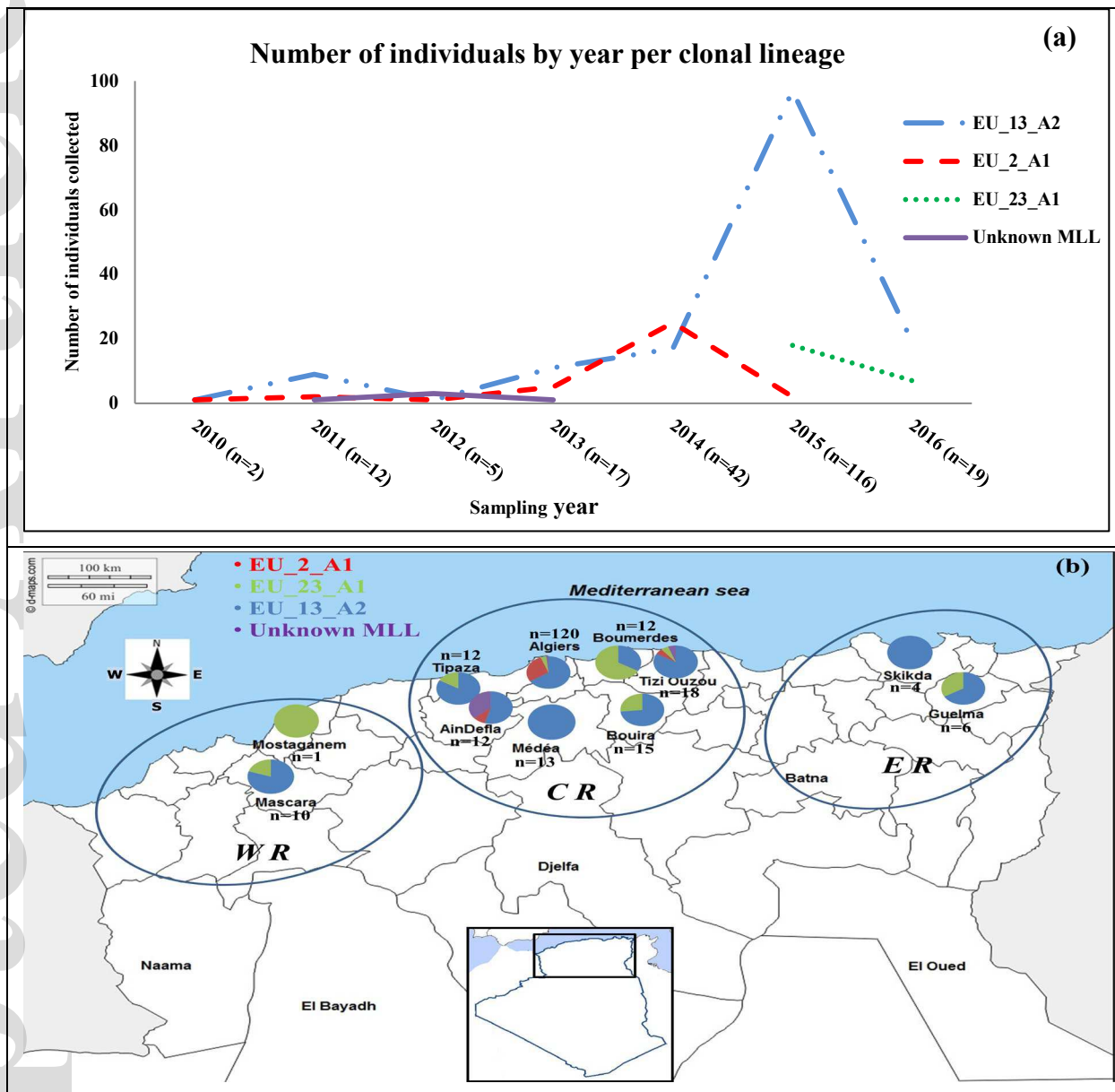
Table7: Major MLGs occurrence frequency and replicates count (over 10) distributed by locality

| Locality | MLLs | MLG ID | Number of MLG replicates | Frequency of occurrence |
|------------|----------|--------|--------------------------|-------------------------|
| Algiers | EU_13_A2 | MLG_17 | 40 | 0.179 |
| Mascara | | | | |
| Tipaza | | | | |
| Tizi Ouzou | | | | |
| Algiers | EU_2_A1 | MLG_22 | 14 | 0.062 |
| Tizi Ouzou | | | | |
| AinDefla | EU_13_A2 | MLG_11 | 12 | 0.053 |
| Algiers | | | | |
| Médéa | | | | |
| Tipaza | | | | |
| AinDefla | EU_2_A1 | MLG_23 | 11 | 0.049 |

MLGs: Multilocus genotypes

MLLs: Multilocus lineage

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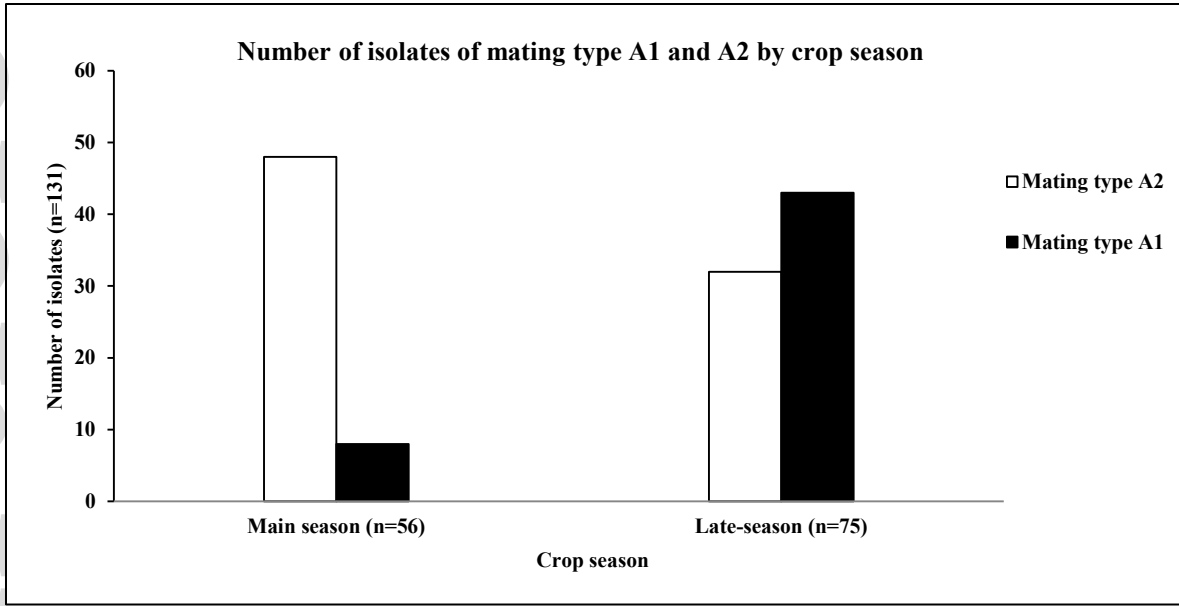


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3 Figure 1: Number of isolates per year and sampling map used in this study. (a): each line
 4 represents a clonal lineage (blue dash with dot (EU_13_A2 (n=152)), green dotted line
 5 (EU_23_A1 (n=18)), red dashed line (EU_2_A1 (n=36)) and purple solid line (Unknown MLL
 6 (n=7)). (b): Map of northern Algeria showing sampling sites by clonal lineage, *WR*: Western
 7 region, *ER*: Eastern region, *CR*: Central region.

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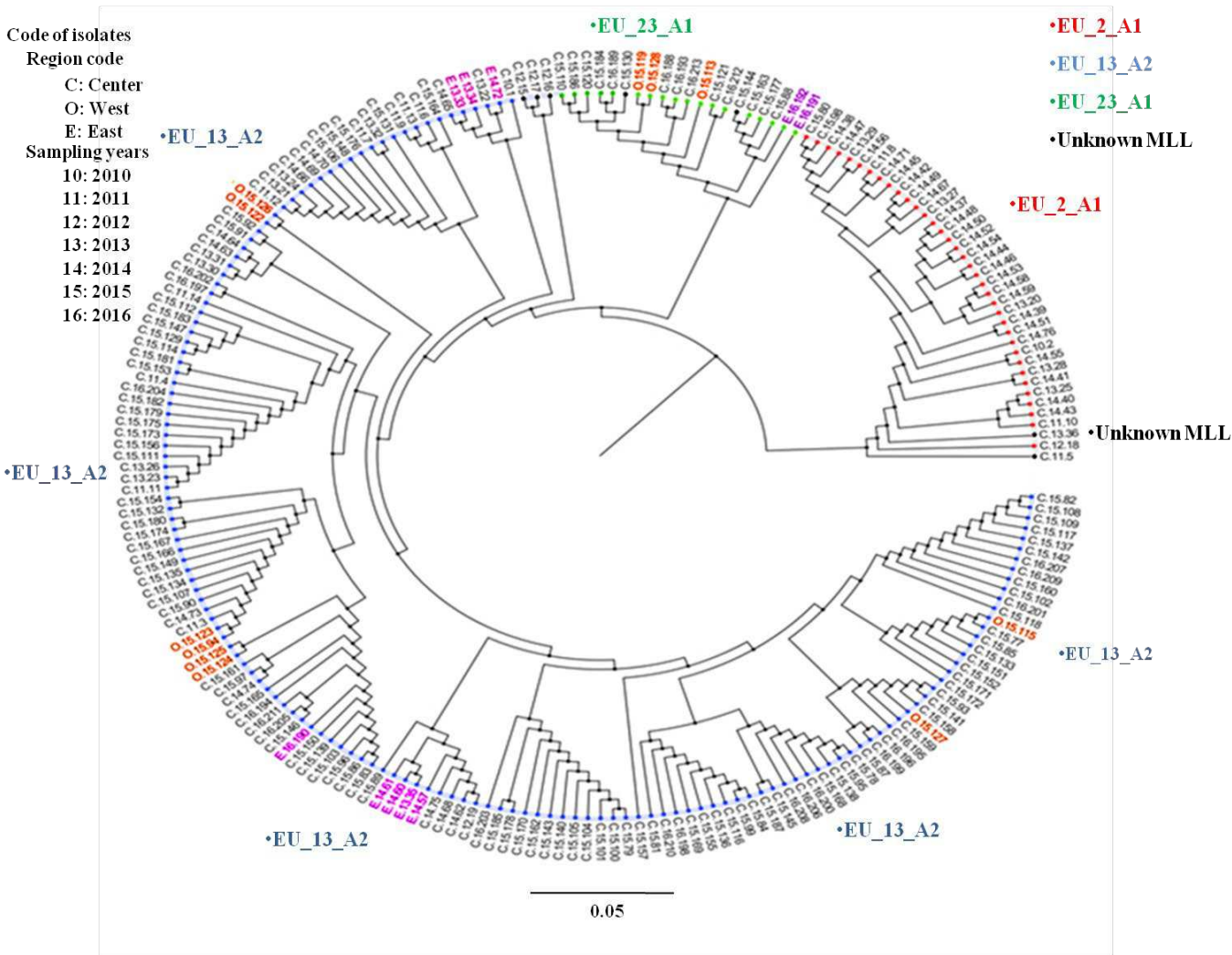
Figure 2: Proportion of both mating type A1 (dark) and A2 (white) by crop season.

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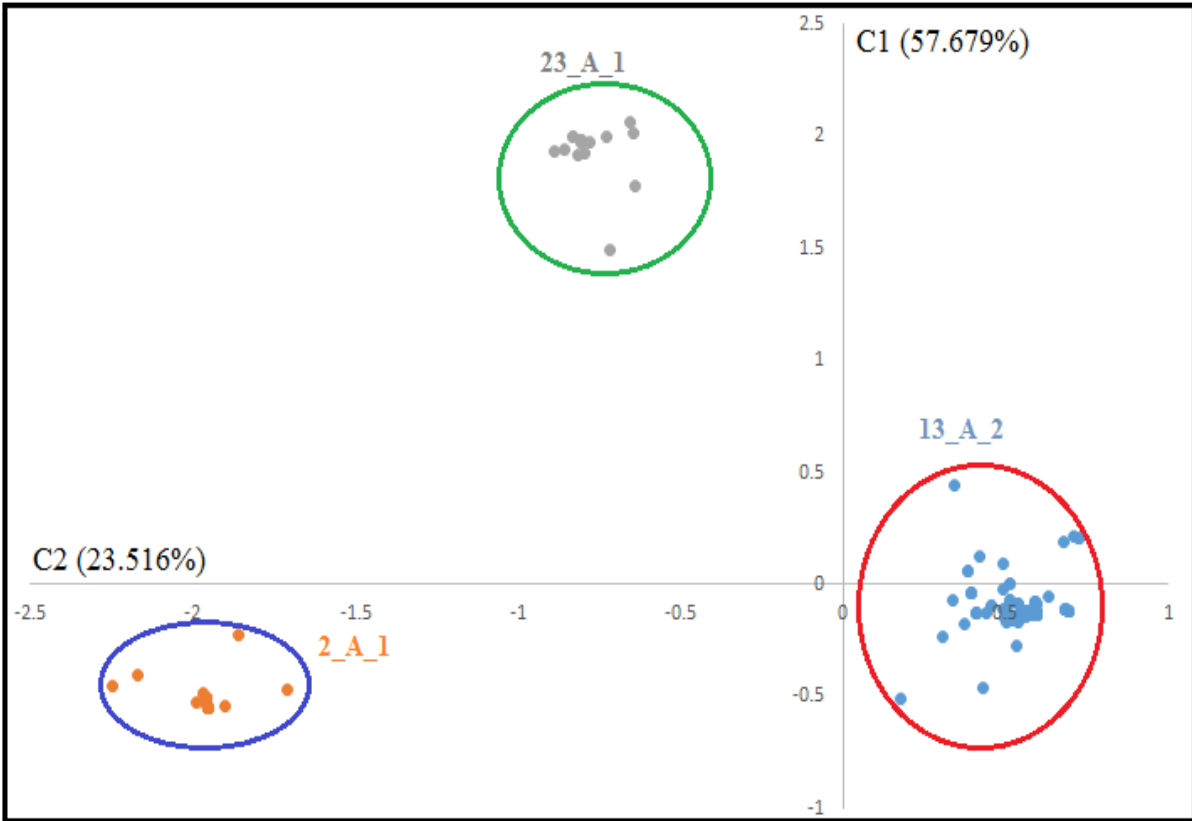
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Figure 3: Individuals neighbor-joining clustering based on bruvo’s distance for the Algerian *Phytophthora infestans* population by region (Central individuals marked in black, west individuals marked in purple and east individuals marked in brown) and per MLLs (light blue dot : EU_13_A2, red dot: EU_2_A1, green dot: EU_23_A1 and black dot : Unknown MLL).



1

2 **Figure 4: Principal component analysis results for the whole dataset (N=206) grouped**
 3 **according to MLL on the two factorial that explain 81.195 % of the total variance. Blue**
 4 **dotted (EU_13_A2), red dotted (EU_2_A1) and green dotted (EU_23_A1). EU_23_A1**
 5 **and EU_2_A1 were negatively correlated to axis 1 while EU_13_A2 was positively**
 6 **correlated with it.**

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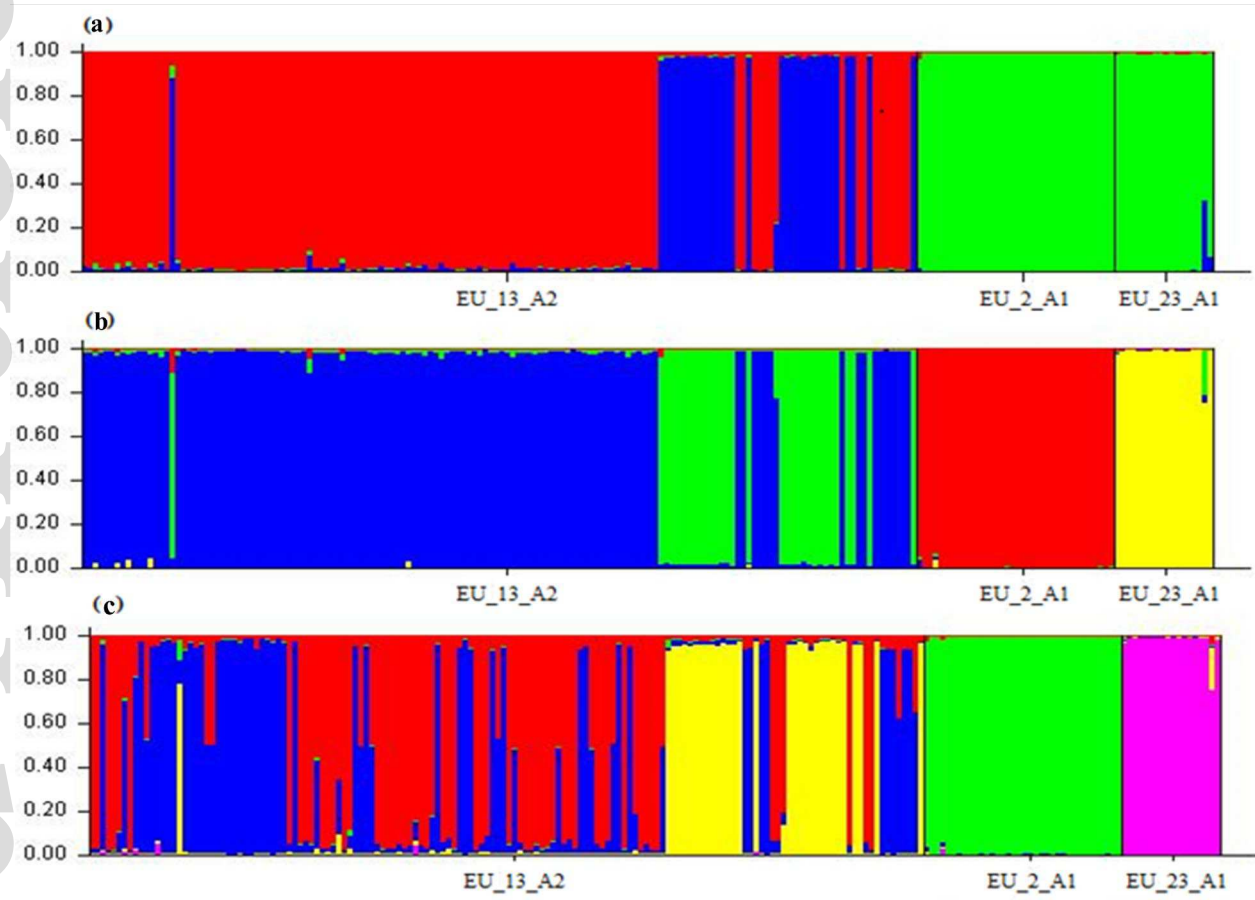


Figure 5: Bar plot indicating the probability of microsatellite assignment based on Structure analysis for the whole dataset grouped by MLLs. (a) $K=3$. (b) $K=4$. (c) $K=5$.