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The Dynamics of Populations of *Phytophthora infestans* (Mont.) De Bary, in the Central Eastern Europe, Part 1: Up To 2010

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ABSTRACT

The Oomycete *Phytophthora infestans* (Mont.) de Bary, 1876 is the most devastating pathogen on potato crop. It was an agent responsible for the Irish Famine in the 1840s. It is a heterothallic hemibiotrophic oomycete. The sexual reproduction offers the pathogen more flexibility and adaptability to the environmental conditions. Before 1980s, the populations of *P. infestans* in Europe were represented by only one clonal lineage, US-1. Later, dramatic changes have been detected in populations of this pathogen, including the introduction of the A2 mating type, and making the sexual reproduction possible. The old genotype US-1 was gradually replaced by the new ones. In this paper, we provide a description of the situation in the Central and Eastern Europe and the changes that happened after the introduction of the A2 mating type, before 2010. A detailed description for the situation in Poland, Hungary, Estonia and Romania is offered.

Keywords: late blight, *Phytophthora infestans*, potato, population dynamics, Central and Eastern Europe.

INTRODUCTION

Among all plant pathogens, *Phytophthora infestans* (Mont.) de Bary, 1876 has, probably the most, impacted human history. In the middle of 1840s, it caused death of a million and the migration of another million people, in the well-known Irish Famine. The price of potato has at least tripled between 1841 and 1846, and the areas cultivated with potato decreased from 2.1 million acres in 1841 to 0.3 million acres in 1847, also the Irish population went from 8.5 million in 1845 to 6.5 million in 1851 (Scholthof, 2007). It causes late blight on potato and tomato, and other *Solanaceae* species. Duncan (1999), qualified *P. infestans* as a threat to human food security. In the field, late blight evolution can be devastating. The potato field can be destroyed during days only. To control it, several interventions with fungicides are needed during the season. The losses and cost of *P. infestans* control are estimated at $6.7 billion (Haas et al., 2009).

P. infestans is still the most devastating pathogen on potato, the 3rd most important food crop in the world (Vleeshouwers et al., 2011), and tomato crops worldwide. In Central and Eastern Europe, potato is a very important agricultural production, often ranking second after wheat (Zimnoch-Guzowska, 2010). In Romania, and maybe also in the other countries in the region, is called the second bread. From the top 10 worldwide potato producers, the Eastern and Central European countries hold a privileged place. Ukraine, Russia, and Poland are ranked the 3rd, 4th, and 9th in the 10 top potato producers in the world, respectively. Belarus is ranked 14th, Turkey occupies the 16th place, and at the 26th place comes Romania. In Europe, the situation is even better,

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Ukraine, Russia, Poland, Belarus, and Romania are the 1st, 2nd, 5th, 7th, and 10th top producers, respectively (Table 1) (FAOSTAT, 2023). As a result, this region is very important for potato production in Europe and worldwide.

Table 1. Top 10 potato producers in Europe in 2020 (FAOSTAT, 2023)

No.	Country	Areas (Ha)	Production (Tonnes)
1	Ukraine*	1 325 200	20 837 990
2	Russia*	1 178 098	19 607 361
3	Germany	273 500	11 715 100
4	France	214 500	11 715 100
5	Poland*	225 740	7 848 600
6	Netherland	164 500	7 020 060
7	Belarus*	253 442	5 231 168
8	Belgium	97 340	3 928 910
9	Denmark	62 800	2 762 900
10	Romania*	174 990	2 698 500

P. infestans is a heterothallic hemibiotrophic oomycete pathogen. By being heterothallic, *P. infestans* needs both mating types A1 and A2 for sexual propagation. The oospores, resulting from the sexual reproduction are hardy, thick-walled structures capable of surviving for many years (Miller, 2001). The oospores can survive extremely cold temperature, but not moderate heat (Miller, 2001). The survival temperature is ranging from -80ºC to 35ºC but not 40-50ºC (Drenth et al., 1995). Sexual reproduction offers to the pathogen more flexibility and adaptability to the environmental conditions.

The durability and sustainability of late blight management is a key for sustainable potato growing. A new strategy of late blight management based on the knowledge about *P. infestans* population composition, dynamics and evolution is necessary. This strategy or strategies must include all the information about the pathogen, host, interactions between them, agricultural practices, and climate. It must also include the modern technologies, for host resistance breeding, prediction and pathogen control.

The central Mexico represents the center of origin of *P. infestans* (Fry et al., 1993). There were two migrations of *P. infestans*, the first was in the 1840s and the second was in the 1970s (Fry et al., 1993). The consequence of the first migration is the Irish Famine in the 1840s. Since then, US-1 occupied the rest of the world outside Mexico. In Europe, *P. infestans* populations suffered huge changes in the last 40 years. The second migration was followed by an increasing diversity of late blight pathogen and by introducing into continental Europe of A2 mating type (Shattock, 2002), offering the pathogen the opportunity for sexual reproduction. The first appearance of *P. infestans* genotypes resistant to phenylamide fungicides was registered in 1980, only one year after the fungicide release (Fry et al., 1993).

The tests generally used for studying *P. infestans* populations are divided into two groups: phenotypic and molecular tests. The first group includes: mating type, virulence and fungicide resistance. The second one includes: isozymes, RG57 probe (based on the RFLP technique), haplotype, AFLP (Amplified Fragment Length Polymorphism), SSR (Simple Sequence Repeat) and SNP (Single Nucleotide Polymorphism). A review detailing these tests and their importance is given by Cooke and Lees (2004).

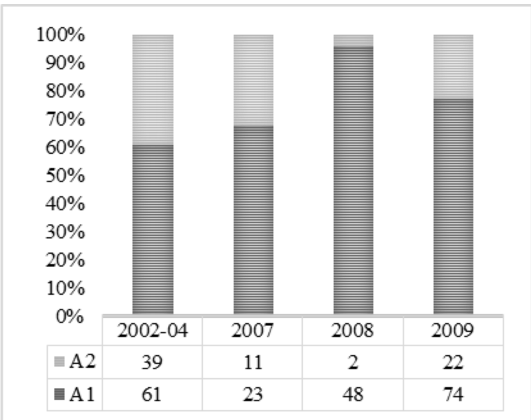
Despite the huge importance of potato producing region (Central and Eastern Europe), and the place hold by the pathogen, as the most devastating pathogen on potato, the research devoted to this pathogen, in this region, is not at the same level in each country, and it is far away behind the Western European countries. Only in Poland and Hungary, the local populations of *P.*

infestans have been studied and in Poland the work is being continued.

Here we collected the data that we could access about *P. infestans* in the Central Eastern European countries before 2010. A second paper is under preparation for the period 2010-2023. During the last period, *P. infestans* population has undergone several alterations, with the emergence of several new races (EU_13_A2, EU_23_A1, and other). Also, the nomenclature of the races has changed, so it is very difficult to track all the races before and after. Here we focused on 2 important features of *P. infestans*: the mating types (A1 and A2) found in each country, and its resistance to the fungicide metalaxyl. Those are the most available data, in approximately all the studies. The other tests are sometimes missing for most of the *P. infestans* population description, exception made for the Polish populations.

Poland

Polish *P. infestans* population suffered a great increase of its genetic diversity during the late 1980s (Sujkowski et al., 1996). The same author analyzed 95 isolates of *P. infestans* between the years 1985-1991 for virulence. Three groups were detected: PO-1, which corresponds to the US-1, isolated before 1988, with an average virulence of 5.5 measured as a number of infected Black's differentials containing genes *R1-R11*; PO-4, that was not detected before 1988, and with a virulence mean of 6.5; the third group, composed of 43 isolates representing 38 genotypes, with virulence average of 6.7, and was also not detected before 1988. The increase of virulence with time was detected in Polish late blight pathogen populations between 1985 and 1991. Śliwka et al. (2006) studied 93 isolates collected between 2002-2004 for mating type, virulence, aggressiveness and metalaxyl resistance. They found that 61% of isolates are A1, and 39% A2; concerning aggressiveness, 63.7% were highly and 27.5% moderately aggressive. In the metalaxyl resistance test, 82% were sensitive, 3.5% intermediate and 14.5% resistant. Regarding virulence, simple races, with one, two or without any virulence factors were not detected. The complex races with 7, 8 and 9 virulence factors were predominant. Chmielarz et al. (2010) characterized a total of 357 isolates collected between 2007-2009, for mating type, virulence, metalaxyl resistance, and haplotypes. In 2007, 68% were A1 and 32% A2, in 2008, 96% A1 and 4% A2, in 2009, 77% A1 and 23% A2 (data corrected, M. Chmielarz - personal communication). Concerning the haplotype, 92% were Ia and 8 were IIa the haplotypes Ib and IIb were not identified. Regarding the metalaxyl resistance, 11%, 14%, and 75% were resistant, intermediate, and sensitive, respectively. Concerning virulence factors, the most abundant were factors against genes *R1*, *R3*, *R4*, *R7*, *R10* and *R11*, in a moderate frequency - virulence factors for *R2* and *R6*, and rare for *R5* and *R9*.



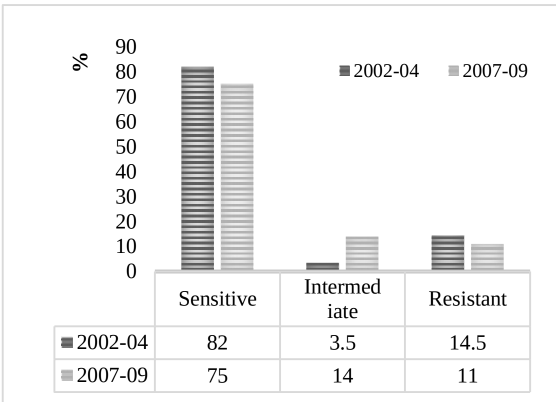


Figure 1. The evolution of Polish *P. infestans* population during the years 2002-2009 concerning resistance to metalaxyl and mating type proportion into the studied populations

The Polish *P. infestans* populations have suffered important changes, before 1988 the mating type A1 was the only mating type present. Between 2002 and 2004, A1 represents 61%, but in the period 2007-2009, the A2 decreased and in the best case did not exceed 32% in 2007. These isolates are generally sensitive to metalaxyl, they are aggressive and virulent, with high potential for sexual reproduction

Hungary

The identification of A2 mating type in Hungary was in 1997, for an isolate collected in 1996, it was metalaxyl tolerant and self-fertile (Bakonyi and Érsek, 1997). The authors think that its introduction was recent. Bakonyi et al. (2002), studied 37 isolates, 17 from potato and 19 from tomato; on potato, 47.06% were A1 and 52.94% A2; on tomato, 21.05% were A1 and 78.55% A2. Resistance to metalaxyl was more present on potato and in the A1 mating type (Bakonyi and Érsek, 1997).

Romania

In Romania, even though potato is the 2nd most important crop in the country, and *P. infestans* is the most important pathogen of potato, information about the pathogen generally, and especially about virulence, aggressiveness, diversity and distribution of the pathogen are still poor. Botez et al. (2004) used RAPD technique for studying the molecular polymorphism in 7 Romanian *P. infestans* isolates, sampled from different potato varieties and from different regions. Later they studied the variability of ten other isolates regarding the mithochondrial haplotype (Botez et al., 2007). In 2008, Botez et al., studied another 10 isolates of *P. infestans* from different regions of Romania. From the 10, 9 were IIa and only one Ia. The last one was the only A2 mating type detected. The rest of the studied isolates were A1. They found also only one isolate resistant to metalaxyl, the others ranged from susceptible to moderately susceptible.

Estonia

In Estonia, from a collection of 101 isolates collected during 2002-2003, 30% were resistant to metalaxyl, 52% intermediate, 19% sensitive and from a subset of 50 isolates, 30 were A1 and 20 were A2 mating type (Runno-Paurson et al., 2009). The analysis performed on the populations collected during 2004-2007, showed that from a set of 424 isolates; 33% were A2 mating type, and the both mating types were found in all the fields (Runno-Paurson et al., 2010). Concerning metalaxyl resistance, a decrease of resistance was detected from 56.1% resistant isolate in 2004 to 15% in 2007; on the other hand, the sensitivity increased from 23.5% in 2004 to 78.8% in 2007 from the isolates tested were sensitive. The most common race found was 1.3.4.7.10. (Runno-Paurson et al., 2010).

Russia

In Russia, Elansky et al. (2001), found that from a total of 485 isolates, of which 2.5% collected before 1996 and the rest were collected between 1997-1998, 77.2% were A1 and 22.8% were A2. However, in many regions there were only A1 or A2 isolates (from 9 sites, 7 sites were A1 mating type). In Moscow region there was a mixture of both mating types with a predominance of A1 mating type (72% of A1, 28% of A2 on potato, on tomato 88% were A1, and only 12% were A2). During 2007-2009 the situation has changed greatly. From a collection of 434 isolates, 58.35% were A1, 41.18% were A2, and 0.46% were self-fertile (Statyuk et al., 2010). However, these numbers do not reflect the distribution of the mating types in a large country like Russia. In two sites, 100% of the isolates tested were A1, and one site was A2. In the other sites the ratios varied from 5.6% to 94.4% of A1 or A2 mating type (Statyuk et al., 2010).

Czech Republic and Serbia

In Czech Republic, the first time A2 was detected in 2003 (Mazakova et al., 2006). In their study on *P. infestans* mating type occurrence and distribution, they reported 70% of A1 and 30% of A2 in 2003, 44% of A1 and 56% of A2 in 2004, and 55% of A1 and 45% of A2 in 2005. In Serbia, among 37 isolates, 75.67% were A2, 24.33% were A1, and 2.7% were self-fertile (Ivanovic et al., 2003). Many isolates (97.3%) were sensitive to metalaxyl, and only 2.7% were intermediate. The isolate collection was made in the year 2000.

For the rest of the countries (Bulgaria, Austria, Ukraine, Turkey, and Croatia) we were not able to find literature concerning the characterization of *P. infestans*, at least in English.

General discussion

The population of *P. infestans* structure is in a continuous dynamic. Despite the lack of studies covering several years (exception made by Poland), the previous affirmation is also true in this region. During this time interval (before 2010) the A2 mating type was present in all the countries where the pathogen populations have been studied (Figure 2), and very likely also in the other countries where the data are unavailable. In this paper, we focused on two major aspect of *P. infestans* populations: the mating types and the resistance to metalaxyl. Also, beside the data describing the Polish *P. infestans* population that are complete, the data concerning pathogen population are incomplete for the rest of the countries. There is always a test, at least, missing.

As a logic result for having both mating types (A1 and A2) in the same place at the same moment, the sexual reproduction may occur. This reproduction of *P. infestans* is feared by everyone. It results in the production of the thick-walled and robust oospores are formed. In contrast to sporangia, they can survive dry and cold conditions without a host, in the soil.

Sexual reproduction leads to a higher risk of genotypic variation in populations of *P. infestans*. As a result, these populations have recently undergone rapid genetic changes due to crosses between genotypes. These crosses have favored the subsequent appearance of new genotypes in all potato growing areas worldwide (Dey et al., 2018). In the next growing season, the germinating oospores can infect newly planted potatoes and cause early epidemics (Brylinska et al., 2016).

Sexual recombination will lead to an increase in genetic variation, and will allow selection to act on individual genetic traits, unlike asexual reproduction, which can only act on the entire genetic make-up of an organism. It also allows the separation of harmful from beneficial mutations and the combination of beneficial mutations from different ancestors (McDonald and Linde, 2002). According to Gavino et al. (2000), the aggressive genotype US-11 resulted from the sexual reproduction between US-6 and US-7.

The combination of sexual recombination (new genotypes) and clonal propagation (maintenance and spread of successful genotypes) will enhance the evolutionary potential of *P. infestans* (McDonald and Linde, 2002). The production of oospores makes *P. infestans* a soil borne plant pathogen (Andersson, 2007), which adds more difficulty and complications to its control (Yuen and Andersson, 2013).

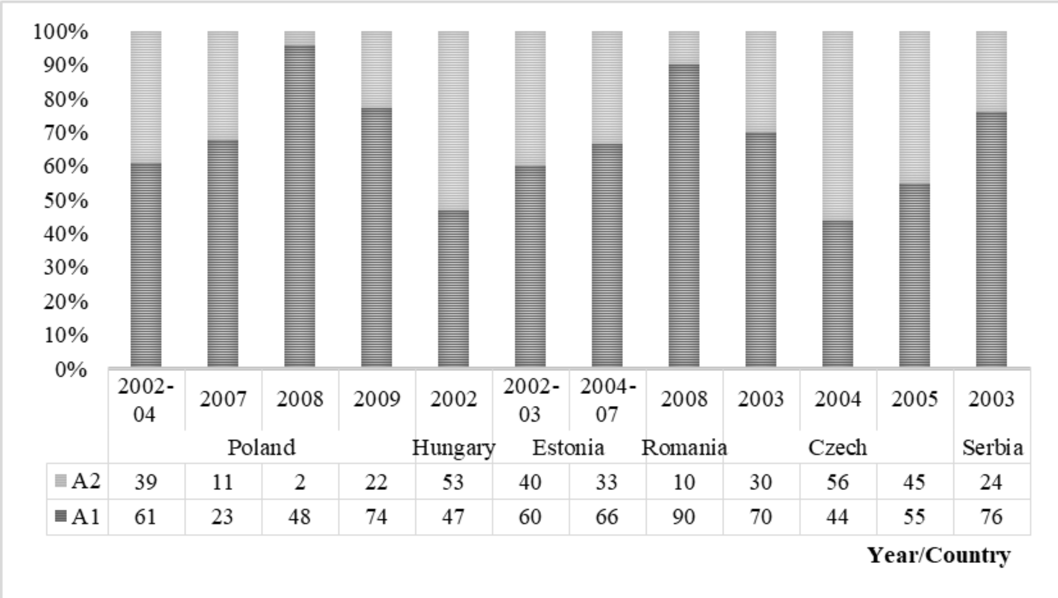


Figure 2. The presence of A2 and A1 in all the countries where the pathogen populations have been studied

There is always emergence of a new race following the introduction of a new potato cultivar with a new resistance gene or following the excess use of fungicides, even before the introduction of the A2 mating type.

CONCLUSIONS

Where the data are available, the *P. infestans* populations in Central and Eastern Europe are undergoing major changes. The importance of population study in this region is however underestimated, though this is one of the most important potatoes producing regions worldwide. A huge need for characterization of *P. infestans* populations is evident. Except for Poland, and recently Estonia, the rest of countries in this region have limited or no information about their *P. infestans* populations. The characterization of *P. infestans* population allows, at first, the comprehension of a major pathogen population evolution, and the improvement and adjusting of a strategy to combat this devastating pathogen. However, the necessity of a new strategy, is required. An integrated strategy for late blight management is needed, with combining all the agricultural techniques and control methods such as resistant cultivars, appropriate chemicals, and better strategies for fungicide applications to avoid the emergence of new races with fungicide resistance capabilities.

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