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Phytophthora infestans POPULATION STRUCTURE: A WORLDWIDE SCALE

Estructura poblacional de *Phytophthora infestans*: una escala global

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ABSTRACT

Phytophthora infestans, the causal agent of late blight disease in potato and other members of the Solanaceae family, is responsible for causing the Irish potato famine and, even today, it causes enormous economic losses all over the world. For the establishment of an adequate pest management strategy, the determination of the pathogen's population structure is required. To characterize *P. infestans* populations worldwide two allozymes, *Gpi* (Glucose-6-phospate isomerase) and *Pep* (Peptidase), the RG57 DNA RFLP fingerprinting probe, as well as resistance to the fungicide metalaxyl and mating type, have been used as markers. *P. infestans* populations in Mexico have been one of the main focuses of research in the population biology of this pathogen because this country has been considered as one of the possible centers of origin of this oomycete. In this review we present the population structure of *P. infestans* in Mexico, Europe, Africa, Asia, North America, and South America, expanding it on the present situation of *P. infestans* in Colombia. Finally, we will discuss different lines of research that are being carried out today with respect to *P. infestans* in Colombia, which have shown the importance of continuing the study of this devastating plant pathogen in our country.

Key words: *Phytophthora infestans*, population structure, late blight.

RESUMEN

Phytophthora infestans, el agente causal del tizón tardío de la papa y otros miembros de la familia de las Solanáceas, es el responsable de la gran hambruna irlandesa y aún hoy sigue causando grandes pérdidas económicas alrededor del planeta. Para establecer estrategias de control adecuadas contra este patógeno se requiere comprender la estructura poblacional del mismo. Mundialmente se han utilizado como marcadores las aloenzimas, *Gpi* (Glucosa-6-fosfato isomerasa) y *Pep* (*Pep*tidasa) y la sonda de *fingerprinting* de RFLP (Polimorfismos de la Longitud de los Fragmentos de Restricción), RG57. De igual forma, la resistencia al fungicida metalaxyl y el tipo de apareamiento, han sido

empleados para caracterizar las poblaciones de *P. infestans*. Las poblaciones de *P. infestans* en México han sido uno de los focos principales de investigación en la biología poblacional de este patógeno debido a que este país ha sido considerado como uno de los posibles centros de origen de este oomiceto. En esta revisión se presentará la estructura poblacional de *P. infestans* en México, Europa, África, Asia, Norte América y Sur América, profundizando en la situación actual de *P. infestans* en Colombia. Finalmente, se discutirá las diferentes líneas de investigación que se llevan a cabo hoy respecto a *P. infestans* en Colombia, las cuales han mostrado la importancia de continuar con el estudio de este devastador patógeno de plantas en nuestro país.

Palabras clave: *Phytophthora infestans*, estructura poblacional, tizón tardío.

INTRODUCTION

Phytophthora infestans (Mont.) de Bary is an oomycete that was considered as a fungus until recently. In the late 1990's, DNA analyses revealed that the oomycetes were more closely related to the brown algae than to the true fungi classifying them in the kingdom Stramenopila (Harper, 2005). *P. infestans* has a diploid vegetative state and its asexual reproduction is carried out by means of motile zoospores. This plant pathogen is heterothallic and its sexual reproduction involves the production of oospores, which act as resistant structures in adverse environmental conditions (Erwin and Ribeiro, 1996).

Phytophthora infestans is the causal agent of the late blight disease in potato (*Solanum tuberosum*) and other members of the Solanaceae family (*S. phureja, S. lycopersicum, S. betaceum, S. melongena, S. quitoense* and *Physalis peruviana*). This disease is famous for causing the Irish potato famine in the nineteenth century and, even now, it is responsible for enormous economic losses all over the world. Fry, 2008, has named this pathogen as the plant destroyer because of the challenge it still represents for the design of effective control strategies. Since 1845, this microorganism has been the target of a large number of studies. The de Bary's work in 1860 allowed the birth of the science of plant pathology and the emergence of a great variety of research groups that have tried to understand this pathogen in each and every aspect of its life cycle, biology, physiology, pathogenicity, epidemiology and taxonomy. Despite the fact that many researchers around the world have focused on finding an efficient way to control this devastating pathogen, pesticides remain the most important control strategy, not only demanding a large economic investment to producers but also being detrimental to the environment.

For the establishment of an adequate pest management strategy, the determination of population structure is required. It is crucial to know whether the growers are facing one or many populations, how these differ from one another, if they are recombining through sexual reproduction and if the pathogen is restricted or not to a specific host. The control of the pathogen depends on its diversity, geographical distribution and population subdivision. Knowing the amount and distribution of the genetic variation in the population of a given pathogen is fundamental to accurately decide the control strategy that must be applied. In general, if the pathogen has high genetic variation, the likelihood of this pathogen overcoming resistance of the host or adapting to fungicides is higher (McDonald and Mc Dermott, 1993).

Molecular Markers traditionally used to study *Phytophthora infestans* at the population level

Traditionally, two allozymes, *Gpi* (Glucose-6-phospate isomerase) and *Pep* (*Pep*tidase), and the RG57 DNA RFLP fingerprinting probe, which provides information on more than 25 different loci, have been used to characterize *P. infestans* populations worldwide (Goodwin *et al.*, 1994a). Nowadays, these markers, as well as resistance to the fungicide metalaxyl and the mating type, have been used to define clonal lineages or genotypes inside *P. infestans*. Based on this, the US-1 lineage, first isolated in the United States, was defined as having an 86/100 *Gpi* allele, a 92/100 *Pep* allele, an A1 mating type and being sensitive to metalaxyl (Goodwin *et al.*, 1994a). At first, all genotypes derived from the US-1 were named US-1.1, US-1.2 and so on. Today, at least 17 lineages known as US-1 to US-17, have been identified in the United States, each one having many variants, corresponding to differences either in the allozyme alleles or the RG57 probe patterns. Furthermore, at the mitochondrial level, a classification system based on a Restriction Fragment Length Polymorphism (RFLP) analysis has been used. According to this system, the *P. infestans* isolates can exhibit four different haplotypes: Ia, Ib, IIa and IIb (Griffith and Shaw, 1988; Carter *et al.*, 1990; Gavino and Fry, 2002).

Until the late 20th century, the US-1 lineage was thought to have a worldwide distribution as shown by Goodwin *et al.*, 1994b, and there was evidence to support the presence of this lineage in Europe, Asia, North, Central and South America at that time. Nonetheless, as stated by Cooke *et al.*, 2004, it remains difficult to establish the real status of global *P. infestans* populations because the markers mentioned above do not have the power to discern this question. Nowadays, with the availability of other molecular markers, the situation is starting to change. Researchers are using Amplified Fragment Length Polymorphisms (AFLP) to understand the dynamics of *P. infestans* populations (Cooke *et al.*, 2003; Mesa *et al.*, 2008) and more recently, Short Tandem Repeats (STR) have been used to monitor the *P. infestans* populations in Europe (Cooke *et al.*, 2004). The Eucablight (European Union Concerted Action on Blight) project (Hansen *et al.*, 2007), which is part of the Potato Late Blight Network For Europe, is an initiative that aims to centralize and homogenize all the information gathered related to *P. infestans*, in order to standardize protocols that permit the comparison of the variation of this pathogen worldwide.

Phytophthora infestans in Mexico

Mexico has been one of the main focuses of research concerning the population biology of *P. infestans*. This country has been considered as one of the possible centers of origin of this pathogen because of three main reasons. The first one is the high diversity that is found in this country. At least until the early 1980's, this was the only place where the two mating types, A1 and A2, could be found allowing sexual reproduction to occur. Sexual reproduction usually increases the genetic diversity of the pathogen, as it is evident in this part of the world, where isolates have the eleven avirulence genes tested by a host differential set, and a high number of fingerprinting patterns can be found (Grünwald and Flier, 2005). Second, *P. infestans* has been reported to cause disease in wild solanaceous species in the central part of the country, the Toluca Valley, where a population subdivision has been found between the isolates from potato and those from wild solanaceous species. This suggests a host preference apparently related to

the presence of R-genes in the native solanaceous species (Flier *et al.*, 2003), which could be used by potato breeders to generate genetically modified potato cultivars. These cultivars should be more resistant to the *P. infestans* attack because of the introgression of R-genes from the wild solanaceous species. Furthermore, in Mexico the sister clade of *P. infestans*, *P. mirabilis, P. ipomoea* and *P. phaseoli* (clade 1c according to Blair *et al.*, 2008) can all be found coexisting in this region and are all thought to have a common ancestor. Because of this, it has been suggested that enough time has passed in this region to allow speciation to occur (Grünwald and Flier, 2005).

P. infestans IN EUROPE

The wide distribution of the US-1 genotype led to the hypothesis that this clonal lineage was the one that caused the Irish famine in 1845. However, Ristaino *et al.*, 2001, using herbarium samples, found evidence that supported the fact that the lineage responsible for this epidemic could not have been the US-1 genotype due to differences in the mitochondrial haplotype. Because of this, the question remains unsolved, although it has been suggested that the catastrophic event in 1845 was the result of a migration event either from USA to Europe (Goodwin *et al.*, 1994a) or from Mexico to Europe. It is well known that *P. infestans* populations in Europe have suffered two migration events. The first one took place in the late 19th century and the second one in the early 1980's as it has been demonstrated in the Netherlands, where a different genotypic composition in the *P. infestans* population was found in isolates collected after the first part of the 1980's (Fry *et al.*, 1991). The same pattern was found in Poland, when isolates collected during 1985-1991 were tested for avirulence genes. Although these isolates are considered US-1 genotype, the complexity of these pathotypes has increased, when compared with isolates from the same lineage collected before 1985 (Sujkowski *et al.*, 1996). Today, it is known that the second migration event comprised isolates from Mexico belonging to the A2 mating type. This event opened the possibility for sexual reproduction to occur and to generate a higher genetic diversity. After the first report of the A2 mating type made in Switzerland (Hohl and Iselin, 1984), the *P. infestans* population in Europe has not only been replaced by a combination of new haplotypes but has also increased its diversity, as it was shown for the Polish *P. infestans* population (liwka *et al.*, 2006). In the same way, a survey performed in Scotland with AFLP's markers has revealed a high level of genetic diversity and a shift from metalaxyl resistant isolates to more susceptible or with intermediate levels of resistance (Cooke *et al.*, 2003). In Great Britain, more than 2,500 isolates were phenotypically and genotypically characterized employing the traditional markers (RG57, allozymes, mating type and metalaxyl sensitivity), but none of the strains corresponded to the US-1 lineage (Day *et al.*, 2004).

In France both mating types are present in potato and tomato, but the A1 mating type is the most frequently detected (Lebreton and Andrivon, 1998). In 2007, metalaxyl resistance has been increasing, with up to 80 % of the isolates in northern France being resistant (Duvauchelle *et al.*, 2009). In this region three mtDNA haplotypes have been recovered. Type Ib, typical of 'old' European populations of *P. infestans*, was detected in isolates recovered before 1992 in tomato, while types Ia and IIa were recovered from isolates collected in 1996 both in tomato and potato. In the same way, in Germany *P. infestans* isolates have been replaced by a new more aggressive population composed of

both A1 and A2 mating types, which belonged to mtDNA haplotypes Ia and IIa (Möller *et al.*, 2009). In southern Germany, a high degree of resistance to metalaxyl has been observed. Both in Germany and France, host specificity on potato or tomato exists among *P. infestans* (Möller *et al.*, 2009).

In Finland and Norway, the A2 mating type was first detected in 1992 and 1993 respectively (Hermansen and Amundsen, 1995; Kankila *et al.*, 1995). Although the A1 mating type predominates in these countries, the relatively high percentage of A2, as well as the distinct genotypes and the large genetic distances between them, point to sexual reproduction of *P. infestans* in both Finland and Norway (Brurberg *et al.*, 1999). In Russia, *P. infestans* samples collected from 1997-1998 showed that isolates from nine different sites outside of Moscow region were monomorphic for mating type, and nearly monomorphic for sensitivity to metalaxyl (Elansky *et al.*, 2001). On the other hand, in the Moscow region, both mating types were found and these isolates were polymorphic for metalaxyl resistance. The US-1 clonal lineage was not detected in this survey and the population of the pathogen near Moscow was highly diverse. From 1991 until 2004, resistance to metalaxyl was studied in 2000 isolates of *P. infestans* from various regions of Russia (Elansky *et al.*, 2007). In this study a decrease in the frequency of resistant strains after 1993-1994 was detected.

P. infestans isolates collected in Estonia during 2004-2007 revealed the presence of both mating types in all fields studied and a large number of multilocus genotypes (Runno-Paurson *et al.*, 2010). Three mtDNA haplotypes (Ia, IIa and IIb) were found, being the Ia type the most commonly found. In this study, 37 % of the isolates were resistant to metalaxyl, 25 % were intermediate and 37 % were sensitive.

Bakonyi *et al.*, 2002 isolated *P. infestans* from single-lesions in potato and tomato in different regions of Hungary. A1 to A2 mating type ratios were 8:9 and 4:15 among strains isolated from potato and tomato, respectively.

P. infestans in Africa and Asia

It is believed that *P. infestans* was introduced to Africa in 1941 on imported potato seeds from the United Kingdom (Cox and Large, 1960). Although secondary migrations have been suggested from Europe to other parts of the world after the late 1980s, implying that the population of *P. infestans* has suffered a shift in other regions, at least in South Africa all the isolates responsible for the epidemics in this country during 1995 and 1996 corresponded to the US-1 lineage, and no evidence of the A2 mating type has been found (McLeoad *et al.*, 2001). Interestingly, even though all the isolates belonged to this clonal genotype, some of them showed resistance when tested for metalaxyl sensitivity, a phenotype that does not correspond to the clonal lineage. This finding suggested that a selection pressure was acting on the population of the US-1 genotype in South Africa. Additionally, a subdivision apparently related to host preference was detected in the population, being the isolates from tomato sensitive to metalaxyl and those from potato ranging from sensitive to resistant (McLeod *et al.*, 2001).

In Uganda and Kenya, *P. infestans* isolates were collected on 1995 from tomato and potato and, in late 1997 and early 1998, from potato (Erselius *et al.*, 1999). All isolates belonged to the US-1 clonal lineage and therefore belonged to the A1 mating type. All tomato isolates showed a variation for the *Gpi* phenotype. The isolates collected on

1997-98 showed a high level of metalaxyl resistance. In a survey performed in 2001 by Ochwo *et al.*, 2002, eight isolates of *P. infestans* were collected from the districts of Mbale and Mbarara in the Eastern and Western highlands of Uganda, all of them belonging to the US-1 clonal lineage.

A population survey of *P. infestans* from commercial potato and tomato fields in Morocco between 1996 and 1998 revealed the presence of the A1 mating type on each year from both potato and tomato, while the A2 mating type was obtained only from potato in 1998 (Sedegui *et al.*, 2000). Four genotypes were identified during this survey: MO-1, MO-2, MO-3 and MO-4. With respect to metalaxyl sensitivity, all isolates collected form potato were either intermediate or insensitive to metalaxyl while those collected from tomato were sensitive to this fungicide.

Between 1992 and 1997 Nishimura *et al.*, 1999, studied the distribution of 336 *P. infestans* isolates in seven Asian countries and found only A1 mating type isolates in India and Taiwan, and only A2 isolates in Korea and Indonesia, while both mating type isolates were detected in Thailand, Nepal, and China. Particularly in China, a recent work showed that the *P. infestans* population in this country was represented by just one A1 mating type genotype when analyzed with microsatellite markers and corresponded to a IIa mitochondrial haplotype. However, when isolates were tested for virulence, a wide range of phenotypes were obtained. In addition, when AFLP's were used, at least eight different patterns could be identified (Guo *et al.*, 2009). Therefore, although no evidence of sexual reproduction in this country was detected, a high level of virulence is present.

In Japan the A2 mating type isolates are dominant over A1 mating type ones (Mosa *et al.*, 1989). Even though A1 and A2 isolates have coexisted in a few locations in Japan (Hokkaido and Tohoku districts), oospores formation has been evidenced only in laboratory conditions (Mosa *et al.*, 1991).

From the year 1983 until the year 2000 a survey was carried out on potato crops in Israel (Cohen, 2002). In this study the A2 mating type was predominantly detected from 1983 until 1991, and it was subsequently replaced by the A1 mating type. The A1 mating type dominated the population from 1993 to 2000. Previous to the coexistence of both mating types, the majority of *P. infestans* isolates were resistant to Metalaxyl. From 1993 on, when both mating types were found in the same population, the first isolates with intermediate sensitivity to this fungicide were detected (Cohen, 2002).

P. infestans in North America

Most of the population studies of *P. infestans* have been conducted in the Unites States. We recommend excellent reviews: Fry and Goodwin, 1997, Fry and Smart, 1999, Mizubuti and Fry, 2006, and Fry, 2008. According to Fry, 2008, the *P. infestans* population in North America has not been shaped yet by the presence of the A2 mating type, since no evidence of sexual reproduction has been found. It has been suggested that the disease might have migrated first into the United States and then to Europe (Mizubuti and Fry, 2006).

Late blight was first detected in the northeastern United States and Canada in the early 1840's (Stevens, 1993). The first migrations probably introduced the US-1 genotype, which has been found worldwide, as well as genotypes US-3 and CDA-1, which appear to be closely related to US-1 (Goodwin *et al.*, 1994a). The second important migration seems

to have taken place from northwestern Mexico in the late 1970's, from where the US-6, US-7 and US-8 genotypes seem to have been introduced (Goodwin, 1997). It appears that this second migration occurred because of the transport of infected tomato fruits across the U.S. - Mexico border. Further migrations from Mexico probably introduced the A2 mating type into the United States and Canada in 1987, although the actual date might be earlier since the search for the A2 mating type in the United States and Canada started because of the first reports of this mating type in isolates from Egypt and several countries in Europe (Deahl *et al.*, 1991). The finding of an A2 mating type in North America did not only open the possibility for sexual recombination to occur but also brought a new strain, US-8, that required significantly more applications of fungicides for its control in comparison with the previously dominant isolate US-1 (Kato *et al.*, 1997).

P. infestans in South America

In South America, *P. infestans* has been widely studied in Peru and Ecuador. In these countries new clonal lineages have been described. In Ecuador, the pathogen has shown low levels of diversity and its population structure is strongly influenced by host preference, with EC-1 associated with potato, EC-2 with wild solanaceous species, in particular with the Anarrhichomenum section, and EC-3 with S. betaceum (Forbes *et al.*, 1997; Ordoñez *et al.*, 2000; Adler *et al.*, 2004). Even though genetic differentiation was found among isolates of *P. infestans* associated with S. ochranthum (Chacón *et al.*, 2006), no geographic subdivision was found in Ecuador (Forbes *et al.*, 1997). On the other hand, in Peru the lineages are neither structured according to any host species (Garry *et al.*, 2005a) nor depend on whether the hosts are cultivated or wild (Garry *et al.*, 2005b). Nonetheless, a higher number of genotypes have been found in Peru than in Ecuador, making the *P. infestans* population from Peru more diverse than the Ecuadorian one (Perez *et al.*, 2001). Peru and Ecuador are considered to be the center of origin of potato (Ames and Spooner, 2008) and thus they have been proposed also to be the center of origin of the *P. infestans* pathogen (Abad and Abad, 1997; Gomez-Alpizar *et al.*, 2007). Recently a new *Phytophthora* species, *P. andina*, has been proposed to coexist with *P. infestans* in Ecuador, affecting wild Solanum species and having the new Ic mitochondrial haplotype (Gómez Alpizar *et al.*, 2007; Gómez Alpizar *et al.*, 2008). However, not enough information has been gathered to support the hypothesis of *P. andina* being a new phylogenetic species.

In southern South America, *Phytophthora* populations seem to be dominated by few clonal lineages. In Brazil, the existence of a new clonal lineage denominated BR1 and corresponding to the A2 mating type was reported on potato. Also, the US1 lineage has been found, but it is restricted to tomato (Reis *et al.*, 2005). Apparently, solanaceous hosts shape the population structure of *P. infestans* in Brazil (Goodwin *et al.*, 1994b). In the same way, in Uruguay a monomorphic or invariant population corresponding to the Brazil lineage BR1 has been identified from isolates collected between 1998 and 1999 (Deahl *et al.*, 2003). Furthermore the A2 mating type has also been reported in Argentina (Forbes *et al.*, 1998) while in Chile to-date only the A1 mating type has been found (Rivera *et al.*, 2002). In Venezuela only one study has been performed on population structure of *P. infestans* and only a single clonal lineage belonging to the A1 mating type was reported (Briceño *et al.*, 2009).

In Colombia the study of *P. infestans* has been limited to a few research groups, including the Laboratorio de Micología y Fitopatología of Universidad de los Andes in Bogotá, which have until recently started to actively investigate this pathogen at different levels. The study of the populations of *P. infestans* in Colombia has focused on metalaxyl sensitivity tests and on the characterization of pathotypes (Jaramillo, 2003; García *et al.*, 2008). Since the year 2005, population studies have incorporated the use of molecular techniques in order to obtain a better resolution of the *P. infestans* population structure in Colombia (Garnica *et al.*, 2006; Vargas *et al.*, 2009).

Recently several studies have been performed, which support the idea that the population of *P. infestans* in Colombia is homogeneous, consisting primarily of the EC-1 lineage. Gilchrist *et al.*, 2009, showed that the isolates from the region of Antioquia between the year 1994 and 2000 corresponded to the mating type A1 but showed two different mitochondrial haplotypes, IIa and Ib. Furthermore, they showed that the Ib haplotype, which corresponded to the US-1 lineage, was associated with tomato and water cucumber (Solanum muricatum). In a survey carried out by Silva *et al.*, 2009, strains of *P. infestans* isolated from potato in the departments of Antioquia, Boyacá, Cundinamarca and Norte de Santander showed to be A1 mating type and IIa mitochondrial haplotype suggesting that they belong to the EC-1 lineage. In this study no differences were found in the ITS neither in the 28S rDNA sequences. Nevertheless, a study performed with markers such as AFLPs in strains from the department of Nariño suggested that population structure is determined by the host, at least for tree tomato plants (Mesa *et al.*, 2008).

L. J. Turkensteen (unpublished data) observed that *P. infestans* populations were resistant to metalaxyl before the introduction of phenylamide-based fungicides between 1985 and 1989 (Flier *et al.*, 2003). In a survey carried out two years ago we found that 52 % of the isolates from the sampled population were sensitive to mefenoxam (metalaxyl-M) and 48 % showed some level of resistance (22 % intermediate and 26 % resistant; Vargas *et al.*, 2009). Mefenoxam response was not associated with host origin, collection site or any of the characteristics such as mtDNA haplotypes, mating type or clonal lineage. At least one resistant isolate was found from each host sampled (Céspedes, unpublished data).

The A2 mating type belonging to the US-8 lineage has recently been reported in Colombia by our group (Vargas *et al.*, 2009). Despite this fact, evidence for sexual reproduction has yet to be detected in the field. Although the Colombian A2 mating type is capable of crossing with most of the A1 Colombian isolates in vitro, the oospore viability was low, suggesting that post-zygotic factors might be involved (Céspedes, unpublished data).

Given the lack of additional information, recent research has focused on understanding the biology and the population structure of *P. infestans* in the Northern Part of the Andean Region and particularly in Colombia. Colombia is the fourth-largest producer of potato in South America (FAO, 2008) and late blight is a disease of great concern. In addition to potato (*S. tuberosum* and *S. phureja*), other members of the family Solanaceae have been reported as hosts to *P. infestans* in Colombia and could also influence the population structure of this pathogen. Over the last decade, several species of Andean exotic fruit have become increasingly important in Colombia both for domestic consumption and for international export. The most important are *Physalis peruviana* (cape gooseberry), a herbaceous perennial plant; *S. betaceum* (tree tomato); and *S. quitoense* (lulo or naranjilla), a perennial shrub and tomato (*S. lycopersicum*). Even

though *P. infestans* was reported growing on cape gooseberry plants, since then, reports of the disease on this host have been sporadic. Recently, data based on histological, molecular and physiological assays performed at our laboratory have shown a non-host interaction between *P. peruviana* and *P. infestans* (unpublished data).

Given that a controversy exists on the origin of *P. infestans* and considering that the center of origin of potato, the principal host of this plant pathogen, is South America, much more research efforts must be carried out in the Northern Andean region of this continent in order to understand more deeply the behavior of this pathogen in this part of the world. Recently we conducted a study on Colombian populations of the pathogen and found that they were not diverse for the genes b-tubulin, CoxI, Ras and Avr3a (Cárdenas *et al.*, 2011). Nevertheless, we found that the Southwestern region of Colombia showed a diverse population of the pathogen using the genes b-tubulin and Avr3a.

In an attempt to study the phylogeography of this pathogen, phylogenetic reconstructions using maximum parsimony (MP), maximum likelihood (ML) and bayesian inference (BI) were made with 4 different loci (COX2, NADH9, Sym6 and rps10) of 36 different isolates around the World (Fig. 1). This analysis suggested that the *P. infestans* isolates could be grouped in two clades that were highly supported. The first clade was originated in Mexico and the second one in the United States. Interestingly, the later clade was subdivided in two additional subclades, one of them grouping all isolates from the United States and the other one included the South American isolates and the isolates from other parts of the world. No other inferences could be done from this analysis due to the low number of samples included. Although additional markers are needed to strengthen the analysis, this approach seems promising (Tabima *et al.*, 2010, unpublished data).

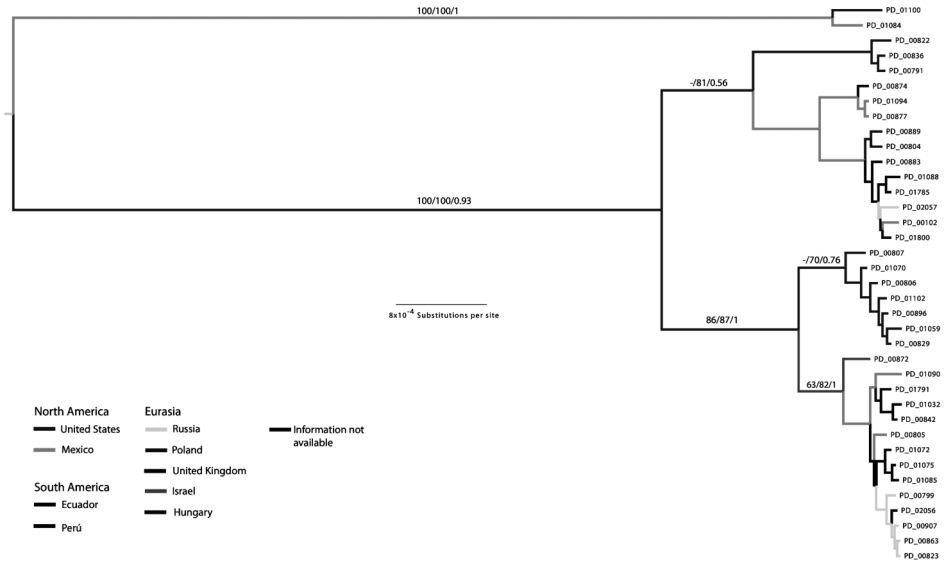

Figure 1. *P. infestans* phylogeographic analysis. Phylogenetic reconstruction using maximum parsimony (MP), maximum likelihood (ML) and bayesian inference (BI) using 4 different loci (COX2, NADH9, Sym6 and rps10) of 36 different isolates around the World.

CONCLUSIONS

Advances in the molecular tools that permit the study of population structure in *P. infestans* have allowed insights into the distribution of the pathogen around the world. Despite this, most studies have been performed using traditional markers that do not offer a complete view on the diversity and distribution of the pathogen. Because of this, new initiatives such as the Eucablight (Hansen *et al.*, 2007) should be promoted on other continents in order to establish a joint effort towards an understanding of the complexity of the disease at a worldwide level. Although significant advances have been achieved on population genetics of *P. infestans* in the past few years, more research is needed to disentangle the population dynamics of the pathogen in the Northern Andean region.

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