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Populations of *Phytophthora infestans* in northern and eastern Europe

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Abstract *Phytophthora infestans* (Mont.) de Bary is an oomycete plant pathogen that causes late blight in potato (*Solanum tuberosum* L.) and tomato (*Solanum lycopersicum* L.). This review documents the population structure of *P. infestans* in northern and eastern Europe, and aims to explain the differences between populations of *P. infestans* in this region and in western Europe. Populations of *P. infestans* are influenced by many factors, e.g., migrations related to the movement of potato seed tubers, possibility of sexual reproduction, changes in climate, and agricultural management practices. All the presented factors may have a significant impact on the *P. infestans* population structure. The knowledge on *P. infestans* populations varies strongly depending on country and time, even within the rather intensively studied region of eastern and northern Europe. Our review indicates some knowledge gaps, such as a lack of data for some countries and gaps in some years in population monitoring. This indicates the need to continue the monitoring of *P. infestans* populations.

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Introduction

The genus *Phytophthora* belongs to oomycetes within the kingdom Stramenopiles, and contains over 100 different species that are pathogens of various plant species. *Phytophthora infestans* (Mont.) de Bary is a hemibiotrophic organism, which attacks both potato (*Solanum tuberosum* L.) and tomato (*Solanum lycopersicum* L.), causing potato and tomato late blight, respectively. This pathogen destroys leaves, stems, tubers, and fruits. Under suitable weather conditions *P. infestans* spreads very fast by air, and it can destroy all plants in large potato fields within a week (Judelson, 2014). Late blight is one of the most economically devastating plant diseases. In 1845-1847, *P. infestans* caused the disaster of the Great Famine in Ireland, destroying potato crops and resulting in the death and mass migration of many people (Haverkort et al., 2008).

P. infestans is a heterothallic organism with two mating types named A1 and A2. Sexual reproduction occurs between isolates of different mating types, which results in the formation of oospores (Judelson, 2014). The thick-walled oospores have a fundamental role in overwintering and the early appearance of late blight in the next season. They can survive in harsh environments for up to two to four years (Danies et al., 2013; Fernández-Pavía et al., 2004; Lehtinen & Hannukkala, 2004; Li et al., 2012; Turkensteen et al., 2000; Yuen & Andersson, 2013). In asexual reproduction, the isolates produce sporangia, and clonal lineages can spread this way (Naveed et al., 2017). Some sources describe a third, parasexual, type of reproduction. This type of reproduction has been described in China, where *P. infestans* is mainly of A1 mating type, however it is able to self-fertilize and thus produce oospores (Zhu et al., 2016). Parasexual isolates produce oospores with isolates of both mating types or alone. Self-fertile isolates have also been described in Brazil (Casa-Coila et al., 2020).

Potato, after wheat, maize, and rice, is the fourth most consumed plant in the world. In 2022, the potato production in Europe exceeded 98 million tonnes and the harvested area was more than 4 million hectares (FAOSTAT, 2024). Potatoes are grown on almost all continents, with the largest production in Asia and Europe. More than 80% of global production takes place on these two continents. Approximately 35% of the global potato harvest has been produced in Europe in recent years (Dzwonkowski, 2017). In 2023 the largest potato producer in Europe was Germany (24% of the total of the EU), followed by France (17.9%) and Netherlands (13.4%) (Eurostat, 2024).

Populations of *P. infestans* are geographically diverse and influenced by many factors, e.g., migration related to the movement of potato seed tubers, possibility of sexual reproduction, changes in climate, and agricultural management practices. The populations of *P. infestans* in the north and east of Europe are different from those populations in other parts of the continent, which may result from different potato production conditions. In western Europe, clonal lineages of *P. infestans* prevail, in contrast to populations in northern and eastern Europe, where the *P. infestans* isolates are diverse (Euroblight, 2024). The aim of this review was to analyze the available literature data on selected factors shaping the *P. infestans* populations in northern (Finland, Norway, Sweden, Denmark, Estonia, Latvia, Lithuania) and eastern (Russia, Poland, Czech Republic) European countries (Fig. 1), and to explain why these populations of *P. infestans* are more genetically diverse, with persistent sexual reproduction and are, so far, not dominated by any of the clonal lineages common in other parts of the world. A list of publications on *P. infestans* populations on which this review is based, classified according to the geographic location, is presented in Supplementary Table S1.

Migration

Migration of *P. infestans* can occur when sporangia are carried by the wind and there are no barriers (like mountains) to block this transmission, or when infected seed tubers are moved and planted in new places. Migration drives gene flow between populations of *P. infestans* and, consequently, increases phenotypic and genotypic diversity in populations of *P. infestans*.

Many different markers have been used for years to assess the genetic diversity of *P. infestans* populations and track its migrations, including isozymes, RG57 restriction fragment length polymorphisms (RFLPs), mtDNA haplotype analysis, amplified fragment length polymorphisms (AFLPs), simple sequence repeats (SSRs) and single nucleotide polymorphisms (SNPs) (Cooke & Lees, 2004). Phenotypic traits, such as mating type, virulence and fungicide resistance, have also been used to determine the population structure of *P. infestans*. Cooke and Lees (2004) proposed that a combination of phenotypic and genotypic markers is the best way to compare different populations of *P. infestans*.

First global migration of *P. infestans* (A1 mating type)

P. infestans is native to the Toluca Valley in Mexico, where both A1 and A2 mating types occur with the same frequency, in a 1:1 ratio, an indication of sexual reproduction. The sexual reproduction is frequent, and genetic diversity in Mexican populations of *P. infestans* is high (Fry et al., 1993).

The first described global migration of this pathogen took place in the 1840s (Fry et al., 1993). The pathogen spread from Mexico to the United States and then to Europe or from Mexico directly to Europe. The first described late blight epidemics in Europe occurred in Belgium in 1845. It was caused by the isolates of a clonal lineage HERB-1 of A1 mating type (Ristaino, 2002). From Belgium, *P. infestans* spread to other European countries, started the Great Famine disaster in Ireland, and by the end of 1845,

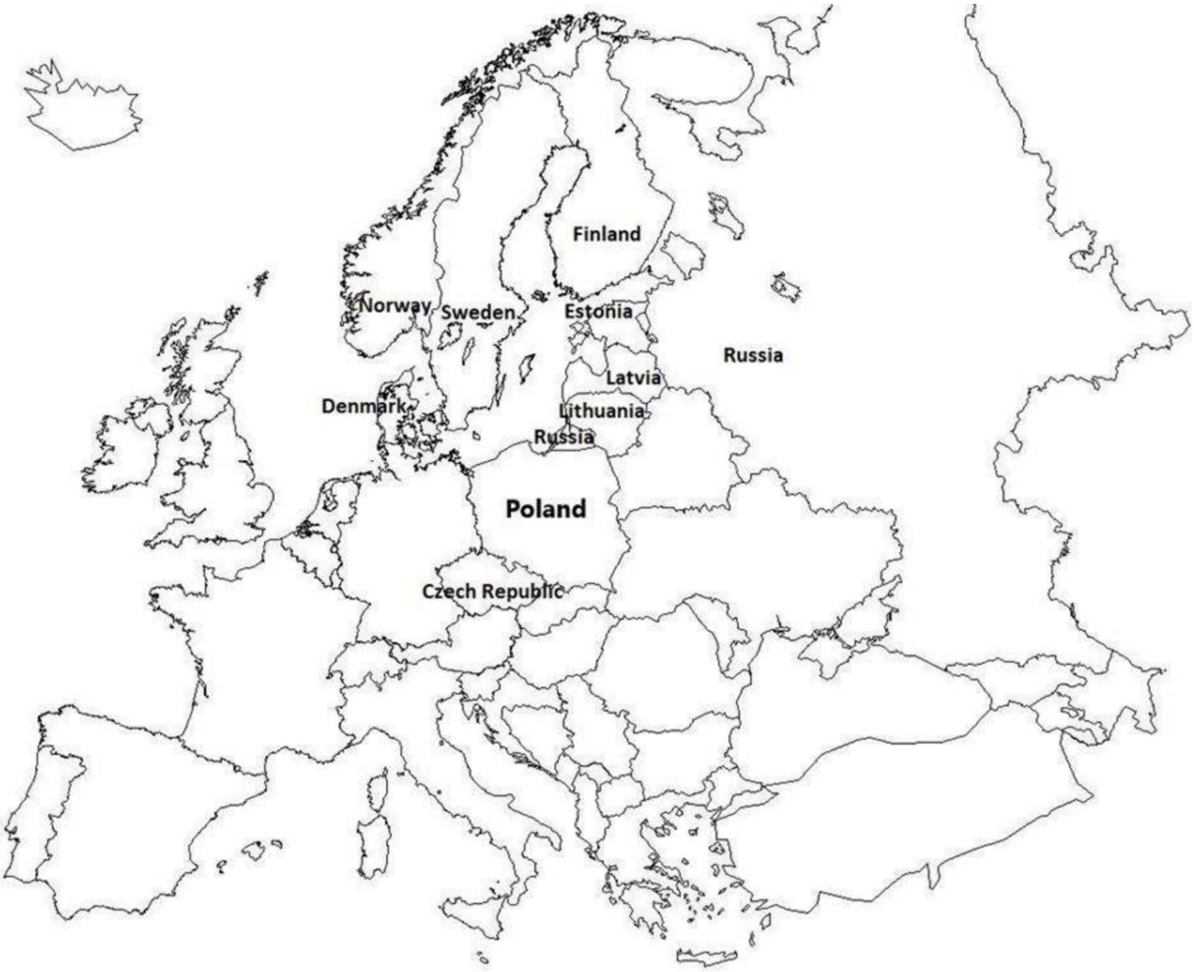

Fig. 1 Geographical location of the countries described in the publication (countries named on the map)

it had reached southern Norway and Sweden (Lamb & Bourke, 1993). From that time on, HERB-1 was the major clonal lineage in Europe; however, after 1890 it was replaced by the US-1 lineage of A1 mating type (Naveed et al., 2017). Yoshida et al. (2013) investigated nineteenth century samples of potato and tomato leaves with lesions of *P. infestans* using Illumina sequencing and concluded that HERB-1 was the dominant genotype for approximately 50 years and could have coexisted with US-1.

Second global migration of *P. infestans* (A2 mating type)

A second global migration of *P. infestans* took place at the end of the 1970s (Fry et al., 1993). The first information about *P. infestans* of A2 mating type outside Mexico came from Switzerland in 1980 (Hohl & Iselin, 1984). The new isolates of A2 mating type changed the *P. infestans* populations in Europe (Ristaino, 2002). The first occurrence of the mating type A2 was not necessarily detected and reported immediately after its first appearance in the local population of *P. infestans*, as there was a lack of constant monitoring of the *P. infestans* population. However, northern and eastern Europe were quickly colonized by the A2 isolates of the pathogen. The potential geographic, climatic or potato trading barriers were insufficient to stop the spread.

In northern Europe, the occurrence of isolates of A2 mating type was first described in Latvia in 1980 (Bimsteine, 2008), in Estonia in 1983 (Goodwin et al., 1994), in Sweden in 1985, in Finland in 1992, in Norway in 1993, in Denmark in 1996 (Nærstad, 2000) and in Lithuania in 2010 (Runno-Paurson et al., 2015). In eastern Europe, the occurrence of isolates of A2 mating type was first reported in Russia in 1985 (Maleeva et al., 1999), in Poland in 1988 (Sujkowski et al., 1994) and in Czech Republic in 2003 (Mazáková et al., 2006) (Table 1).

From Europe, the A2 mating type of *P. infestans* moved to Africa, Asia and South America with potato seed tubers (Fry et al., 1993).

Spread of clonal lineages

P. infestans propagates asexually and sexually. The asexual life cycle is most common for this pathogen and causes rapid progression of the disease. Sporangia are produced in asexual reproduction and can then be transported by wind for several kilometers. As a result of asexual reproduction, clonal lineages are formed. A clonal lineage is a group of isolates that are descendants of one clonally reproducing isolate. Clonal lineages often exhibit features that allow them to spread rapidly, such as the ability to overcome host resistance and resistance to fungicides (Judelson, 2014).

The most aggressive clonal lineages can spread very quickly and come to dominate the entire population of *P. infestans* in a country in a very short time. In recent years, the clonal lineages EU13_A2, EU34_A1, EU37_A2, EU41_A2 and EU36_A2 have been noteworthy.

The clonal lineage EU13_A2 was found in Netherlands and in Germany in 2004 and spread rapidly in other parts of Europe (Cooke et al., 2012). After the Netherlands, EU13_A2 was detected in Great Britain in 2005, in France, Poland and Hungary in 2006, in Germany, Denmark, Scotland, Slovenia and Sweden in 2007, in Latvia and Lithuania in 2010, in Greece and Northern Ireland in 2011, and in other European countries in 2013 (Euroblight, 2024). The EU13_A2 clonal lineage has appeared in eastern European countries (Chmielarz et al., 2014, Euroblight, 2024), but it has never dominated these populations. Among northern European countries, EU13_A2 clonal lineage has only been reported in Denmark (Nielsen et al., 2014).

In Great Britain, the EU13_A2 clonal lineage was recorded for the first time in July 2005, and this lineage took over 75% of the Great Britain population of *P. infestans* in less than three years (Cooke et al., 2012). In 2003-2008, the authors collected 4654 isolates from 1100 locations and tested samples using 11 SSR markers. It was found that a high rate of sequence variation in the genome of EU13_A2, together with an unusual pattern of extended biotrophic growth, may be the causes of the high aggressiveness and ability to break resistance in potato cultivars in this clonal lineage. Isolates of the EU13_A2 clonal lineage show resistance to phenylamide fungicides (Cooke et al., 2012). Lees et al. (2012) tested 49 cultivars known in Great Britain with published late blight resistance assessments, 42 new cultivars and 11 control cultivars for their resistance to *P. infestans* isolates of the EU13_A2 genotype. The resistance rating was statistically significantly lower in the 49 cultivars with known resistance and two of the control cultivars, Lady Balfour and Stirling, when challenged

Table 1 The first literature information about isolates of the A2 mating type in the countries of northern and eastern Europe

Country	Part of Europe	First labeled detection (year)	Reference
Latvia	northern Europe	1980	(Bimsteine, 2008)
Estonia	northern Europe	1983	(Goodwin et al., 1994)
Sweden	northern Europe	1985	(Nærstad, 2000)
Finland	northern Europe	1992	(Nærstad, 2000)
Norway	northern Europe	1993	(Naerstad, 2000)
Denmark	northern Europe	1996	(Naerstad, 2000)
Lithuania	northern Europe	2010	(Runno-Paurson et al., 2015)
Russia	eastern Europe	1985	(Maleeva et al., 1999)
Poland	eastern Europe	1988	(Sujkowski et al., 1994)
Czech Republic	eastern Europe	2003	(Mazáková et al., 2006)

with the EU13_A2 genotype compared to an A1 genotype (Lees et al., 2012).

Fungicide resistance can drive the establishment and spread of a clonal lineage. Puidet et al. (2023) found reduced sensitivity to fluazinam of the EU37_A2 clonal lineage based on isolates collected from potato fields in the UK and France in 2023. Abuley et al. (2023) tested the sensitivity to mandipropamid of 72 *P. infestans* isolates collected in Denmark and concluded that the EU43_A1 genotype is resistant to this fungicide.

A new clonal lineage, EU41_A2, is the first example of the *P. infestans* genotype spreading and establishing in the northern Europe. It first appeared in Denmark in 2013 (Hansen et al., 2017). In the following years the genotype was detected in Norway, Sweden, and Finland (Euroblight, 2024). This genotype was reported in 2020 in three locations in Poland (Marta Janiszewska, Plant Breeding and Acclimatization Institute – National Research Institute, Poland, unpublished) and in Germany (Euroblight.net). In 2021, it was identified in Great Britain (Euroblight, 2024). Puidet et al. (2022) investigated the phenotypic traits (mating type, resistance to fungicide and virulence) of the isolates of this new clonal lineage of *P. infestans*, to explain its rapid expansion and establishment, despite sexual recombination existing in the population of *P. infestans* in northern Europe. The authors hypothesized that the invasive success of EU41_A2 in sexual Nordic populations of *P. infestans* may be influenced by climate change (Puidet et al., 2022).

Clonal lineage EU36_A2 is the main clonal lineage in the *P. infestans* population in northwest Europe from 2019 to 2023 (Troussieux et al., 2022, Euroblight, 2024). This genotype is distributed in Great Britain, the Netherlands, Germany, and France. It was also found in Greece and Portugal, and in 2021 it was found in southwest Poland. EU36_A2 has not been found in other eastern and northern European countries (Euroblight, 2024).

In eastern Europe, the important genotype was EU34_A1. In a study by Janiszewska et al. (2021), 237 isolates of *P. infestans* were collected in Poland in 2000-2014. Eighty-seven of the isolates belonged to the 34_A1 genotype, which was detected in all study years except 2012. High subclone variability was observed within the 34_A1 genotype. It seems that there are no barriers for migration for the *P. infestans* clonal lineages to eastern Europe, and some lineages have established and spread locally in the region but never come to dominate in the populations. According to Euroblight (2024), the population of the 13_A2 genotype was largest in 2008 and amounted to about 80% in the whole of Europe; isolates of EU34_A1 were less than 30%; isolates of EU36_A2 were 40%; isolates of genotype EU37_A2 were 15% and isolates of 41_A2 genotype never exceeded 10% in 2004-2022 in Europe.

Local migrations

Local migrations between and within countries and related gene flow increases the genetic diversity of *P. infestans* in the studied region. *P. infestans* migration between countries was studied by Brurberg et al. (2011) in Norway, Sweden, Finland and Denmark, and the results showed a large diversity in the *P. infestans* population in each country. In 2003, 743 isolates of *P. infestans* were collected from 320 organic and conventional fields. Nine SSR loci (Pi02, Pi04, Pi16, Pi26, Pi33, 4B, 4G, G11, D13) were checked for 200 isolates of *P. infestans*. In Sweden, the authors detected one unique allele at the G11 locus, but the frequency of this allele was low. They also found five unique alleles in Norway in 14 isolates. None of the genotypes found in these countries were dominant in the *P. infestans* population. The most common genotype was represented by seven isolates from Denmark. Within each country the authors found large diversity of *P. infestans* populations, and between the studied countries the populations of *P. infestans* were similar to each other (Brurberg et al., 2011). Similar findings have also been described by Sjöholm et al. (2013), where the authors indicated different levels of gene flow between the countries of northern Europe. Limited gene exchange has been observed between Sweden and Denmark despite their close geographic location. The greatest gene flow was observed between Denmark and Finland. Due to the occurrence of sexual reproduction, the effects of migration on populations of *P. infestans* were not as visible as in other parts of Europe, where only asexually reproducing isolates were present (Sjöholm et al., 2013).

The flow of genes in the *P. infestans* population takes place also within regions. Migration can cause changes in the population of *P. infestans* manifested by the changed occurrence of the mating types and resistance to metalaxyl. Hannukkala et al. (2009) checked the response of *P. infestans* from Finland and Russia to fungicides metalaxyl-M and propamocarb-hydrochloride in 2006 and 2007. In 2006, metalaxyl resistant isolates had not been detected in the fields in Russia and Finland but resistant isolates subsequently appeared. In 2007, the authors detected 32% and 23% frequency of metalaxyl resistant isolates in Russia and Finland, respectively. The authors suspected that the increased frequency of metalaxyl resistant isolates in Finland in 2007 could have been caused by an increased use of metalaxyl fungicides in 2005 and 2006. The reason for the occurrence of metalaxyl resistant isolates in Russia is not clear, as no chemical control was used in the studied fields. The emergence of metalaxyl resistant isolates in Russian fields could have been a result of migration isolates between the countries and sexual recombination (Hannukkala et al., 2009).

The smallest-scale migration of *P. infestans* is the transfer of isolates between fields. From 2001 to 2007, Runno-Paurson et al., (2014) tested the resistance to metalaxyl of 179 isolates from Estonia and 451 isolates from Finland, and found metalaxyl resistant isolates even in the fields where fungicides with metalaxyl were not used. Runno-Paurson et al., (2014) agreed with Möller et al. (2009) that this could be a consequence of migration of resistant isolates from sprayed fields to unsprayed fields. Möller et al. (2009) found different genotypes of the *P. infestans* at different stages of the growing season in the same field and detected isolates of *P. infestans* belonging to the new pathotype in neighbouring fields.

Isolates of *P. infestans* migrate between fields, regions and countries, which indicates the possibility of the same population occurring throughout Europe. However, despite efficient migration routes, the *P. infestans* populations in Europe in different regions differ significantly.

Sexual reproduction of *P. infestans*

A necessary condition for sexual reproduction is the presence of isolates of two mating types in the same location, while high genetic diversity may be an indication of recombinant isolates arising from it, and these two elements have been widely studied. As a result of sexual reproduction, the *P. infestans* isolates may inherit new combinations of traits, improving their adaptation to environmental conditions and increasing their fitness. The high genetic diversity resulting from sexual reproduction in the population of *P. infestans* may limit the spread of clonal lineages in such populations.

Sexual reproduction of *P. infestans* in northern Europe

Lehtinen et al. (2008) reported that sexual reproduction in *P. infestans* populations occurred with high probability in Denmark, Finland, Norway and Sweden in 2003. In these countries, 40% of the monitored potato fields were infected with *P. infestans* isolates of both mating types, and the frequency of mating types A1 and A2 was approximately 40% to 60% (Lehtinen et al., 2008). In Finland, the acceleration of disease onset was attributed to the presence of A2 mating type isolates and the survival of *P. infestans* as oospores (Hannukkala, 2014). Research published by Widmark et al. (2011) described isolates from Sweden collected in 2001-2002. *P. infestans* samples were taken from the area where sexual reproduction was suspected, and an experimental field was artificially inoculated with those isolates. Three weeks later, leaflets showing late blight symptoms were collected from the experimental field and 151 obtained progeny isolates were analyzed by SSRs and mating type as markers. The analysis revealed the presence of eight genotypes, including three new genotypes (19% of all progeny isolates obtained). Oospores from the soil of the experimental field collected a year later yielded six new genotypes that had not been identified in isolates from previous years. The isolates collected from the experimental field three weeks post inoculation and a year later were recombinants of the parental isolates that were used for inoculation. This study confirmed the sexual reproduction of *P. infestans* in the field, and demonstrated the possibility of obtaining new recombinant isolates of *P. infestans* from overwintering oospores (Widmark et al., 2011). The results, described by Sjöholm et al. (2013) in 2008 in Nordic countries (Denmark, Finland, Norway, and Sweden), also indicated the existence of sexual reproduction in northern Europe and showed the absence of clonal lineages in the *P. infestans* population.

Research conducted in Estonia indicated that *P. infestans* is reproducing sexually in that country. From 2001 to 2007, Runno-Paurson et al., (2012) collected 180 samples of *P. infestans* from eastern Estonia, and 59% and 38% of the isolates were of mating types A1 and A2, respectively, while 3% of isolates were self-fertile (Runno-Paurson et al., 2012). In a different publication, Runno-Paurson et al., (2016) suggested the possible risk of oospore production by *P. infestans* in Estonia during the 2004 growing season. Seventy isolates were collected from eight fields, and in every field between 17% to 78% of the isolates were of the A2 type (Runno-Paurson et al., 2016), indicating a high likelihood of sexual reproduction. A dataset analyzed by Kiiker et al. (2018) consisted of 141 *P. infestans* isolates collected from 23 potato farms, in Estonia, in the years 2010-2012. The isolates of mating type A2 made up 48% of the samples, and this proportion was stable over the years. Isolates of both mating types were obtained in 87% of the investigated locations. The population of *P. infestans* was highly diverse, and the majority of the multilocus genotypes, defined by 12 SSR loci, occurred only once in the samples from the three years, which indicates a highly variable population. The almost 1:1 ratio of mating types, high percentage of fields with both mating types, and a large number of different genotypes suggested that sexual reproduction was highly probable (Kiiker et al., 2018). In a subsequent publication, Runno-Paurson, Nassar, et al., (2022) collected samples in the years 2001–2014 in Estonia and observed fluctuations in the mating types. In later years, from 2010 to 2014, the A2 mating type dominated (Runno-Paurson, Nassar, et al., 2022). In Runno-Paurson et al., (2023) over a three-year period, 193 isolates were collected from three Estonian islands. The distribution of mating types did not differ from the 1:1 ratio and both A1 and A2 mating types were found in all three study years (Runno-Paurson et al., 2023).

Across the border from Estonia is Latvia, and sexual reproduction of *P. infestans* is also likely there. Between 2010 and 2012, 181 *P. infestans* isolates were collected from 23 fields from different locations in Latvia. The ratio of A1 to A2 type was close to 1:1 among the analyzed isolates. Both mating types occurred in most of the fields (Aav et al., 2015).

In a study by Kiiker et al. (2019), isolates of *P. infestans* were collected in 2010-2012 in Latvia and Lithuania. Samples were taken from 15 potato fields in Lithuania and 21 fields in Latvia. Samples were genotyped with the SSR 12-plex marker set. SSR loci were examined for linkage disequilibrium, which did not result in significant association between markers, suggesting dominant sexual recombination in the population.

In Lithuania, Runno-Paurson et al., (2015) collected 93 *P. infestans* samples in 2010-2012. Both mating types were identified in 45% of the fields and there were no statistically significant differences in frequency between mating type A1 and mating type A2. The possibility of sexual reproduction in the Lithuanian *P. infestans* population was postulated (Runno-Paurson et al., 2015).

Sexual reproduction of *P. infestans* in eastern Europe

Sexual reproduction is possible in the Russian population of *P. infestans.* This population showed a high level of genetic diversity and the presence of isolates of both A1 and A2 mating types in different regions of Russia. Elansky et al. (2015) collected 567 *P. infestans* isolates in 2000-2009 from 16 different locations in Russia. In three locations only isolates of A1 mating type were found, while no locations were found with only A2 mating isolates, in four locations the authors found isolates capable of producing oospores with both reference isolates (i.e., parasexual reproduction), and in two locations they found isolates which did not generate oospores. In 13 locations, both the A1 and A2 mating types were observed. Genetic variation was measured using polymorphisms of two peptidases (Pep 1 and Pep 2) and glucose-6-phosphate isomerase (Gpi1), and the diversity in the population was high (Elansky et al., 2015). From 2010 to 2013 in the Pskov Region in North-West Russia, Runno-Paurson, Agho, et al. (2022) monitored the *P. infestans* population over four seasons and found that the presence of the A2 mating type increased from 33% to 48% during the tested seasons. In 90% of surveyed fields in the Pskov Region, the *P. infestans* isolates of both mating types occurred, which also suggested sexual reproduction. The high genetic diversity is also confirmed by the detection of 65% of unique SSR multilocus genotypes in the tested samples (Runno-Paurson, Agho, et al., 2022).

In Poland, from 1985 to 1991, Sujkowski et al. (1994) analyzed 247 *P. infestans* isolates. Isolates collected in the years 1985-1987 belonged to a single clonal lineage of mating type A1 based on allozyme and DNA fingerprint analyses. In 1988, in Poland, isolates with the A2 mating type were detected for the first time and, as a result of sexual reproduction, genotype diversity increased in 1988 and reached its highest point in 1990. In the years 2002–2004, in the study by Śliwka et al. (2006), 61% of the 93 analyzed *P. infestans* isolates were of mating type A1 and 39% of mating type A2. Later, according to Chmielarz et al. (2014), A2 isolates were in majority in 2006, while in 2008 and 2009 the A1 mating type dominated in Poland, but both mating types still occurred. In addition, 66 of the 96 isolates tested with SSR markers had unique genotypes (Chmielarz et al., 2014). Brylińska et al. (2016) analyzed 365 *P. infestans* isolates collected between 2010 and 2012 from three different regions of Poland, and the results showed great genetic variation in the population of *P. infestans*. In the Siedlce region, the proportion of A2 to A1 isolates was not statistically significantly from 1:1. In the Młochów region, the A1 mating type accounted for 75% and in the region Boguchwała for 77% of tested isolates. The lack of a 1:1 ratio of mating types may be due to the detection of isolates from clonal lineages, especially in Młochów, where the potato cultivation was most intensive with strong chemical control of late blight. The authors identified 299 unique SSR genotypes, 69% of isolates of the A1 mating type among all the isolates collected and 31% of tested isolates of the A2 mating type, thus supporting the hypothesis of the possible occurrence of sexual reproduction of *P. infestans* in this country (Brylińska et al., 2016).

Research conducted by Mazáková et al. (2006) in Czech Republic found a changing ratio of *P. infestans* mating types A1:A2 in the local population, being 70:30 in 2003, 44:56 in 2004 and 55:45 in 2005. The proportions in 2004 and 2005 were close to a 1:1 ratio. Isolates of mating type A2 were mainly found in the fields with potato seed tubers from the Netherlands (Mazáková et al., 2006). In the Czech Republic, in the years 2012-2014 and 2016, the isolates of A2 mating type dominated in population of *P. infestans* (Sedlák et al., 2017). The *P. infestans* isolates of both mating types were found in the same locations with frequencies of mating types A1 (40%) and A2 (60%). In a study of Sedlák et al. (2017), the authors confirmed the occurrence of oospores in the Czech Republic, but a study by Mazáková et al. (2018) did not detect any oospores. Mazáková et al. (2018) suggested dry weather in the study seasons was the reason. Results show that oospores can survive in soil in the Czech Republic, but other factors such as soil moisture and temperature or crop rotation can affect their survival (Mazáková et al., 2018). The information obtained on the survival of oospores and the ratio of mating types indicate the possibility of sexual reproduction in the Czech Republic.

Weather conditions

Weather conditions are one of the most important factors in the development of late blight. Optimal conditions for *P. infestans* are high air humidity (>90%) and a temperature close to 16 °C (Pacilly et al., 2016). Sporangia can survive at many temperatures (3-30 °C), but UV radiation and long-lasting drought are limiting factors. Wind is important in spreading sporangia (Modesto et al., 2016). Weather conditions can influence the time of occurrence of the first symptoms in the season, the duration of the late blight epidemics, the possibility of migration, and the survival of oospores.

Humidity

It is assumed that high air humidity (above 90%) is necessary for the development of late blight, however some authors suggest that air humidity is a limiting factor up to a certain level, and then other factors have a greater impact on the development of late blight.

Lehsten et al. (2017) investigated the linear relationship between air humidity and late blight development. For 30 years, in Finland from 1988 to 2011 and in Sweden from 1983 to 2012, Lehsten et al. (2017) recorded the first symptoms of disease in experimental fields and noted the weather conditions (e.g., temperature and humidity). Observations in the first years of the experiment showed a very weak relationship between the timing of the first occurrence of late blight in the season and weather conditions, but in recent years the relationship has been very strong. Using the Cox's proportional hazards model, they have shown that the first symptoms of the disease have appeared earlier in each year. The research has led to two important conclusions. First, it was found that in Sweden before 1994 and in Finland before 2001, the incidence of late blight disease was irregular, because *P. infestans* reproduced asexually with seed tubers as the primary inoculum source. In later years, the incidence of the disease was closely related to the weather, because *P. infestans* began to reproduce sexually with oospores serving as the primary inoculum being present in the soil and activated whenever the weather was suitable. Secondly, it was then shown that the development of late blight increases with increasing humidity, in a range from 40 to 88%, and not, as previously stated, only when air relative humidity is above 90% (Minogue & Fry, 1981). It is likely that individual isolates in a population of *P. infestans* have different ranges of humidity in which they can survive (Lehsten et al., 2017).

Janiszewska et al. (2021) observed a moderate abundance of *P. infestans* in years with low humidity, which indicates that other factors (the effects of temperature, host, pathogen, and human factors) may have a greater impact on the population than humidity alone.

Temperature

Differences in the spread of *P. infestans* clonal lineages can be attributed to better adaptation to the temperature of some genotypes, e.g. the spread of clonal lineage EU41_A2 in northern European countries (Euroblight, 2024).

Wu et al. (2020) studied the adaptation of *P. infestans* to low and high temperatures in laboratory conditions. The results obtained after adaptation to low temperatures (8-12 °C) indicated a strengthening of the positive relationship between the growth rate of the pathogen and aggressiveness. The aggressiveness of *P. infestans* increased with growth rate on media. At elevated temperatures (26-30 °C) growth inhibition was observed, which indicates the existence of a thermal niche limit. The pathogen adapts quickly to an increase in temperature, but it is currently impossible to determine what genetic or physiological mechanisms are responsible for this (Wu et al., 2019*)*.

Oospores overwintering in the field conditions

The overwintering of oospores in field conditions is an important factor in distinguishing the populations of *P. infestans* between western Europe and eastern and northern Europe. Oospores increase the diversity of the population of *P. infestans* and overwintering oospores were more frequently observed in eastern and northern Europe than in western Europe.

In the growing seasons of 2000 and 2001 in Norway, the oospores remained viable after being buried in the potato fields for 20 to 31 months (Hermansen et al., 2002). In 2001, in Swedish winter conditions, oospores produced during the summer epidemic can survive the winter and cause infection next year (Widmark et al., 2011). From 2007 to 2009 in Russia, oospores retained their infectious ability on tuber slices after overwintering in field conditions (Kuznetsova et al., 2010). During 2012-2014 and 2016 in the Czech Republic, oospore viability under field conditions was significantly higher in a region with higher temperature and lower humidity (29 to 43%, Prague-Suchdol) than in a region with a thicker and longer-lasting amount of snow in winter (15 to 44%, Svitavy) (Mazáková et al., 2018).

Agricultural management practices

The population of *P. infestans* is influenced by various cultivation practices, such as the resistance level of potato cultivars, the quality of potato seed tubers used, and the type and amount of chemical protection applied against late blight.

Potato cultivars

The arms race between the potato and *P. infestans* continues, and breeders try to create new cultivars to settle the war on the potato side. Genes *R1-R11* were the first identified genes for resistance against late blight, found in wild potato species *S. demissum* (Malcolmson & Black, 1966). To prevent late blight, resistance genes against *P. infestans* (*Rpi* genes) were introduced into potato cultivars. However, the time taken for resistance to be broken by the pathogen was shorter than the time it took to breed a new cultivar. Cultivars Pentland Ace, Pentland Dell and Epoka, grown on a large scale in Europe, quickly lost their resistance to *P. infestans* (Malcolmson & Black, 1966; Rudkiewicz, 1985).

Stellingwerf et al. (2018) showed that potato cultivars applied a strong selection pressure to the clonal lineage, and thus the cultivars grown in a given location can shape the populations of *P. infestans* in that area. The authors studied the selection pressure of potato genotypes in a population of *P. infestans* dominated by several clonal lineages in Ireland. From 2012 to 2016, 56 potato genotypes were compared. It was shown that the *P. infestans* genotype was influenced by the host genotype. Isolates of *P. infestans* from resistant potato genotypes, such as cultivars Sárpo Mira and Bionica, were more often of the EU13_A2 clonal lineage than from EU6_A1 and EU8_A1 ones, compared to samples from susceptible control potato cultivar King Edward or from other less resistant potato genotypes. EU13_A2 was favored by selection on resistant potato cultivars as it was able to overcome their resistance (Stellingwerf et al., 2018). While in the past, especially before 1985, the set of potato cultivars grown in eastern Europe differed significantly from the set of cultivars in western Europe, now the differences are fading away. A common EU catalogue of cultivars and marketing by western European companies led to a increase in acreage of their cultivars, usually more susceptible to late blight. On the other hand, in northern Europe, apart from traditional or locally bred potato cultivars, western cultivars were always present. There is a lack of data coordinating the population structure of *P. infestans* to the potato cultivar structure in the region. This issue requires further studies, as the potato cultivars grown in a given area may strongly influence the *P. infestans* population structure.

Fungicides

The use of a given fungicide in a specific area may affect the emergence of fungicide-resistant isolates and the *P. infestans* population structure.

In a survey conducted in 1990-1996 and in 2003, high percentages of metalaxyl resistant isolates were found in Sweden and Norway, which proves that the applied fungicide exerts a strong selection pressure on *P. infestans* population; while the lower occurrence of resistant isolates in Finland was related to the low use of metalaxyl in this country (Hermansen et al., 2000; Lehtinen et al., 2008). In unprotected potato fields in Poland 30% of the *P. infestans* isolates were resistant to metalaxyl, whereas in the protected field 50% of the isolates were resistant to metalaxyl, and all intermediately resistant isolates originated from protected fields (Śliwka et al., 2006). In the years 2004-2005 in Estonia, there were four times more metalaxyl resistant isolates found in large conventional fields with intensive chemical control than were found in organic fields (Runno-Paurson et al., 2010).

Among the isolates of four clonal lineages (EU37_A2, EU13_A2, EU1_A1 and EU6_A1) collected in 2016 and 2017 in France and the UK, the clonal lineage EU37_A2 was determined to be resistant to fluazinam (Puidet et al., 2023). The authors indicated that EU37_A2 was under selection pressure, which was confirmed by the fact that the occurrence of this genotype reduced following restrictions in the use of fluazinam.

The use of the fungicide mandipropamid has resulted in the spread of mandipropamid-resistant isolates and loss of efficacy of this fungicide. Isolates of the EU43_A1 genotype found in Denmark were resistant to mandipropamid and this *P. infestans* genotype is widely distributed across the main potato growing region (Jutland) in the country (Abuley et al., 2023).

Quality of the potato seed tubers

The quality of potato seed tubers is an important factor influencing populations of *P. infestans*, as various isolates of *P. infestans* migrate along with the import and export of seed tubers over an unlimited distance. Poor quality of potato seed tubers leads to a higher diversity of *P. infestans* populations.

Runno-Paurson et al., (2010) collected 196 isolates of *P. infestans* in 2004-2005 in Estonia from organic, small, and large-scale conventional fields. In the small-scale conventional fields, farmers did not use certified seed material and in large-scale conventional fields farmers used potato seed tubers imported from western Europe. In the large-scale conventional fields the three rarest virulence factors in Estonia, R5, R8 and R9, were found. This result is surprising, but a possible explanation was that in western Europe the clonal lineages with high virulence dominate in the populations of *P. infestans*, and such clonal lineage(s) were imported with the seed tubers (Runno-Paurson et al., 2010). The results contained in this publication differ from the results presented in other Runno-Paurson publications for subsequent years. In a more comprehensive study, Runno-Paurson et al., (2013) investigated the effect of potato seed tuber quality on the *P.*

infestans population. Potato seed tubers of high and low phytosanitary quality were planted in two different open fields in Estonia in 2001-2007. High quality seed consisted of healthy, certified seed potato tubers imported from Western Europe that were propagated two years after meristem phase. The low quality seed tubers were propagated from commercial certified seed tubers, multiplied for several consecutive years, and included diseased potatoes and untested tubers of unknown origin. During the years 2001-2007, 387 isolates of *P. infestans* were collected. The quality of potato seed tubers in this study had no effect on the resistance to metalaxyl and the proportion of mating types in the population of *P. infestans.* Low quality potato seed tubers influenced the diversity of pathotypes of the obtained *P. infestans* isolates. Higher quality potato seed tubers increased average virulence. Additionally, the Shannon diversity index was higher, indicating a higher genetic diversity in the *P. infestans* population, in the group of isolates obtained from plants grown from potato seed tubers of low phytosanitary quality, than in those from potato seed tubers of high phytosanitary quality (Runno-Paurson et al., 2013).

Cultivation system

Potato production can take place on a large-scale or small conventional farm, an organic farm, or in a garden. Usually, these systems differ in fertilization, aftercrop, cover crop, crop rotation etc. Any of these factors can cause differences in the population structure of *P. infestans* in these potato crops. In contrast to western Europe, high-input large conventional cultivation of potatoes is not the dominant system in northern and eastern Europe.

In a study by Lehtinen et al. (2007), the authors collected 1726 isolates of *P. infestans* in Finland from organic fields, conventional fields and home gardens, from 1997 to 2000. The authors examined the phenotypic and genetic variability of populations of *P. infestans*, and found that the frequency of mating types depends on the type of fields. Samples collected in organic fields and gardens more often contained isolates of both mating types A1 and A2, while those collected in conventional fields were dominated by one mating type (the proportions were not 1:1).

The results of Brylińska et al. (2016) suggest an impact of the dominating cultivation system in a region on the population of *P. infestans*. The research was conducted in three regions of Poland, Boguchwała, Siedlce and Młochów, from 2010 to 2012. Samples were collected from gardens (55%), experimental fields (29%), organic fields (7%) and intensive production fields (9%) in Boguchwała. In Siedlce, the samples were collected from gardens (44%), production fields (42%) and organic fields (14%). In Młochów, the samples were collected from large production fields (69%), gardens (24%) and experimental fields (7%). In the Młochów region, where large, high-input production dominated, the diversity among *P. infestans* isolates was smaller than in other locations, and more isolates were resistant to metalaxyl. In large, intensively cultivated and protected fields, selection pressure caused the spread of clonal lineages. In small home gardens, allotments and small farms, the population of *P. infestans* was genetically more diverse and likely sexually recombining (Brylińska et al., 2016).

Runno-Paurson et al. (2015) collected 93 isolates of *P. infestans* in 2010-2012 in Lithuania from experimental field plots and small or large-scale conventional fields, and did not observe an influence of agricultural management practices on the population of *P. infestans* (Runno-Paurson et al., 2015). The first reason for the different results of the works of Brylińska et al. (2016) and Runno-Paurson et al., (2015) may be the different sampling schemes. Brylińska et al. (2016) collected the samples in three regions with different dominating cultivation systems and the migration of *P. infestans* between these regions was limited or impossible. Fields sampled in Lithuania differed in cultivation practices, but were not geographically separated. The isolates of *P. infestans* could have migrated between fields and the tested population sample was uniform in the work of Runno-Paurson et al., (2015). The second reason for the different results may be that in Lithuania, the authors collected samples mainly from small-scale crops and the disproportion between the compared groups of isolates may account for the lack of statistical differences (Runno-Paurson et al., 2015).

From 2010 to 2013 in the Pskov region of north-western Russia, Runno-Paurson, Agho, et al., (2022) characterized the mating type, sensitivity to metalaxyl, population genetic diversity and genotype of 238 isolates of *P. infestans.* In Russia, the use of metalaxyl is low, and small-scale conventional fields prevailed in the agroecosystem. In 2010 and 2012, the samples were collected mainly from small-scale farm fields, but in subsequent years mainly from large-scale conventional fields. Based on the results, it was concluded that a high genotypic diversity of *P. infestans* population may be connected with agriculture management practice. The authors found more unique multilocus genotypes of *P. infestans* on small conventional farms (71%) than on large conventional farms (60%). This is probably due to the fact that farmers in small conventional fields grew potatoes each year without using crop rotations (Runno-Paurson, Agho, et al., 2022).

Summary

The feature that most distinguishes northern Europe and eastern Europe from western Europe is their agricultural management practices. The biggest producers of potato in Europe are five countries (Germany, Poland, France, Netherlands and Belgium) (Goffart et al., 2022), four of which are from western Europe. In western Europe, the industrial model of potato cultivation prevails, with up to 20 applications of fungicides against *P. infestans* per season, the use of certified potato seed tubers, and cultivation carried out on large-scale fields.

On the other hand, in northern Europe and eastern Europe, only a few fungicide applications are used per season and, in some countries, it is completely limited. Nevertheless, countries such as Denmark also chemically protect the fields, following blight management decision support systems, and the number of applications is usually high because Denmark has a high risk of late blight (Schepers et al., 2019). Some potato seed tubers imported from western Europe are used, but also potato seed tubers from an unknown source or farm-saved seeds are used, cultivation usually takes place on small fields and scattered at small distances from each other. Regarding seed tubers, Norway is an exception as it does not allow any import of seed tubers from abroad.

Infected potato seed tubers brought from western European countries enable migration of *P. infestans* and mixing of western European genotypes with genotypes of local populations, which results in a greater diversity of genotypes of *P. infestans* in eastern and northern European countries. Through potato seed tubers, genotypes of *P. infestans* also migrate between individual fields in the countries of northern and eastern Europe. The fast migration of the A2 isolates of *P. infestans* in 1990, and current migrations of the clonal lineages of pathogen from western Europe, indicate that there are no barriers for migration to eastern and northern Europe for this organism.

Sexual reproduction was found in all studied countries from northern and eastern Europe, resulting in the formation of oospores, and overwintering of these oospores has been demonstrated. This, in turn, increases the diversity of the population. In western Europe, asexual reproduction predominates, but sexual reproduction also occurs.

Different types of climate are associated with different weather conditions, which means different temperature and humidity. Weather conditions are also an important factor in the spread and life of *P. infestans*. According to the European climatic zones created by Schneider et al. (2013) on the basis of EUCA15000, western Europe is classified as a temperate oceanic climate zone, Poland and the Czech Republic as a transitional temperate zone, Latvia, Lithuania and Estonia as a temperate continental zone, and the northern countries as a boral zone. In the temperate oceanic climate, we observe the dominance of clonal lineages, which may lead to the assumption that the climate has a significant influence on the population of *P. infestans*. Climate change is an important factor shaping pathogen populations, affecting their ranges of occurrence, migrations, and overwintering success. Oospores have a limit to their survival at certain temperatures, but this limit can shift. Selective pressure from temperature can promote strains that are better adapted to higher temperatures. As temperatures rise, the entire *P. infestans* population may change.

It is difficult to separate the effects of climate differences from the effects of different agricultural practices in the described countries. Both factors may shape the population of *P. infestans*.

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Data Availability All data supporting the finalings of this study are available within the paper and its supplementary files.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

References

Aav, A., Skrabule, I., Bimšteine, G., Kaart, T., Williams, I. H., & Runno-Paurson, E. (2015). The structure of mating type, metalaxyl resistance and virulence of *Phytophthora infestans* isolates collected from Latvia. *Zemdirbyste-Agriculture, 102*, 335–342.

Abuley, I. K., Lynott, J. S., Hansen, J. G., Cooke, D. E., & Lees, A. K. (2023). The EU43 genotype of Phytophthora infestans displays resistance to mandipropamid. *Plant Pathology, 72*(7), 1305–1313.

Bimsteine, G. (2008). *Phytophthora infestans* populations in Latvia. In *Proceedings of the proceedings of the Latvian Academy of Sciences* (p. 223).

Brurberg, M. B., Elameen, A., Le, V. H., Nærstad, R., Hermansen, A., Lehtinen, A., & Yuen, J. (2011). Genetic analysis of Phytophthora infestans populations in the Nordic European countries reveals high genetic variability. *Fungal Biology, 115*(4-5), 335–342.

Brylińska, M., Sobkowiak, S., Stefańczyk, E., & Śliwka, J. (2016). Potato cultivation system affects population structure of *Phytophthora infestans*. *Fungal Ecology, 20*, 132–143.

Casa-Coila, V. H., Gomes, C. B., Lima-Medina, I., Rocha, D. J. A., & Reis, A. (2020). Characterization of mating type and the diversity of pathotypes of *Phytophthora infestans* isolates from southern Brazil. *Journal of Plant Diseases and Protection, 127*, 43–54.

Chmielarz, M., Sobkowiak, S., Dębski, K., Cooke, D., Brurberg, M., & Śliwka, J. (2014). Diversity of Phytophthora infestans from Poland. *Plant Pathology, 63*, 203–211.

Cooke, D. E., Cano, L. M., Raffaele, S., Bain, R. A., Cooke, L. R., Etherington, G. J., Deahl, K. L., Farrer, R. A., Gilroy, E. M., & Goss, E. M. (2012). *Genome analyses of an aggressive and invasive lineage of the Irish potato famine pathogen*. Public Library of Science San Francisco.

Cooke, D. E. L., & Lees, A. K. (2004). Markers, old and new, for examining Phytophthora infestans diversity. *Plant Pathology, 53*(6), 692–704.

Danies, G., Small, I., Myers, K., Childers, R., & Fry, W. (2013). Phenotypic characterization of recent clonal lineages of *Phytophthora infestans* in the United States. *Plant Disease, 97*, 873–881.

Dzwonkowski, W. (2017). Ewolucja produkcji ziemniaków w Polsce i UE (evolution of potato production in Poland and the EU). *Zeszyty Naukowe Szkoły Głównej Gospodarstwa Wiejskiego w Warszawie, 17*, 71–80.

Elansky, S., Pobedinskaya, M., Kokaeva, L., Statsyuk, N., & Dyakov, Y. (2015). *Phytophthora infestans* populations from the European part of Russia: Genotypic structure and metalaxyl resistance. *Journal of Plant Pathology, 97*, 449–456.

EuroBlight (2024) https://agro.au.dk/forskning/internationale-platforme/euroblight/pathogen-monitoring/genotype-frequency-map/. Accessed 20 Aug 2024.

Eurostat (2024) https://ec.europa.eu/eurostat/statistics-explained/index.php?title=The_EU_potato_sector_-_statistics_on_production,_prices_and_trade/. Accessed 20 Aug 2024.

FAOSTAT (2024) Food and agriculture data. https://www.fao.org/faostat/en/#data/QCL/. Accessed 20 Aug 2024.

Fernández-Pavía, S., Grünwald, N., Diaz-Valasis, M., Cadena-Hinojosa, M., & Fry, W. (2004). Soilborne oospores of *Phytophthora infestans* in Central Mexico survive winter fallow and infect potato plants in the field. *Plant Disease, 88*, 29–33.

Fry, W. E., Goodwin, S. B., Dyer, A. T., Matuszak, J. M., Drenth, A., Tooley, P. W., Sujkowski, L. S., Koh, Y. J., Cohen, B. A., Spielman, L. J., Deahl, K. L., Inglis, D. A., & Sandlan, K. P. (1993). Historical and recent migrations of Phytophthora infestans: Chronology, pathways, and implications. *Plant Disease, 77*, 653–661.

Goffart, J. P., Haverkort, A., Storey, M., Haase, N., Martin, M., Lebrun, P., & Demeulemeester, K. (2022). Potato production in northwestern Europe (Germany, France, the Netherlands, United Kingdom, Belgium): Characteristics, issues, challenges and opportunities. *Potato Research, 65*(3), 503–547.

Goodwin, S. B., Cohen, B. A., & Fry, W. E. (1994). Panglobal distribution of a single clonal lineage of the Irish potato famine fungus. *Proceedings of the National Academy of Sciences, 91*, 11591–11595.

Hannukkala, A. (2014). Changes in epidemiology and population structure of *P. infestans* in Finland 1847-2011. *PPO-Special Report* (pp. 153–158).

Hannukkala, A. O., Rastas, M., & Hannukkala, A. E. (2009). Phenotypic characteristics of Finnish and North-Western Russian populations of *Phytophthora infestans* in 2006-2007. *PPO-Special Report no., 13*, 191.

Hansen, J., Lassen, P., Kessel, G., Cooke, D., Andrivon, D., & Roselyne, C. (2017). *Potato blight tracking in Europe*. Euroblight Newsletter.

Haverkort, A. J., Boonekamp, P. M., Hutten, R., Jacobsen, E., Lotz, L. A. P., Kessel, G. J. T., & Van der Vossen, E. A.

G. (2008). Societal costs of late blight in potato and prospects of durable resistance through cisgenic modification. *Potato Research, 51*, 47–57.

Hermansen, A., Hannukkala, A., Nærstad, H., & Brurberg, M. B. (2000). Variation in populations of *Phytophthora infestans* in Finland and Norway: Mating type, metalaxyl resistance and virulence phenotype. *Plant Pathology, 49*, 11–22.

Hermansen, A., Nordskog, B., & Brurberg, M. B. (2002). Studies on formation and survival of oospores of Phytophthora infestans in Norway. *PPO-Special Report*, (8), 77–80.

Hohl, H. R., & Iselin, K. (1984). Strains of Phytophthora infestans from Switzerland with A2 mating type behaviour. *Transactions of the British Mycological Society, 83*(3), 529–530.

Janiszewska, M., Sobkowiak, S., Stefańczyk, E., & Śliwka, J. (2021). Population structure of *Phytophthora infestans* from a single location in Poland over a long period of time in context of weather conditions. *Microbial Ecology, 81*, 746–757.

Judelson, H. S. (2014). Phytophthora infestans. In *Genomics of plant-associated Fungi and oomycetes: Dicot pathogens* (pp. 175–208). Springer: Springer-Verlag.

Kiiker, R., Hansen, M., Williams, I. H., Cooke, D. E., & Runno-Paurson, E. (2018). Outcome of sexual reproduction in the *Phytophthora infestans* population in Estonian potato fields. *European Journal of Plant Pathology, 152*, 395–407.

Kiiker, R., Skrabule, I., Ronis, A., Cooke, D. E. L., Hansen, J. G., Williams, I. H., Mänd, M., & Runno-Paurson, E. (2019). Diversity of populations of Phytophthora infestans in relation to patterns of potato crop management in Latvia and Lithuania. *Plant Pathology, 68*, 1207–1214.

Kuznetsova, M., Ulanova, T., Rogozhin, A., Smetanina, T., & Filippov, A. (2010). Role of oospores in the overwintering and year-on-year development of the late blight pathogen on tomato and potato. *PPO-Special Report, 14*, 223–230.

Lamb, H., & Bourke, A. (1993). *The spread of potato blight in Europe in 1845-6 and the accompanying wind and weather patterns*. Met Éireann.

Lees, A., Stewart, J., Lynott, J., Carnegie, S., Campbell, H., & Roberts, A. (2012). The effect of a dominant *Phytophthora infestans* genotype (13_A2) in Great Britain on host resistance to foliar late blight in commercial potato cultivars. *Potato Research, 55*, 125–134.

Lehsten, V., Wiik, L., Hannukkala, A., Andreasson, E., Chen, D., Ou, T., Liljeroth, E., Lankinen, Å., & Grenville-Briggs, L. (2017). Earlier occurrence and increased explanatory power of climate for the first incidence of potato late blight caused by *Phytophthora infestans* in Fennoscandia. *PLoS One, 12*, e0177580.

Lehtinen, A., Hannukkala, A. (2004). Oospores of Phytphthora infestans in soil provide an important new source of primary inoculum in Finland.

Lehtinen, A., Hannukkala, A., Andersson, B., Hermansen, A., Le, V., Naerstad, R., Brurberg, M., Nielsen, B., Hansen, J., & Yuen, J. (2008). Phenotypic variation in Nordic populations of *Phytophthora infestans* in 2003. *Plant Pathology, 57*, 227–234.

Lehtinen, A., Hannukkala, A., Rantanen, T., & Jauhiainen, L. (2007). Phenotypic and genetic variation in Finnish potato-late blight populations, 1997–2000. *Plant Pathology, 56*, 480–491.

Li, Y., Van Der Lee, T., Evenhuis, A., Van den Bosch, G., Van Bekkum, P., Förch, M., van Gent-Pelzer, M., Van Raaij, H., Jacobsen, E., & Huang, S. (2012). Population dynamics of *Phytophthora infestans* in the Netherlands reveals expansion and spread of dominant clonal lineages and virulence in sexual offspring. *G3: Genes| Genomes| Genetics, 2*, 1529–1540.

Malcolmson, J. F., & Black, W. (1966). New R genes in Solanum demissum Lindl. And their complementary races of *Phytophthora infestans* (Mont.) de Bary. *Euphytica, 15*, 199–203.

Maleeva, Y. V., Naumoff, D., Yatsentiuk, S., Dolgova, A., & Kolesnikov, A. (1999). Changes in the composition of populations of *Phytophthora infestans* (Mont.) de Bary in Russia in the 1990s based on the results of mitochondrial DNA analysis. *Russian Journal of genetics c/c of Genetika, 35*, 1007–1014.

Mazáková, J., Táborský, V., Zouhar, M., Ryšánek, P., Hausvater, E., & Doležal, P. (2006). Occurrence and distribution of mating types A1 and A2 of *Phytophthora infestans* (Mont.) de Bary in the Czech Republic. *Plant Protection Science, 42*, 41.

Mazáková, J., Zouhar, M., & Ryšánek, P. (2018). Significance of sexual reproduction of *Phytophthora infestans* in the Czech Republic. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis, 66*, 1191–1197.

Minogue, K., & Fry, W. (1981). Effect of temperature, relative humidity, and rehydration rate on germination of dried sporangia of *Phytophthora infestans*. *Phytopathology, 71*, 1181–1184.

Modesto, O. O., Anwar, M., He, Z., Larkin, R. P., & Honeycutt, C. W. (2016). Survival potential of *Phytophthora infestans* sporangia in relation to environmental factors and late blight occurrence. *Journal of Plant Protection Research.*

Möller, K., Dilger, M., Habermeyer, J., Zinkernagel, V., Flier, W., & Hausladen, H. (2009). Population studies on *Phytophthora infestans* on potatoes and tomatoes in southern Germany. *European Journal of Plant Pathology, 124*, 659–672.

Nærstad, H. (2000). Variation in populations of *Phytophthora infestans* in Finland and Norway: Mating type, metalaxyl resistance and virulence phenotype. *Plant Pathology, 49*, 11–22.

Naveed, K., Rajputt, N. A., Khan, S. A., & Ahmad, A. (2017). Population structure of *Phytophthora infestans* on worldwide scale: A review. *Pakistan Journal of Phytopathology, 29*, 281–288.

Nielsen, B.J.; Cooke, D.E.; Hansen, J.G. (2014). Monitoring the Danish population of potato late blight pathogen, *Phytophthora infestans* in 2011-2012 and occurrence of 13_ A2. In Proceedings of the Proceedings of the fourteenth EuroBlight Workshop, PPO-Special Report; pp. 159-162.

Pacilly, F. C., Groot, J. C., Hofstede, G. J., Schaap, B. F., & van Bueren, E. T. L. (2016). Analysing potato late blight control as a social-ecological system using fuzzy cognitive mapping. *Agronomy for Sustainable Development, 36*, 1–18.

Puidet, B., Mabon, R., Guibert, M., Kiiker, R., Loit, K., Le, V. H., & Andrivon, D. (2023). Investigating phenotypic traits as potential drivers of the emergence of EU_37_A2, an invasive new lineage of *Phytophthora infestans* in Western Europe. *Plant Pathology, 72*(4), 797–806.

Puidet, B., Mabon, R., Guibert, M., Kiiker, R., Soonvald, L., Le, V. H., Eikemo, H., Dewaegeneire, P., Saubeau, G., & Chatot, C. (2022). Examining phenotypic traits contributing to the spread in northern European potato crops of EU_41_A2, a new clonal lineage of *Phytophthora infestans*. *Phytopathology, 112*, 414–421.

Ristaino, J. B. (2002). Tracking historic migrations of the Irish potato famine pathogen, *Phytophthora infestans*. *Microbes and Infection, 4*, 1369–1377.

Rudkiewicz, F. (1985). *Zaraza ziemniaka (Phytophthora infestans (Mont) de Bary)* (pp. 381–398). Biologia Ziemniaka. Państwowe Wydawnictwa Naukowe.

Runno-Paurson, E., Agho, C. A., Nassar, H., Hansen, M., Leitaru, K., Hallikma, & Niinemets, Ü. (2023). The variability of Phytophthora infestans isolates collected from Estonian islands in the Baltic Sea. *Plant Disease*.

Runno-Paurson, E., Agho, C. A., Zoteyeva, N., Koppel, M., Hansen, M., Hallikma, T., Cooke, D. E., Nassar, H., & Niinemets, Ü. (2022). Highly diverse *Phytophthora infestans* populations infecting potato crops in Pskov region, north-West Russia. *Journal of Fungi, 8*, 472.

Runno-Paurson, E., Hannukkala, A., Kotkas, K., Koppel, M., Williams, I., & Mänd, M. (2014). Population changes and phenotypic diversity of *Phytophthora infestans* isolates from Estonia and Finland. *Journal of Plant Pathology, 96*, 85–95.

Runno-Paurson, E., Hannukkala, A., Trdan, S., Williams, I., Koppel, M., & Mänd, M. (2012). The structure of mating type, virulence, metalaxyl resistance of *Phytophthora infestans* in a long-term phenotypic study in distinct location in eastern Estonia. *Journal of Plant Diseases and Protection, 119*, 45–52.

Runno-Paurson, E., Hannukkala, A. O., Kotkas, K., Koppel, M., Williams, I. H., & Mänd, M. (2013). Impact of phytosanitary quality of seed potato and temporal epidemic progress on the phenotypic diversity of *Phytophthora infestans* populations. *American Journal of Potato Research, 90*, 245–254.

Runno-Paurson, E., Kiiker, R., Joutsjoki, T., & Hannukkala, A. (2016). High genotypic diversity found among population of *Phytophthora infestans* collected in Estonia. *Fungal Biology, 120*, 385–392.

Runno-Paurson, E., Nassar, H., Tähtjärv, T., Eremeev, V., Hansen, M., & Niinemets, Ü. (2022). High temporal variability in late blight pathogen diversity, virulence, and fungicide resistance in potato breeding fields: Results from a long-term monitoring study. *Plants, 11*(18), 2426.

Runno-Paurson, E., Remmel, T., Ojarand, A., Aav, A., & Mänd, M. (2010). The structure of *Phytophthora infestans* populations from organic and conventional crops. *European Journal of Plant Pathology, 128*, 373–383.

Runno-Paurson, E., Ronis, A., Hansen, M., Aav, A., & Williams, I. H. (2015). Lithuanian populations of *Phytophthora infestans* revealed a high phenotypic diversity. *Journal of Plant Diseases and Protection, 122*, 57–65.

Schepers, H., Hausladen, H., Hansen, J. G., Abuley, I. K., Andersson, B., Liljeroth, E., & Vanhaverbeke, P. (2019). Epidemics and control of early & late blight, 2017 & 2018 in Europe. In *Proceedings of the seventeenth EuroBlight workshop*. Wageningen University & Research.

Schneider, C., Laizé, C. L. R., Acreman, M. C., & Flörke, M. (2013). How will climate change modify river flow regimes in Europe? *Hydrology and Earth System Sciences, 17*(1), 325–339.

Sedlák, P., Mazáková, J., Sedláková, V., Ryšánek, P., Vejl, P., & Doležal, P. (2017). Virulence and mating type of *Phytophthora infestans* isolates in the Czech Republic. *Scientia Agriculturae Bohemica, 48*, 185–192.

Sjöholm, L., Andersson, B., Högberg, N., Widmark, A.-K., & Yuen, J. (2013). Genotypic diversity and migration patterns of *Phytophthora infestans* in the Nordic countries. *Fungal Biology, 117*, 722–730.

Śliwka, J., Sobkowiak, S., Lebecka, R., Avendaño-Córcoles, J., & Zimnoch-Guzowska, E. (2006). Mating type, virulence, aggressiveness and metalaxyl resistance of isolates of *Phytophthora infestans* in Poland. *Potato Research, 49*, 155–166.

Stellingwerf, J., Phelan, S., Doohan, F., Ortiz, V., Griffin, D., Bourke, A., Hutten, R., Cooke, D., Kildea, S., & Mullins, E. (2018). Evidence for selection pressure from resistant potato genotypes but not from fungicide application within a clonal *Phytophthora infestans* population. *Plant Pathology, 67*, 1528–1538.

Sujkowski, L. S., Goodwin, S., Dyer, A., & Fry, W. (1994). Increased genotypic diversity via migration and possible occurrence of sexual reproduction of *Phytophthora infestans* in Poland. *Phytopathology, 84*, 201–207.

Troussieux, S., Gilgen, A., & Souche, J.-L. (2022). A new biocontrol tool to fight potato late blight based on *Willaertia magna* C2c Maky lysate. *Plants, 11*, 2756.

Turkensteen, L., Flier, W., Wanningen, R., & Mulder, A. (2000). Production, survival and infectivity of oospores of *Phytophthora infestans*. *Plant Pathology, 49*, 688–696.

Widmark, A. K., Andersson, B., Sandström, M., & Yuen, J. (2011). Tracking *Phytophthora infestans* with SSR markers within and between seasons–a field study in Sweden. *Plant Pathology, 60*, 938–945.

Wu, E. J., Wang, Y. P., Shen, L. L., Yahuza, L., Tian, J. C., Yang, L. N., Shang, L. P., Zhu, W., & Zhan, J. (2019). Strategies of *Phytophthora infestans* adaptation to local UV radiation conditions. *Evolutionary Applications, 12*, 415–424.

Wu, E. J., Wang, Y. P., Yahuza, L., He, M. H., Sun, D. L., Huang, Y. M., Liu, Y. C., Yang, L. N., Zhu, W., & Zhan, J. (2020). Rapid adaptation of the Irish potato famine pathogen *Phytophthora infestans* to changing temperature. *Evolutionary Applications, 13*, 768–780.

Yoshida, K., Schuenemann, V. J., Cano, L. M., Pais, M., Mishra, B., Sharma, R., & Burbano, H. A. (2013). The rise and fall of the Phytophthora infestans lineage that triggered the Irish potato famine. *elife, 2*, e00731.

Yuen, J., & Andersson, B. (2013). What is the evidence for sexual reproduction of *Phytophthora infestans* in Europe? *Plant Pathology, 62*, 485–491.

Zhu, W., Shen, L.-L., Fang, Z.-G., Yang, L.-N., Zhang, J.-F., Sun, D.-L., & Zhan, J. (2016). Increased frequency of self-fertile isolates in *Phytophthora infestans* may attribute to their higher fitness relative to the A1 isolates. *Scientific Reports, 6*, 1–10.