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Genotypic Analysis of Russian Isolates of *Phytophthora infestans* from the Moscow Region, Siberia and Far East

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With one figure

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Abstract

Phytophthora infestans samples were collected during 1997 and 1998 at multiple sites in Russia from Sakhalin Island in the Far East across Siberia (nine sites, 160 isolates) to the Moscow region (four sites, 325 isolates). In addition, 12 isolates that were obtained previously were included. All isolates were analysed for mating type, and sensitivity to metalaxyl. Isolates from within any of the nine sites outside of the Moscow region were monomorphic for mating type and nearly monomorphic for metalaxyl resistance. In contrast, both A1 and A2 isolates were detected in the Moscow region, and these isolates were also polymorphic for metalaxyl resistance. In two sites in Siberia only A2 mating type strains were detected, in the other six sites in Siberia and in Sakahlin Island, only A1 mating types were detected. A subset of isolates ($n = 191$) was also analysed for pathotype (virulence to 10 R-genes, each in a distinct differential genotype). All isolates were highly complex (mean number of virulences approximately 8.4 of a maximum number of 10). All isolates ($n = 43$) from Sakahlin Island were virulent to all 10 of the R-genes tested. A further subset of isolates ($n = 70$, including 12 isolates collected before 1997) was analysed for genotype at the *Glucose-6-phosphate isomerase* and *Peptidase* loci, mtDNA haplotypes, and RFLP pattern using the RG57 probe. The US-1 clonal lineage (previously dominant) was not detected in the 1997–98 sample. The populations of *P. infestans* near Moscow in 1997 and 1998 was highly diverse with 15 unique genotypes (including both mating types) among a sample of 18 isolates. In contrast, the populations of *P. infestans* in Siberia had limited diversity, with only three multilocus genotypes detected and most populations were dominated by the SIB-1 clonal lineage. This lineage accounted for 31 of the 39 strains collected in Siberia that were assayed for multilocus genotype.

Introduction

Phytophthora infestans (Mont.) de Bary, the causal pathogen of the late blight disease of potato (*Solanum tuberosum* L.) and tomato (*Lycopersicon esculentum* Mill.) is the most damaging microbial pest of potato and tomato crops world-wide, especially in Russia and Eastern Europe. In the mid-1800 s, late blight caused wide-spread potato crop failures throughout Northern Europe, including Ireland where it was responsible for the Irish Potato Famine. In the last 150 years many changes in agriculture and plant pest control have significantly decreased crop losses due to late blight. For example, certified seed programmes, crop rotation, use of fungicides and grower education have all contributed to controlling losses in potato yields due to late blight. More recently, fungicides which are particularly effective against *P. infestans*, and plant breeding programmes, which select for late blight resistance in host plants have made great strides in controlling late blight in potatoes. Unfortunately, within the last 10–20 years *P. infestans* isolates resistant to metalaxyl (previously, one of the most effective fungicides) have been found and these strains have jeopardized the previous achievements.

These important changes in *P. infestans* populations have been observed in many potato-growing regions of the world over the last two decades. For example, in Europe before 1980, the US-1 clonal lineage was the predominant lineage (Fry et al., 1992; Goodwin et al., 1994), but more recently, other *P. infestans* genotypes

have replaced US-1. In such places as Poland and the Moscow region of Russia, US-1 has not been detected in field populations since 1988 and 1994, respectively (Sujkowski et al., 1994; Elansky, 2000). These changes in Europe were probably caused by the introduction of exotic strains of *P infestans*. These exotic strains probably originated from Mexico, which is considered to be the centre of origin of *P. infestans* (Goodwin et al., 1994). European *P. infestans* populations are currently highly diverse, having both A1 and A2 mating types and many different genotypes (Sujkowski et al., 1994; Elansky et al., 1999a,b; Maleeva et al., 1999). Furthermore, these new genotypes show virulence to a broader range of potato cultivars (Sujkowski et al., 1994).

There is now evidence from Poland and western Russia that new strains have been introduced and that oospores are being produced by *P. infestans* in the field (Bagirova and Dyakov, 1998; Smirnov and Elansky, 1999; Zarzycka and Sobkowiak, 1999). Although there is information regarding the changes in *P. infestans* populations in Europe and western Russia, similar information about Siberia and far eastern Russia is lacking. In this report, phenotypic and genotypic data is presented for *P. infestans* samples taken from multiple locations across Russia, including Siberia and into far eastern Russia.

Materials and Methods

Isolate collection

Isolates of *P. infestans* were collected in commercial fields of potatoes and tomatoes during 1997–98 at different locations across the Russian territory (Fig. 1). Only single, young, small lesions of late blight from tomato and potato were collected to reduce the possibility of isolating mixed genotypes. For purposes of comparison, 12 isolates collected previously (seven in 1995 and five in 1993) were included.

Phenotypic analyses

All isolates were characterized for mating type and resistance to the fungicide metalaxyl. Mating type was determined by growing the isolates together with tester strains of known mating type in a Petri dish containing oatmeal agar (i.e. each sample isolate was paired with known mating types, A1 and A2). Each pairing was assessed for oospore formation 10–15 days later, by microscopic examination. Isolates forming oospores on plates with the A1 mating type were registered as A2; isolates that formed oospores with the A2 mating type were registered as A1.

The sensitivity of *P. infestans* isolates to the phenylamide fungicide metalaxyl was evaluated in radial growth assays similar to that described by Matuszak et al. (1994). Each isolate was transferred to oatmeal agar medium supplemented with 0, 1, 10 or 100 mg active ingredient of metalaxyl per litre. Four agar plugs (3–6 mm in diameter) containing *P. infestans* were placed equidistant on each plate. The radial growth from each plug was recorded at 5 and 10 days after inoculation. The relative growth of each isolate growing in fungicide supplemented media was obtained by

Fig. 1 Locations of sampling sites

dividing the radial growth of the isolate growing in metalaxyl media by the radial growth of the same isolate growing in media without fungicide. The isolates were recorded as sensitive (S) when the relative radial growth at 10 mg/l metalaxyl was less than 10%. They were recorded as semi-resistant (SR) when the radial growth at 10 mg/ metalaxyl was greater than 10% but less then 40% of the growth without metalaxyl. Isolates were scored as resistant (R) when radial growth on medium with 10 mg/l was more than 40% of the growth without metalaxyl.

The specific virulence pathotype (compatibility with 10 specific R-genes) of each isolate was determined on a subset of the collection ($n = 191$) using detached leaflets. Different potato genotypes containing individual resistance genes were obtained from the International Potato Center in Lima, Peru. These potato genotypes were accessions: 702514 (no known R-gene), 800986 (containing gene, R1), 800987 (R2), 800988 (R3), 800989 (R4), 800990 (R5), 800991 (R6), 800992 (R7), 800993 (R8), 800995 (R10), 800996 (R11), 800997 (R1R2), 800998 (R1R3), 800999 (R1R4), 801000 (R2R3), 801001 (R2R4), and 801002 (R3R4). Leaflets were collected from the middle portion of plants at 6–8 weeks of age. Leaflets were placed in moist chambers with the abaxial surface uppermost, and inoculated with a suspension of a standardized concentration of sporangia ($0.5–1.5 \times 10^5$ sporangia/ml). The sporangia were obtained from cultures that were grown on oatmeal agar for 10–14 days at 16–20°C. Two drops (approximately 50 μl each) of the sporangial suspension were placed on each leaflet, and then incubated at 18°C. The interaction between the oomycete and each potato genotype was scored 5 to 6 days after inoculation. Each test included the susceptible cultivar 702514 (containing no known R-genes) as a control. Only data from tests in which the oomycete produced large, profusely sporulating lesions on the susceptible cultivar were used. Compatibility was defined as the ability of the isolate to produce large, profusely sporulating lesions on leaflets with R genes. An interaction was scored incompatible if the isolate did not grow, or gave a hypersensitive reaction. All virulence test experiments were repeated three times.

Neutral marker assessments

Fifty-eight of the isolates collected in 1997 and 1998 and the 12 isolates from previous collections were tested for genotype at the *Glucose-6-phosphate isomerase* (*Gpi*) *and Peptidase* (*Pep*) loci, for mitochondrial haplotype (mtDNA) and genomic DNA restriction length fragment polymorphism (RFLP) fingerprint using probe RG57. The genotypes at the *Gpi*, and *Pep* loci were analysed by cellulose acetate gel electrophoresis (Helena Laboratories, Beaumont, TX, USA) using the protocols published earlier (Fry et al., 1992; Goodwin et al., 1995). Tester genotypes included US-1 and US-8, which had *Gpi* genotypes of 86/100 and 100/111/122, respectively, and *Pep* genotypes of 92/100, and 100/100, respectively. It was difficult to distinguish between the 96/96 genotype and the 100/100 genotype for *Pep*. Consequently, only the 100/100 designation was used, but it might also include individuals of the 96/96 genotype.

RFLP analysis of the 70 isolates was performed using the RG57 probe (Goodwin et al., 1992). This probe recognizes a dispersed, moderately repetitive and highly polymorphic DNA element that allows the characterization of up to 30 different bands in a single hybridization experiment (Fry et al., 1992; Goodwin et al., 1992). Extraction of genomic DNA was according to the protocol described by Goodwin et al. (1992). DNA was digested with the restriction endonuclease *Eco*RI, and subjected to agarose gel electrophoresis and transferred to a nylon membrane (Amersham, Buckinghamshire, UK). Labelling and detection were carried out using the Renaissance non-radioactive detection kit as described by the manufacturer (New England Nuclear, Boston, MA, USA).

Identification of mtDNA haplotype was carried out for the 70 isolates using a variation of the method described by Griffith and Shaw (1998). This method allows for the detection of four mtDNA haplotypes (Ia, Ib, IIa, and IIb). The primers used for amplification of region P2 were F2 (5′-TTCCCTTTGTCCTCTACCGAT-3′) and R2 (5′-TTACGGCGGTTTAGCACATACA-3′), and primers F4 (5′-TGGTCATCCAGAGGTTTATGTT-3′) and R4 (5′-CCGATACCGATACCAGCACCAA-3′) were used to amplify the P4 region. The polymerase chain reaction (PCR) cycling programme used was the same for both primer combinations: 1 × (90°C for 9 min), 40 × (90°C for 30 s, 52°C for 30 s, 72°C for 90 s), 1 × (72°C for 5 min). For restriction enzyme analysis 10 μl of PCR reaction mix was mixed with 6 μl of water, 2 μl of the appropriate 10× Buffer, and 2 μl (10 units/μl) of enzyme. Digestions were performed at 37°C overnight. Ten microlitres of the digested DNA sample were loaded into a 2% agarose gel in 1× TAE buffer, containing 0.1 μl/ml ethidium bromide). The gel was run at 10 V/cm and restriction patterns were visualized using an UV-transilluminator.

Results

Phenotypic analyses

Of the 485 isolates, 160 were from Siberia and the Russian Far East and 325 were from the Moscow region (Fig. 1). In seven of the nine sites in Siberia and the Russian Far East, only A1 mating type isolates were collected (Table 1). In the other two sites only A2 mating type isolates were detected (Table 1). Both A1 and A2 mating type isolates were collected in the Moscow Region with A1 mating types accounting for 72 and 88% of the isolates from potato and tomato, respectively (Table 1). Most isolates from Siberia and the Russian Far East were highly resistant to metalaxyl (Table 1), and in some sites all isolates were highly resistant. In contrast, isolates from the Moscow region were polymorphic for metalaxyl resistance and fewer than 30% of the isolates were highly resistant to metalaxyl.

Table 1
Frequencies of A1 and A2 mating types and of metalaxyl resistance in isolates of *Phytophthora infestans* collected from different locations in Russia in 1997 and 1998

Sampling sites	Sakhalin	Vladivostok	Khabarovsk	Birobijahn	Chita	Irkutsk	Krasnoyarsk	Omsk	Ekaterinburg	MR[a](P)	MR[b](T)
Percentage of A1	100	100	0	0	100	100	100	100	100	72	88
Percentage of A2	0	0	100	100	0	0	0	0	0	28	12
Resistance to fungicide metalaxyl (% SR + R)	100	90	0	0	100	0	39	100	47	22	32
Number of tested isolates	57	10	25	4	7	9	18	15	15	168	157

[a]MR (P), Moscow region, isolates from potato;
[b]MR (T), Moscow region, isolates from tomato.

Isolates from all locations were very complex in terms of pathotype. Most isolates were compatible with (specifically virulent to) most R-genes. The mean number of specific virulence genes per isolate ranged from 5.5 for isolates from Birobijahn (these isolates were collected from tomato) to 10 (presence of all tested virulence genes) in isolates from Sakhalin Island (Table 2).

Neutral marker assessments

Analysis of 58 isolates for multilocus genotypes (*Gpi* and *Pep* loci, DNA fingerprint as determined by probe RG57 and mtDNA haplotype) revealed a highly clonal population structure in Siberia and the Russian Far East (Table 3). One multilocus genotype (identified here as SIB-1, Table 3) predominated or was present in several different locations, including Krasnoyarsk, Ekaterinburg, Irkutsk, Chita, Omsk, and Sakhalin Island (Fig. 1, Table 3). SIB-1 was the most widespread genotype in Siberia and the Russian Far East, accounting for 31 of the 40 individuals collected in 1997–98 from this region that were characterized. Another multilocus genotype (SIB-2) collected in Khabarovsk accounted for eight of the remaining nine individuals collected in 1997–98 and analysed for these neutral markers (Table 1). All isolates from Siberia and Russian Far East contained only the IIa mtDNA haplotype.

In contrast, *P. infestans* isolates collected from around the Moscow region were very diverse. For example, both mating types A1 and A2 were found at many locations in the sample from 1997 and 1998 in the Moscow region. Although only one genotype (100/100) at the *Gpi* locus was identified in all Moscow isolates collected in 1997 and 1998, three *Pep* genotypes, 92/92, 92/100, 100/100 were observed. Two mtDNA haplotypes, Ia and IIa, were detected in *P. infestans* isolates from the Moscow region collected in 1997–98. RFLP analysis using the RG57 probe identified many differences. From the 18 isolates collected in 1997–98 and subjected to full neutral marker analysis, there were 16 unique multilocus genotypes. When isolates collected previously (1993 and 1995) were included in the analysis, the number of distinct genotypes compared with the total number of isolates analysed rose to 23 unique genotypes among 27 isolates.

There was some polymorphism for metalaxyl resistance in the SIB-1 clonal lineage. For example, isolates of the SIB-1 genotype from Sakhalin Island were all resistant, but all SIB-1 isolates from Irkutsk were highly sensitive. There was also probably polymorphism in SIB-1 for metalaxyl resistance within isolates from Krasnoyarsk and from Ekaterinburg (Tables 1 and 3). For example only the SIB-1 clonal lineage was detected in these locations, but in the total sample there was polymorphism for metalaxyl resistance.

Discussion

Populations of *P. infestans* in the Moscow region differed markedly from those in Siberia and far eastern

Table 2
Frequencies of specific compatibility (virulence) to potato R-genes in isolates of *Phytophthora infestans* from different locations in Russia in 1997 and 1998

Sampling sites		Sakhalin	Vladivostok	Khabarovsk	Birobijahn	Chita	Irkutsk	Krasnoyarsk	Omsk	Ekaterinburg	MR[a]
Host plant		P[b]	P	P	T[c]	P	P	P	P	P	P
Virulence	R1	100	100	100	75	100	100	100	87	100	98
to	R2	100	100	92	25	100	100	100	80	93	98
resistance	R3	100	100	88	100	100	100	67	93	93	93
gene	R4	100	90	100	100	80	67	100	93	73	95
	R5	100	50	20	25	20	89	78	73	80	51
	R6	100	80	40	0	0	100	78	7	87	68
	R7	100	40	92	75	80	67	44	80	87	72
	R8	100	100	100	50	80	67	33	0	93	57
	R10	100	100	100	50	40	67	94	33	100	96
	R11	100	70	100	50	40	89	89	67	100	79
Mean number of virulences/isolate		10	8.3	8.3	5.5	6.4	8.4	7.8	6.2	8.9	8.1
Number of tested isolates		43	10	25	4	5	9	18	15	15	47

[a]MR, Moscow region; [b]P, potato; [c]T, tomato.

Table 3
Multilocus genotypes of isolates of *Phytophthora infestans* collected in different locations in Russia in 1997 and 1998

Genotype	Location	Mating type	*Gpi* genotype	*Pep* genotype	RG 57 fingerprint	mtDNA haplotype	No. of isolates
Isolates from potato							
SIB 1	many[a]	A1	100/100	100/100	100010001100110100011 0011	IIa	31
SIB 2	Khabarovsk	A2	100/100	100/100	100010000100110100011 0011	IIa	5
SIB 3	Vladivostok	A1	100/100	100/100	110010101000110100011 0011	IIa	1
MO 1	M1 (1997)[b]	A2	100/100	100/100	100010001100110100011 0011	IIa	1
MO 2	M1 (1997)	A2	100/100	100/100	100010000100110100011 0011	Ia	1
MO 3	M1 (1997)	A1	100/100	100/100	101010000100110100011 0011	IIa	1
MO 4	M1 (1997)	A1	100/100	92/100	101011101100110100011 0011	IIa	3
MO 5	M2 (1997)	A1	100/100	100/100	100010100100110101011 0011	IIa	1
MO 6	M2 (1997)	A1	100/100	100/100	101010100100110100011 0011	Ia	1
MO 7	M4 (1997)	A1	100/100	92/100	100010001100110000011 0011	IIa	1
MO 8	M4 (1997)	A1	100/100	92/92	101011000100110000011 0011	IIa	1
MO 9	M1 (1998)	A1	100/100	92/100	100010000100110100011 0011	IIa	1
MO 10	M2 (1998)	A1	100/100	100/100	101011000000110000011 0011	Ia	1
MO 11	M3 (1998)	A1	100/100	92/100	101010100100110000011 0011	Ia	1
MO 12	M3 (1998)	A2	100/100	100/100	101010100100110100011 0011	Ia	1
Isolates from tomato							
SIB 2	Birobijahn	A2	100/100	100/100	100010000100110100011 0011	IIa	3
MO 13	M2 (1997)	A1	100/100	100/100	101010100000110100011 0011	Ia	1
MO 14	M3 (1998)	A1	100/100	100/100	001010100100110000011 0011	Ia	1
MO 15	M3 (1998)	A1	100/100	100/100	011011100100110001011 0011	Ia	1
MO 16	M3 (1998)	A1	100/100	100/100	100010000000110100011 0011	IIa	1
Isolates from old collections							
US 1	M3 (1993)	A1	86/100	92/100	101010101100110100011 0011	Ib	2
SIB 1	several[c]	A1	100/100	100/100	100010001100110100011 0011	IIa	5
MO 17	M3 (1993)	A1	86/100	100/100	101010101100110100011 0011	Ib	1
MO 18	M3 (1995)	A1	100/100	100/100	101011100100110100001 0011	IIa	1
MO 19	M3 (1995)	A1	100/100	100/100	101010100000110101011 0011	IIa	1
MO 20	M3 (1995)	A2	100/100	100/100	101010100000110100011 0011	IIa	1
MO 21	M3 (1995)	A2	100/100	100/100	101010100000110001011 0011	IIa	1

[a]Genotype SIB-1 was detected in:: Sakhalin, Omsk, Vladivostok, Chita, Irkutsk, Krasnoyarsk, Ekaterinburg (Fig. 1);
[b]'M' refers to Moscow region with each of four sites identified in Fig. 1. The year of collection is identified in the parentheses;
[c]SIB-1 had been detected in the Moscow region in 1993 (three isolates), and in Tomsk (Fig. 1) in 1995 (two isolates).

Russia. Populations were very diverse near Moscow, with nearly each isolate (16 of 18) in the small sample having a unique multilocus genotype. Thus, this study extends and confirms an earlier report (using mating type and allozymes as markers) of high diversity in *P. infestans* populations in the Moscow region (Elansky et al., 1999a). When data from previously collected isolates were added to the current study, only the SIB-1 and US-1 clonal lineages were not unique in the Moscow Region. In contrast, isolates collected in Siberia and the Russian Far East were primarily of the SIB-1 clonal lineage. A second lineage (SIB-2) was also

detected several times in Siberia. SIB-1 was found all along the Trans-Siberian railway, and SIB-2 was found in the Russian Far East near the Chinese border (Birobijahn and Khabarovsk, Fig. 1). Isolates with the same multilocus genotype as SIB-1 and SIB-2 were also detected in the Moscow region. There was one isolate from Vladivostock, which was the SIB-3 genotype (the only occurrence of this genotype). The most common method of transporting potatoes across Russia is by rail, which most likely helped spread SIB-1 over such a huge territory.

There are probably two factors contributing to the high levels of diversity in the Moscow region. First, it seems highly likely that there have been introductions of 'exotic' strains of *P. infestans* to this region: the US-1 lineage that was previously dominant is now no longer dominant, and was not detected in the samples of 1997 and 1998. The mechanism of introduction is not known with certainty, but the constant importation of tomato fruits and potato tubers to Moscow from various locations around the world provides ample opportunity for introduction. Second, sexual reproduction probably contributes to this high level of diversity. There is direct evidence that *P. infestans* matings are occurring in the Moscow region, because oospores have been detected in field samples (Bagirova and Dyakov, 1998; Smirnov and Elansky, 1999). Oospores not only add to the genetic diversity in a population, but can act as a source of inoculum that can over-winter and infect the potato or tomato crop in the following year. Thus, the combination of imported genotypes and *P. infestans* sexual reproduction has appeared to make the Moscow region the centre of *P. infestans* diversity in Russia.

Isolates from across Russia were complex in their pathotype. The mean number of specific virulences in isolates from different locations ranged from 5.5 in Birobijahn to 10 in isolates from Sakhalin Island. (The maximum number of specific virulences that were detected was 10.) The present data are also consistent with the expectation that specific resistance genes are probably selecting compatible individuals in the pathogen population. Resistance genes R-1, R-2, R-3, and R-4 are currently deployed in Russian potato cultivars. The frequency of compatibility to these four resistance genes was 0.92. In contrast, the frequency of compatibility to resistance genes R-5, R-6, R-7, R-8, R-9, and R-11 was 0.69. There was no relationship between pathotype and genotype as determined by neutral markers.

The present results confirm that metalaxyl resistance is under strong selection pressure. All isolates from Sakhalin Island had high levels of resistance to metalaxyl, and metalaxyl has been used there intensively. However, in the Moscow region, the frequency of isolates with high levels of resistance has declined in comparison with earlier periods. Metalaxyl-resistant strains predominated in the Moscow region when the fungicide was widely used at the end of the 1980s and the beginning of the 1990s (Elansky et al., 1999a,b). Since that period, the use of metalaxyl has decreased significantly, mainly for economic reasons, and in turn the frequency of highly resistant individuals has also declined, and in 1999 typically only 20–30% of isolates in the Moscow region were highly resistant (Elansky et al., 1999a,b).

In summary, over the last decade there have been significant changes in *P. infestans* genotypes throughout Russia. The situation appears to be more dynamic and diverse in the potato- and tomato-growing regions around Moscow than in Siberia or far eastern Russian. This may be due to a number of factors, including more ready excess to foreign imports (Moscow is and has been a trade centre for centuries), and the earlier introduction of A2 mating types into the Moscow region. Both mating types are common in the Moscow region, whereas populations were monomorphic for mating type in locations across Siberia and far eastern Russia. There seems to be no evidence for sexual reproduction occurring in Siberian and far eastern *P. infestans* populations. The common practice of using local seed tubers in these areas helps to maintain a more constant gene pool of the pathogen. It should be noted that the US-1 lineage was present in Ekaterinburg in 1990 (Goodwin et al., 1994), but has since been replaced by SIB-1. Thus, it is important to continue to monitor the genotypic changes in *P. infestans* populations across Russia, so that migration and evolution of the late blight pathogen in one of the largest potato-growing regions of the world can be understood and better managed.

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