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Temporal changes in phenotypic diversity of *Phytophthora infestans* in northern Estonia

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Abstract

Phytophthora infestans is one of the most serious and economically important pathogens in potato fields worldwide, including Estonia. Under favourable conditions, the pathogen causes a destructive foliar blight and can also have a destructive effect on tubers. *Phytophthora infestans* was isolated from potato leaves from the northern region of Estonia during 2001–2008. In the six years 2003–2008, the proportions of A1 and A2 mating types among 180 isolates tested were 57% and 43%, respectively. We found a consistent directional change in the proportions of A2 mating types which increased during the study years. Both mating types were found in almost all sampled fields in the study area. The results indicated that the ratio of *P. infestans* A1:A2 mating types is suitable for sexual reproduction. Race diversity calculated by the normalized Shannon diversity index showed a very low value (0.27), still considerable differences between years were found.

Keywords: *Phytophthora infestans*, mating type, virulence, population changes.

Introduction

Late blight, caused by the plant pathogen *Phytophthora infestans* (Mont.) de Bary, is one of the most devastating diseases of potato worldwide. The pathogen causes a destructive foliar blight and can also have a destructive effect on tubers. The pathogen can be transported long distances in infected plant material. In Estonia, under favourable cool and moist conditions, control of the late blight pathogen by fungicides is necessary to achieve high yield with good quality in conventional potato production (Koppel, 1997). Such control is expensive, as, under weather conditions conducive to infection, the canopy must be treated weekly to prevent the disease once inoculum is present (Lehtinen et al., 2007). Growing more resistant potato varieties is one of the most effective strategies to control late blight, to protect potato yield and to prevent harm to the environment.

The fungal-like oomycete *P. infestans*, can reproduce both sexually and asexually. For sexual reproduction, *P. infestans* requires both A1 and A2 mating types to produce gametangia (Fry, Goodwin, 1997). The centre of diversity of this oomycete is located in the highlands of Mexico (Fry, Goodwin, 1997), from where both mating types originate. At least two different migration events occurred from Mexico. The first is postulated to have occurred before 1845, after which *P. infestans* swept through Europe and Ireland resulting in the death of over one million people due to starvation, and emigration of 1.5 million people to other parts of Europe or North America (Drenth et al., 1994). The second

migration occurred in the 1970s to 1990s, bringing the A2 mating type out of Mexico and also transferring genetically diverse and aggressive strains (Fry et al., 1993). Sexual reproduction results in oospores which can overwinter in the soil (Andersson et al., 1998; Lehtinen, Hannukkala, 2004). The effects of this change in the population were observed in potato fields, where epidemics started earlier and the number of fungicide treatments for control of the blight increased, probably partly because of oospore-derived infections (Hannukkala et al., 2007).

In this study, we tested the hypotheses that: 1) temporal changes occur in population parameters at a particular location over an eight year period; 2) the mating type ratio in northern Estonia allows sexual reproduction to occur. Results are compared with the findings of similar studies performed in previous years in Estonia and in other European countries.

Materials and methods

Collection and isolation of isolates. In total, 218 isolates of *Phytophthora infestans* were collected in eight consecutive years, 2001–2008, from Saku in northern Estonia (Table 1). All eight potato fields were located at the Department of Plant Biotechnology EVIKA of the Estonian Research Institute of Agriculture. All the isolates originated from leaves. The study area is characterized by high genetic diversity of the host plants including several genotypes that have race specific genes (Runno-Paurson et al., 2009). Conventional agrotechnical methods were used on these fields with fungicides being applied once or twice per growing season in all years, except in 2006. Planted potato seeds were of high quality, multiplied from meristem plants (Rosenberg, Kotkas, 1986) and shifted after two years of growing.

Nine to forty-eight leaflets, each with a single lesion (one per plant) were collected from all fields. In 2004, 2005, 2007 and 2008, isolates were collected at different stages of the epidemic: at the beginning of the outbreak and again 2–3 weeks later. An approximately equal number of isolates was taken early and late in the season. In the early stages of the outbreak, approximately 10–15% of the leaf area of the infected plants and less than 10% of the plants were infected with late blight. In the later stage, about 20–30% of the leaf area and more than 50% of the plants were infected. The plants were selected by randomising the distance from field edges, and from each plant the blighted leaf was also randomly chosen, excluding those that had several or no lesions.

Table 1. Origin and characteristics of *Phytophthora infestans* isolates collected from northern Estonia during 2001–2008

	Number of isolates tested for	
Year	Mating type	Virulence
2001		18
2002		10
2003	33	25
2004	33	37
2005	33	34
2006	14	13
2007	46	48
2008	21	20
Total	180	205

Isolations were carried out by placing a fragment of infected leaf tissue between ethanol and flame-sterilized tuber slices. Tubers of susceptible varieties without known R genes were used (Berber). The slices were placed into sterile Petri dishes with a moist filter paper disk on top and incubated for 6–7 days at 16°C in a growth chamber until the mycelia had grown through the slices. A small sample of mycelia from the tuber slices was transferred with a sterile needle to rye B agar (Caten, Jinks, 1968). The pure cultures were preserved at 5°C and transferred to rye agar after every two months. All phenotypic tests were carried out in October–November of the year of isolation.

Phenotypic analyses. Mating types were determined by the method described in Runno-Paurson et al. (2009). Observed oospore formation in single isolate pure cultures was interpreted as the occurrence of self-fertility of the isolates. The tester isolates were the same as those described in Lehtinen et al. (2007). The specific virulence of each of the 196 isolates was determined using Black's differential set of potato genotypes containing resistance genes R1-R11 (provided by the Scottish Agricultural Science Agency) (Malcolmson, Black, 1966). Laboratory procedures were performed as described in Runno-Paurson et al. (2009).

Data analysis. Statistical analyses were performed with SAS/STAT version 9.1 (SAS Institute Inc., USA). Differences in the prevalence of the two mating types among *P. infestans* isolates between years were tested using a logistic analysis (GENMOD procedure in SAS) with a multinomial response variable (A1, A2, or both).

Separate logistic analyses were used to test for the difference in the prevalence of virulence against different R genes (virulent vs. non-virulent) between years, and for the dependence of mating type on race prevalence (unique vs. prevalent). The virulence complexity dependence of different years was analysed with one-way ANOVA. Regression analyses were used to compare the normalized Shannon index values during the study years. Race diversity was calculated with the normalized Shannon diversity index (Sheldon, 1969).

Results

Mating type. Mating type determination of a total of 180 isolates collected during 2003–2008, showed that, on average, 43% of the tested isolates per year were of the A2 mating type and 57% were A1 mating type (Table 2). Self-fertile isolates were not found. Significant differences ($\chi^2 = 55.77$, d.f. = 5, $p < 0.0001$) were found in the proportion of A1 and A2 mating types between years. In 2003, only the A1 mating type was found but, thereafter, the A2 mating type was also found each year (Table 2). Although the A1 mating type continued to be dominant (82%) in 2004, thereafter the frequency of the A2 mating type increased rapidly and remained at a high level (43–73%) (Table 2).

Table 2. Percentages of mating types among isolates of *Phytophthora infestans* from northern Estonia during 2003–2008

Year	Mating type %		Number of isolates
	A1	A2	
2003	100	0	33
2004	82	18	33
2005	27	73	33
2006	57	43	14
2007	39	61	46
2008	33	67	21
Total	57 ± 3.7*	43 ± 3.7	180

* – mean ± SE

Virulence. All 11 known virulence factors were found among the 205 isolates tested for virulence. Almost all were virulent on differentials with genotypes R1, R2, R3, R4, R7, R10 and R11. Virulence factors 5 (2%), 8 (9%) and 9 (3%) were rare. A difference in the prevalence of virulence factors 2, 5, 6, 8 and 9 was observed between collection years (factor 2: $\chi^2 = 25.45$, d.f. = 7, $p = 0.00063$; factor 5: $\chi^2 = 49.98$, d.f. = 7, $p < 0.0001$; factor 6: $\chi^2 = 19.40$, d.f. = 7, $p = 0.0070$; factor 8: $\chi^2 = 94.11$, d.f. = 7, $p < 0.0001$; factor 9: $\chi^2 = 28.49$, d.f. = 7, $p = 0.00018$). The relatively rare virulence factors R2 and R6 were found every year (Table 4). The rarest virulence factor R5 was found in only two years (2001 and 2003) as was the virulence factor R9 (2001 and 2005).

The mean number of virulence factors per isolate was 6.7 ± 0.08 (mean, ±SE), but varied significantly ($F_7 = 7960$, $p < 0.0001$) between years. Complex races predominated in 2001 (8.4), 2002 (7.9) and 2004 (7.2) (Table 4). The most common race was 1.3.4.7.10.11 representing 59% of the studied strains and occurred in almost all study years, except in 2001 and 2004. The overall normalized Shannon diversity index was 0.27. The diversity index was highest in isolates from 2001 (0.92) (Table 5). The value of the normalized Shannon diversity index decreased significantly from 2003 to 2008 ($b = -0.68$, $R^2 = 0.465$, $F_{(7)} = 6.073$, $p = 0.04$).

Discussion

The frequency of mating types of *P. infestans* European populations has changed in recent years; several studies have reported a rapid increase in the proportion of the A2 mating type. The average percentage of 43% A2 mating type in the current study was higher than found in previous studies in Estonia in 2002–2003 (Runno-Paurson et al., 2009) and in 2004–2007 (Runno-Paurson et al., 2010 a). The average percentage of A2 mating type in years where both mating types were found (52%) is also high. Our results confirm the overall trend of an increase in A2 mating type within European populations. In Poland, A1 dominated in the years 2001–2004, but increase of the A2 mating type occurred in 2005–2006 with 66% of tested isolates being A2 (Sliwka et al., 2006; Lebecka et al., 2007). This trend continued in 2007–2009 with 73% of A2 mating type (Chmielarz et al., 2010). The same trend has been observed in the UK, where, since 2005, the proportion of A2 mating type isolates increased dramatically from their low occurrence in middle 1990s (Lees et al., 2009). A new genotype 13-A2 (also named 'Blue-13') was first found in the UK in 2005 and then spread very rapidly to comprise approximately 80% of population in 2008 (Lees et al., 2009). Similarly, in the Irish Republic and in Northern Ireland, the genotype 13-A2 has spread rapidly since 2007 (Kildea et al., 2010). In Finland,

the mean proportion of A2 mating type was quite low, approximately 18–23%, during 1993–1999 (Hermansen et al., 2000; Lehtinen et al., 2007), but a notable shift took place in 2000, when A2 became the dominant type (Lehtinen et al., 2007).

In the current study, mating types were studied over the six year period 2003–2008. Both mating types were detected in most (five out of six) of the studied plots. We found a consistent directional change in the proportions of A2 mating type increasing during this period. In 2003, the A2 mating type was not found. Thereafter, it increased to 18% in 2004 and then abruptly further to 73% in 2005. Since then, the proportion of A2 mating type has remained high. In four observed years, the ratio of the A1 and A2 mating types appeared to be close to 50:50, the most effective ratio for sexual reproduction. The constant A2 mating type prevalence in the current study is a clear indication of soil borne contamination with oospores. Based on this long-term study, it is clear that there is an increased risk of an early outbreak of late blight in this location, and these findings are not exceptional. Although good crop rotation is practised in these fields with potatoes planted only every three years, these results suggest that a longer interval between potato crops is needed. Chemical treatment of late blight was used only once or twice per growing season, and severe late blight infections were noticed in most years, except in 2006. Insufficient fungicide use may be an additional risk factor promoting increased oospore production, reducing the effectiveness of crop rotation (Lehtinen et al., 2007).

Sexual reproduction increases genetic diversity. The high genotypic diversity and rare genotypes found among Estonian populations of *P. infestans* have been observed in several studies (Runno-Paurson et al., 2009; Runno-Paurson et al., 2010 a). The high numbers of rare genotypes detected every year indicate that oospores may act as an infection source in commercial potato fields (Zwankhuizen et al., 2000). A cropping systems study by Runno-Paurson et al. (2010 b) showed that several aspects of pathogen diversity, such as genotypic diversity, race complexity and the diversity of mtDNA haplotypes, appeared to be highest in large conventional fields. Even though pathogen diversity tended to be higher in large conventional fields in our study, the plants were still more affected in organic fields and allotments. This can be important because continuous potato cropping in fields where the crop is not protected or control is insufficient as in small scale conventional and organic fields or allotments further increases the risk of oospore-derived infections and may cause earlier attacks and consequent yield loss (Runno-Paurson et al., 2009).

Table 3. Race frequencies among isolates of *Phytophthora infestans* from northern Estonia during 2001–2008

Year of isolation	Races	Number of virulence factors	Number of isolates
2001	1.2.3.4.5.6.7.8.9.10.11	11	1
	1.2.3.4.5.6.7.8.10.11	10	1
	1.2.3.4.6.7.8.9.10.11	10	1
	1.2.3.4.6.7.8.10.11	9	1
	1.2.3.4.5.7.8.10.11	9	2
	1.2.3.4.6.7.10.11	8	2
	1.2.3.4.7.8.10.11	8	2
	1.3.4.7.8.9.10.11	8	1
	1.2.3.4.7.10.11	7	1
	1.3.4.7.8.10.11	7	2
	1.2.3.7.10.11	6	1
	1.3.4.7.10.11	6	3
2002	1.2.3.4.6.7.8.10.11	9	2
	1.2.3.4.7.8.10.11	8	1
	1.2.3.4.6.7.10.11	8	3
	1.3.4.7.8.10.11	7	3
	1.3.4.7.10.11	6	2
2003	1.2.3.4.6.7.8.10.11	9	1
	1.2.3.4.5.6.7.10.11	9	1
	1.2.3.4.6.7.10.11	8	3
	1.2.3.4.7.10.11	7	1
	1.3.4.7.10.11	6	19
2004	1.2.3.4.6.7.8.10.11	9	1
	1.2.3.4.6.7.10.11	8	20
	1.3.4.7.8.10.11	7	1
	1.3.4.7.10.11	6	15
2005	1.2.3.4.6.7.9.10.11	9	1
	1.2.3.4.6.7.10.11	8	8
	1.3.4.7.9.10.11	7	2
	1.3.4.7.8.10.11	7	2
	1.2.3.4.7.10.11	7	1
	1.3.4.6.7.10.11	7	1
	1.3.4.7.10.11	6	19
2006	1.2.3.4.6.7.10.11	8	2
	1.2.3.4.7.10.11	7	1
	1.3.4.7.10.11	6	10
2007	1.2.3.4.6.7.10.11	8	3
	1.2.3.4.7.10.11	7	2
	1.2.4.6.7.10.11	7	1
	1.3.4.6.7.10.11	7	1
	1.3.4.7.10.11	6	41
2008	1.2.3.4.6.7.10.11	8	3
	1.2.3.4.7.10.11	7	4
	1.3.4.7.10.11	6	11
	1.2.4.7.10.11	6	1
		Total number of isolates	205
		Total number of races	18

Table 4. Frequencies of specific compatibility (virulence) to potato R genes in isolates of *Phytophthora infestans* from northern Estonia during 2001–2008

Virulence to resistance gene	Year of isolation							
	2001	2002	2003	2004	2005	2006	2007	2008
R1	100	89	76	86	97	81	100	91
R2	85	56	18	49	29	19	13	38
R3	100	89	76	86	97	81	98	86
R4	92	89	76	86	97	81	100	95
R5	31	0	3	0	0	0	0	0
R6	39	44	15	49	29	13	10	14
R7	100	89	76	86	97	81	100	95
R8	69	67	3	5	6	0	0	0
R9	23	0	0	0	9	0	0	0
R10	100	89	76	86	97	81	100	91
R11	100	89	76	86	97	81	100	91
The mean number of virulences/isolate	8.4^{a}	7.9^{ac}	6.5^{bc}	7.2^{ac}	6.7^{bc}	6.4^{bd}	6.2^{bd}	6.3^{bd}
Number of isolates tested	18	10	25	37	34	13	48	20

Note. [a] – values with different superscripts differ significantly (Turkey HSD test, $p < 0.05$) from each other.

Table 5. Racial diversity of isolates of *Phytophthora infestans* from northern Estonia during 2001–2008

Year	HS*
2001	0.92
2002	0.64
2003	0.26
2004	0.25
2005	0.37
2006	0.27
2007	0.16
2008	0.37
Total	0.27

* – the normalized Shannon diversity index for race diversity calculation

In the current study, the frequencies of virulence factors are similar to those reported recently in Estonia (Runno-Paurson et al., 2009; Runno-Paurson et al., 2010 a; Runno-Paurson et al., 2010 b) and in Denmark and Sweden (Lehtinen et al., 2008), except for virulence factor 9. The two most common races 1.3.4.7.10.11 and 1.2.3.4.6.7.10.11 were prevalent in almost all study years in the current study. Both races have also been common in recent years in Nordic (Lehtinen et al., 2008) and Russian populations (Vedenyapina et al., 2002; Zoteyeva, Patrikeeva, 2008). These two races represent 80% of the studied strains (Table 3), which is uncommon for Estonian population compared to previous studies (Runno-Paurson et al., 2009; Runno-Paurson et al., 2010 a), where race structure has been highly diverse.

The mean number of virulence factors per isolate was, on average, 6.7, similar to that found for the Estonian population in previous population studies in 2002–2003 (6.3, Runno-Paurson et al., 2009) and in 2004–2007 (6.6, Runno-Paurson et al., 2010 a). A decrease in the mean number of virulence factors per isolate over time was found. In 2001, 2002 and 2004, the mean number was very high (8.4, 7.9 and 7.2, respectively). In 2005, it decreased considerably and stayed low until the end. The predominance of complex races in these three years, together with very favourable conditions for late blight, could explain the early start of the epidemic and the severity of the infection. Subsequently, in 2006–2008, weather conditions were unfavourable for disease development and spread and therefore late blight emerged in potato fields at the end of August when most potato varieties had finished their growth. In such dry weather conditions apparently only a few strains survived over winter

and spread. *P. infestans* populations can go through narrow 'bottle necks' at the end of the season, especially when dry weather before harvest restricts tuber infections. Therefore, blight populations in a particular year can be quite different from those in the previous one if the genotypes that survive have had only a marginal role in epidemics of the previous year (Zwankhuizen et al., 2000).

Race diversity calculated by the normalized Shannon diversity index showed a very low value (0.27) compared to other results from Estonia in 2002–2003, 0.92 (Runno-Paurson et al., 2009) and in 2004–2007, 0.54 (Runno-Paurson et al., 2010 a). Still, considerable differences between years were found. The diversity index was much higher in the first two study years (2001 and 2002). This finding can be explained by collection year 2001 when most of the races were unique and found only once per season. In subsequent years, the diversity index decreased to extremely low levels and stayed quite low, varying between 0.16–0.37 during 2003–2008.

Conclusions

1. Both mating types were found at almost all the sampled fields in the study area confirming results from previous studies that there is great potential for sexual reproduction in Estonian potato fields.

2. The ratio of *Phytophthora infestans* A1:A2 mating types is suitable for sexual reproduction in northern Estonia and therefore could cause soil borne infections. The probable occurrence of oospore formation makes it important to apply crop rotation as a preventative measure in the current field areas.

3. Consistent directional change was found in the proportions of mating types over the study period.

4. Race diversity and the mean number of virulences per isolate were much higher in the first two sampling years of 2001 and 2002 than subsequently.

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Bulvių maro (*Phytophthora infestans* (Mont.) de Bary) fenotipų įvairovės pokyčiai šiaurinėje Estijoje

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Santrauka

Phytophthora infestans yra vienas svarbiausių bulvių patogenų pasaulyje, taip pat ir Estijoje. Esant palankioms sąlygoms, patogenas sukelia žalingą ligą – bulvių marą, kuris pirmiausia pasireiškia ant lapų, taip pat gali turėti neigiamą poveikį ir bulvių gumbams. *P. infestans* patogenas buvo izoliuotas iš bulvių lapų, surinktų 2001–2008 m. Estijos šiauriniame regione. Per šešerius metus (2003–2008 m.) tarp tirtų 180 izoliatų santykis tarp A1 ir A2 lytinio dauginimosi tipų buvo atitinkamai 57 ir 43 %. Nustatytas nuoseklus A2 lytinio dauginimosi tipo proporcijų pokytis, kurios tyrimų metais didėjo. Abu lytinio dauginimosi tipai buvo nustatyti beveik visuose laukuose, iš kurių imti ėminiai. Tyrimų rezultatai parodė, kad *P. infestans* A1 ir A2 lytinio dauginimosi tipų santykis yra palankus lytinei reprodukcijai. Rasių įvairovė, apskaičiuota naudojant *Shannon* įvairovės indeksą, buvo labai maža (0,27), tačiau tarp metų buvo nustatyti esminiai skirtumai.

Reikšminiai žodžiai: *Phytophthora infestans*, lytinio dauginimosi tipas, virulentiškumas, populiacijos pokyčiai.