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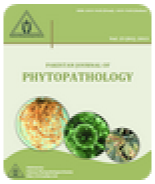

POPULATION STRUCTURE OF *PHYTOPHTHORA INFESTANS* ON WORLDWIDE SCALE: A REVIEW

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ABSTRACT

Phytophthora infestans is a destructive pathogen that causes late blight of potato worldwide. Several sexually and asexually reproducing lineages of the pathogen have been identified and new lineages are more virulent as compared to their parental lineages. A new highly aggressive clonal lineage EU13_A2 has spread into potato fields of Europe, Africa and Asia in place of the older lineages. In North America, 24 clonal lineages US1to US24 have been identified. Despite of sexual reproduction, the overall population of *P. infestans* in potato and tomato fields is dominated by asexual lineages. Breeding has been done to transfer 'R' genes into commercial potato cultivars through classical breeding and by pyramiding of genes. Defender is the only potato cultivar that has foliar and tuber resistance to late blight. Genetically modified potato with *RB* gene from *Solanum bulbocastanum* has been developed but it lacks tuber resistance to disease. This review discusses population structure of *P. infestans* worldwide and breeding efforts to produce late blight resistant potato.

Keywords: *Phytophthora infestans*, population;lineage, resistance breeding, Defender

INTRODUCTION

Genus *Phytophthora* (Class *Oomycota*) has been very famous with regards to the diseases caused by its different species. It includes more than 100 species with *Phytophthora infestans* being the most important. It causes late blight (LB) in potato and tomato that result in significant yield losses in different parts of the world. The costs associated with yield losses and protection measures against LB are estimated to be over 6 billion dollars worldwide (Haverkort *et al.,* 2008). *Phytophthora infestans* was responsible for Irish famine in 1845-49 that resulted in the death of millions of people in Ireland and the migration of another one million people to other parts of Europe and United States (Vanhaute *et al.,* 2006). LB starts initially as gray-green, water-soaked lesions on leaf margins and stems which enlarge at advanced stages and become dark brown to black (Fig. 1a and b). The spots finally become brittle with a rough leathery surface covering the whole plant. Lesions are commonly found at the junction of leaf and stem where water accumulates and on clusters of leaves at the top of the stem (Schumann and D'Arcy, 2000). High air humidity >90% and low temperatures 15 to18^{0}C accompanied with rains are very conducive for LB development, killing the entire potato fields within a week.

P. infestans is a heterothallic oomycete with two mating types, A1 and A2. The fungus has a coenocytic diploid mycelium and reproduces both sexually and asexually (Fry *et al.,* 2008). *P. infestans* is usually diploid but higher ploidy levels have been reported from European isolates. Sexual reproduction occurs when two compatible strains of both mating types A1 and A2 interact, resulting in the formation of thick-walled, resistant oospores (Nowicki *et al.,* 2012). The oospores can survive in dry and cold conditions in the absence of host for several years and play a role in overwintering of the fungus and in initiating the next disease cycle (Lethinen and Hannukkala., 2004; Anderson *et al.,* 2009). Sexual reproduction results in the evolution of the pathogen as a result of sexual recombination

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producing more virulent isolates. Sexual reproduction has resulted in resistance breakdown in potato varieties which were previously LB resistant. In asexual reproduction, sporangia are produced which can germinate directly on host surface through the formation of germ tubes or indirectly by producing zoospores. Sporangia act as main inoculum source when temperatures are above 10^0C and humidity is in the range of 75% to 80% (Judelson and Blanco, 2005). Zoospores are produced in cold conditions at low temperatures of 4-12^0C and high humidity >90% (Walker and van West, 2007). Although sexual reproduction occurs, but the frequency is very low and asexual reproduction is mainly responsible for disease outbreaks. In potato, sporangia or zoospores infect tubers as they wash down into the soil with rain or irrigation water. Diseased tubers become dark brown to purplish black and are invaded by soft rot bacteria which convert the entire tuber flesh into soft fleshy mass. Infected tubers serve as an important inoculum source from one season to the next (Kirk, 2003).

Until 1980, only A1 mating type was present in Europe and North America and A2 was only restricted to Mexico. First report of A2 mating type outside Mexico came from Switzerland in 1981 (Hohl and Iselin, 1984). The assumption was that importation of potato from Mexico to Europe in 1977 was responsible for arrival of A2 mating type into Europe and USA. Since 1981, A2 mating type has been found in Asia, Africa, Europe, North and South America (Nowicki *et al.,* 2012). Populations of *P. infestans* in potato fields have changed dramatically as a result of migration, sexual reproduction, climate change and potato cultivation systems. Allozymes, *Glucose-6-phosphate isomerase* (Gpi), *Peptidase* (Pep), RG-57 DNA probe, fungicide sensitivity, mating type, and haplotypes are used to define lineages of *P. infestans.* Simple sequence repeat markers (SSRs) are also being used to characterize *P. infestans* populations worldwide (Li *et al.,* 2013a).

The first migrations from Mexico to USA and Europe probably introduced the US-1, US-3 and CA-1 lineages from US to Europe. The second migration took place during late 1970's bringing US-6, US-7 and US-8 lineages from Mexico into Europe. Later migrations from Mexico probably introduced the A2 mating type into the United States and Canada during 1980's (Fry *et al.,* 1993; Danies *et al,* 2013). Previously it was thought that epidemics of 1845-49 were caused by US-1 due to its prevalence in fields. However, the data showed that the epidemics of 1845-47 in Ireland were caused by the clonal lineage HERB-1 of the A1 mating type that was the dominant lineage in Europe between 1845 to 1896. HERB-1 was replaced by US-1 in early 1900's due to the development of LB resistant potato varieties (Yoshida *et al.,* 2013).

P. infestans secretes numerous effectors that modulate host defense for establishing successful infection. There are over 18,000 genes in its genome with nearly 560 genes encoding RXLR effectors and over 180 genes encode CRN effectors (Haas *et al.,* 2009). The large repertoires of effectors in its genome indicate their important roles during infection process. Effectors secreted by haustoria of *P. infestans* include both apoplastic and cytoplasmic effectors (Nowicki *et al.,* 2012). Cytoplasmic effectors get across the host cell's plasma membrane and function inside the plant cell, where they induce metabolic changes that favor pathogen development. After transport into the host cytoplasm, the effectors manipulate host cellular processes to cause chlorosis, cell death and browning of infected tissues (Torto *et al.,* 2003). This review discusses population structure of *P. infestans* in different parts of the world and breeding efforts for producing LB resistant potato.

Figure 1. Symptoms of late blight infection on potato plant showing late black lesions at advanced stages of disease.

Population structure of *P. infestans* in North and South America: *P. infestans* probably originated from Mexico where both mating types A1 and A2 are present in equal proportions and sexual reproduction occurs (Goss *et al.,* 2014). Several migrations from Mexico to North America and Europe have introduced *P. infestans* outside of its native place (Yoshida *et al.,* 2013). US-1 predominated in Europe and North America until 1990's however; new lineages were reported after 1980's from North America. US-1, US-6, US-7 and US-8 were most common lineages in United States from 1985-96 associated with LB outbreaks (Hu *et al.,* 2012; Kawchuk *et al.,* 2011; Alkher *et al.,* 2015). Cespedes *et al.,* (2009) reported that population of *P. infestans* in Central Columbian Andean region is mainly clonal with a huge diversity of races. High possibility of sexual reproduction was detected due to the existence of both mating types and upto 48 % of the strains showed resistance to mefenoxam.

The pathogen population in North America is still today dominated by asexually reproducing lineages although both mating type are present in fields and sexual reproduction takes place. In British Columbia, seven clonal lineages CA-1 to CA-7 have been identified in potato fields (Forbes *et al.,* 1997). Dramatic changes took place in the population structure of the pathogen in United States when US-8 displaced US-1 and US-7 and predominated during 1994-96 (Peters *et al.,* 2014). US-8 is more aggressive and metalaxyl resistant that displaced the US-1 lineage in United States after 1985. In US, US-8 of A2 mating type was present in only 2% of samples in 1992 but its proportion increased in 1996. US-1 was previously dominant in United States and Canada but it was present in only 8% of the samples collected during 1996. US-8 is a good pathogen of potato however it grows poorly on tomato and it was the dominant lineage in United States until 2009. It is assumed that US-7 and US-8 were introduced into United States from Mexico during 1992 along with trade of infected plant materials. US-1, US-6 and US-8 were dominant in potato fields in Oregon and Washington during1992 to 1996. The study showed a genetic change in the population structure of *P. infestans* which comprised only of US-1 in 1992 to US-6 and US-8 in 1996. Until now, 24 clonal lineages of *P. infestans* belonging to both mating types A1 and A2 have been identified in North America that include US-1, US-2, US-3-------US-24 (Saville *et al.,* 2015). Since 2009, US-8 has been replaced with newly emerged lineages US-22, US-23 and US-24 in Canada and United States (Danies *et al.,* 2013; Gevens and Seidl, 2014). Alkher *et al.,* (2015) studied *P. infestans* population changes in Canada and it was found that new lineages US-22, US-23 and US-24 have displaced US-8 that was previously dominant. In British Columbia, US-11 and CA-12 were dominant and most of the isolates showed resistance to mefenoxam. Events of sexual recombination were also detected in isolates collected from tomato fields in some of the lineages. Co-existence of both mating types A1 and A2 and sexual reproduction has resulted in pathogen evolution in North America during last few years (Peters *et al.,* 2014). In South America, EC-1, EC-2, and EC-3 have been found. In Ecuador, EC-1 was dominant lineage in potato fields (>95%) whereas US-1 was present in 5% of the samples (Alder *et al.,* 2004; Forbes *et al.,* 1997). *P. infestans population* in potato and tomato fields in Brazil is dominated by two clonal lineages US-1 and BR-1(Reis *et al.,* 2005). In a study conducted in North Andes countries in Columbia and Venezuela from different hosts. The results showed very little genetic diversity was detected within the population and the population was entirely clonal with very little within-clone variation (Cardenas *et al.,* 2011).

Population structure of *P. infestans* in Europe: The asexual lineage HERB-1 predominated in potato crops in Europe from 1845-1896, and was responsible for the potato famine in Ireland. However, HERB-1 was displaced due to development of resistant potato varieties during 1890's by US-1(Yoshida *et al.,* 2013). All European isolates collected prior to 1970 belonged to US-1 with the exception of Mexico where other lineages were reported (Fry, 2008). Another genotype 6_A1 of Ib haplotype was found in Netherlands in 2002 and in Great Britain and Ireland in 2008. Ib haplotype had disappeared from potato crops during 1990s and in the first decade after 2000, however it again re-emerged associated with 6_A1. The Ib haplotype was associated with US-1 until 1970's however, new haplotypes Ia, IIa and IIb were reported after the worldwide spread of A2 mating type during 1980's. The re-emergence of 6_A1 in Great Britain, Ireland and Netherlands has probably resulted as a result of migration of the pathogen (Cooke *et al.,* 2012; Kildea *et al.,* 2013). 13_A2 and 6_A1 were found as the most common lineages in British gardens accounting upto 86% of all isolates (Stroud *et al.,* 2016). In Nordic countries in Europe, both mating types A1 and A2 occur in 1:1 ratio increasing the chances of sexual reproduction. Existence of a large number of multilocous genotypes showed that sexual reproduction has resulted in increased genetic variability (Fry, 2008; Brurberg *et al.,* 2011). In Denmark, both mating types A1 and A2 are present but recombination analysis showed that clonal reproduction dominates in most of the fields (Montes *et al.,* 2016).

Present populations of *P. infestans* in Britain, France and Netherlands are dominated by asexual lineages mainly US-22, US-23, US-24 and EU13_A2 (Montarry *et al.,* 2010; Yuen and Anderson, 2013). EU13_A2 is a highly aggressive asexual lineage (also known as Blue_13) of A2 mating that was found in United Kingdom and it has displaced the older lineages exceeding 75% population proportion within three years. EU13_A2 has rapidly spread throughout Europe and has become dominant lineage in Ireland, Netherlands and United Kingdom (Cooke *et al.,* 2012). Population studies show that *P. infestans* is still mainly clonal in France, Switzerland and United Kingdom (Flier *et al.,* 2007).

Runno-Paurson *et al.,* (2016), studied population structure of *P. infestans* in potato fields in Estonia by using SSR markers. Both mating types A1 and A2 were present in fields indicating high chances of sexual reproduction. From Ireland, different genotypes 13_A2, 5_A1, 6_A1 and 8_A1 have been reported (Cooke *et al.,* 2012). In Netherlands, only A1 mating type (US-1) was present before 1980 however, new lineages NL-001(Blue_13), NL-002, NL-003 to NL-008 have recently been reported. EU13_A2 has displaced the older lineages over a ten year period from 2000-2009 and sexual reproduction has resulted in increased genetic diversity in Netherlands. The dominant position of EU13_A2 is attributed to its superior fitness in combination with resistance to frequently used metalaxyl and a Blue-13 favorable choice of commonly grown cultivars (Li *et al.,* 2013).

Population structure in Asia and Africa: US-1 was the dominant lineage in potato crops in Asia and Africa until 1980. In recent years, new lineages have been reported from different countries in Africa including Ethiopia and Rwanda. *P. infestans* population analysis from eight Sub-Saharan African countries: Burundi, Kenya, Malawi, Mozambique, Tanzania, Rwanda, South Africa and Uganda revealed that most of the isolates were of US-1 lineage and its variants (US-1.1 to US-1.11). KE-1 that was previously found in Kenya in 2007 was also detected and it showed some similarities to earlier variants from Rwanda. Isolates collected from potato fields were metalaxyl resistant whereas isolates collected from tomato fields were metalaxyl-sensitive (Pule *et al.,* 2013). US-1 is slowly being replaced in East Africa with KE-1 and EU13-A2. US-1 was not found in Ethiopia on either potato or tomato whereas KE-1 which was identified in only two fields in 2007 was detected in all fields in 2011. US-1 has also disappeared from potato in Eastern Uganda and a high proportion of the population (44.4%) collected from potato fields in Uganda was metalaxyl resistant and belonged to KE-1. KE-1 has completely displaced US-1 on potato in Kenya (Mukalazi *et al.,* 2001; Njoroge *et al.,* 2016).

In Japan, different lineages have been classified as US-1, JP-1, JP-2, JP-3 and JP-4 based on DNA polymorphisms. JP-3 and JP-4 have been the main cause of LB in Japan since 2005. It is assumed that these lineages entered Japan from outside. From Korea, KR-1 was reported (Gotoh *et al.,* 2005; Akino *et al.,* 2014). JP-1 has also been detected in potato samples from China, Korea, Philippines and Taiwan. A2 mating type is replacing A1 in Japan and Korea (Koh *et al.,* 1994). In Taiwan, population of *P. infestans* has undergone dramatic changes from 1991- to 2006. Until 1997, only US-1 and its variants (US-1.1, US-1.2, US-1.3 and US-1.4) were present in potato and tomato. However after 1998, US-11and TW-1 new lineages appeared and became dominant in few years displacing the old US-1 lineage (Chen *et al.,* 2008; 2009). Four different mtDNA haplotypes: Ia, IIa, Ib and IIb have been found in China. IIa was first time reported from Japan and its introduction into China has probably resulted due to plant material trade. High genetic diversity of *P. infestans* in China is attributed to multiple migration events (Guo *et al.,* 2010). Genetic structure of *P. infestans* in a potato germplasm nursery in Northwestern China was studied by studying DNA haplotypes and through SSR markers. Both mating types A1and A2 and self-fertile isolates were present but sexual reproduction was not detected. The overall *P. infestans* population showed very little genetic diversity and the isolates showed resistance to metalaxyl. Migration and asexual reproduction were found to be the predominant mechanisms influencing population structure (Tian *et al.,* 2015a). Population structure analysis from Gansu province in China showed high percentage of A1 mating type and self-fertile isolates. Ia (25%) and IIa (75%) haplotypes were found and a high percentage of the isolates were metalaxyl resistant (Han *et al.,* 2013). In a study conducted in Northern China, SG-1 was found as the most dominant lineage with a frequency upto 75.2% in potato fields. Phenotypic and genotypic analysis showed that asexual reproduction was present whereas sexual reproduction was not detected. Recently, a European lineage EU-13 A2 has spread in China and has become the dominant lineage within few years (Li *et al.,* 2013b; Tian *et al.,* 2015b).

In Thailand, the population structure analysis showed the dominance of US-1 and the isolates showed sensitivity to metalaxyl (Petchaboon *et al.,* 2014). From Pakistan, both mating types of *P. infestans* A1 and A2 have been reported. A study done in Khyber Pakhtunkhwa (KPK) province showed that the isolates of *P. infestans* differ in their virulence in inducing disease on potato (Majeed *et al.,* 2014). *P. infestans* population in India comprises both mating types A1 (90%) and A2 (10%), however there has been a drift in its population structure during the last decade. Isolates collected prior to 2000 were metalaxyl sensitive, whereas isolates collected after 2004 were metalaxyl tolerant and Ia haplotype has replaced the Ib haplotype. High variability exists in regions with high pathogen build-up and where exchange of plant materials is higher (Chimote *et al.,* 2010). LB epidemics in India after 2008 are attributed to recent introduction of EU_13 which is replacing US-1. LB infected potato and tomato samples collected from South India between 2010 to 2012 comprised of A2 mating type, Ia haplotype and metalaxyl resistant isolates. Minor variants of 13_A2 were also found and named as 13_A2-3, 13_A2-3b, 13_A2 3c and 13_A2-1(Chowdappa *et al.,* 2015).

Future prospects: *P. infestans* has evolved with the passage of time resulting in the emergence of more aggressive isolates with potential to overcome LB resistance genes. One of the significant factors that has resulted in pathogen evolution is migration from one region to another along with trade of potato tubers. Emphasis should be made to prevent the movement of pathogen from country to another along with infected plant parts. Several new lineages have developed resistance to metalaxyl and mefenoxam due to their widespread use for LB management. Need is to develop bio-control strategies which are environment friendly and offer better disease control. Strict quarantines should be imposed so that no foreign diseased potato tubers will be allowed to enter other disease free regions. Improper applications of phenylamides have created a selective pressure on the pathogen, resulting in phenylamide-resistant isolates in some countries. LB resistant potato varieties are not available in many countries and resistance is not durable in field conditions. Breeding efforts should be made to incorporate resistance (R) genes from wild potato into cultivated potato through gene pyramiding and genetic engineering. Availability of complete genome sequence of *P. infestans* has provided in-depth understanding of the pathogen infection process. Analysis of the putative effector proteins has resulted in the discovery of genes involved in virulence. Creating genetically modified potato for LB resistance is difficult as the GM clones differ from their parental clones in tuber size, texture, quality and yield as well. Long term success to achieve LB resistance is difficult as *P. infestans* is a diverse and evolving pathogen.

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