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Phenotypic variation in Nordic populations of *Phytophthora infestans* in 2003

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A total of 743 single-lesion isolates of *Phytophthora infestans* were collected in summer 2003 from Denmark, Finland, Norway and Sweden. Most of the isolates were tested for mating type, and subsets were tested for sensitivity to fungicides and virulence (host specific pathogenicity). Approximately 60% of the isolates were A1 mating type in each country. Both mating types were present in 40% of the fields where more than one isolate was tested, indicating strong potential for sexual reproduction. The proportion of metalaxyl-resistant isolates dropped to under 15% from the 60% observed in the early 1990s in Norway and Finland, possibly due to lower selection pressure because of decreased use of metalaxyl. Propamocarb-HCl sensitivity remained unchanged in the Nordic countries compared to the situation in 1997–2000 in Finland. Four isolates collected from Finland and Sweden were able to sporulate in the presence of this fungicide at a concentration of 1000 mg L^{-1}. In Norway and Finland the frequencies of virulence factors and pathotypes remained nearly unchanged since the 1990s, but the mean number of virulence factors per isolate increased from 5·6 to 6·3. In Denmark and Sweden virulence factors 2 and especially 6 were more common than in Norway and Finland. In addition, in the Swedish population the frequencies of pathotypes were quite even while in other countries pathotype 1,3,4,7,10,11 was most prevalent.

Keywords: mating type, metalaxyl resistance, pathotype, potato late blight, propamocarb-HCl resistance, virulence

Introduction

Potato late blight caused by the oomycete *Phytophthora infestans* is a severe disease of potato. Under favourable conditions it can kill unprotected potato haulm in a couple of weeks. In addition, rain can spread sporangia from affected foliage to tubers and cause tuber blight. In the Nordic countries it is common for late blight to cause a 50% yield reduction in unprotected fields due to a shorter growing season and rotted tubers. Therefore fungicides are used routinely in commercial potato production.

The main initial sources of late blight inoculum are considered to be infected tubers which survive to the next season in cull piles, storage or soil (Zwankhuizen *et al*., 1998). A new primary source of inoculum appeared in Europe when the old clonal lineage of *P. infestans* was replaced by a new more diverse population during the 1980s (Goodwin, 1997). The new population possesses both mating types and is able to reproduce sexually in potato in the Nordic countries (Brurberg *et al*., 1999; Hermansen *et al*., 2000). Sexual reproduction results in oospores which can overwinter in soil (Andersson *et al*., 1998; Lehtinen & Hannukkala, 2004).

Sexual reproduction has further increased the high evolutionary potential of *P. infestans* (McDonald & Linde, 2002). However, *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 during one season can be quite different from the previous one if the genotypes that survive have had only a marginal role in epidemics of the previous year (Zwankhuizen *et al*., 2000). High reproductive potential during an epidemic allows migrating genotypes to become common or even dominate the population during a season. The

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Country	Fields	Isolates[a]	Mating type	Sensitivity to metalaxyl	Sensitivity to propamocarb-HCl	Virulence
DK	61	61	49	57	57	39
FI	94	264	217	251	251	42
N	117	329	328	75	75	50
S	48	89	88	74	74	46
Total	320	743	682	457	457	177

Table 1 Number of fields sampled, and isolates of *Phytophthora infestans* collected and tested for mating type, sensitity to fungicides metalaxyl and propamocarb-HCl, and virulence in Denmark (DK), Finland (FI), Norway (N) and Sweden (S)

[a]The number of isolates tested within a country varies from the number collected due to difficulties in culturing in the individual tests.

latter, together with high phenotypic diversity, makes *P. infestans* 'a moving target' (Cooke & Lees, 2004) for the resistance breeders and chemical companies. Thus there is a need to frequently monitor phenotypic changes in *P. infestans* populations to decide the best control strategies.

In this study Nordic *P. infestans* populations were characterized for mating type, sensitivity to metalaxyl and propamocarb-HCl and virulence, to answer the following questions: (i) does the mating type ratio, and in particular the frequency of fields with both mating types, suggest occurrence of sexual reproduction?; (ii) what is the population level of metalaxyl and propamocarb-HCl sensitivity?; (iii) which R-genes are the Nordic *P. infestans* populations able to overcome?; and (iv) do populations in Nordic countries differ from each other with respect to phenotypic characteristics?

Material and methods

Sampling and isolations

During summer 2003, 743 isolates of *P. infestans* were collected from 320 potato fields (both conventional and organic production) in the four Nordic countries (Table 1). Isolates were collected early in the epidemic. Three to six leaflets, each with one single lesion, were collected to achieve at least one pure isolate from each field.

Isolations were made by trapping *P. infestans* from a piece of sporulating tissue (5 mm in diameter) cut from the margin of leaf lesion and placing it abaxial side up under a tuber slice (cv. Bintje in Denmark, Sweden and Finland, and cv. Laila in Norway) in a Petri dish. Tuber slices were incubated 4–7 days at 18°C. Small pieces of mycelium were collected from the upper side of the potato slice and transferred to agar medium. Media used differed between the countries. For isolation, rye B media (Caten & Jinks, 1968) amended with 0·2 g L^{-1} ampicillin and 10 mg L^{-1} pimaricin was used in Sweden, and a mixture (50/50) of pea agar (protocol from Corbiére & Andrivon, 2003) and rye B agar in Norway and Denmark. After isolation, rye B agar without antibiotics was used in Sweden, pea agar in Norway and a mixture of pea and rye agar in Denmark. In Finland only modified rye medium without antibiotics was used (Hermansen *et al.*, 2000).

All phenotypic tests were carried out between August 2003 and July 2004. Each participating group determined the mating type of their own isolates. One isolate per field was selected for other phenotypic tests which were carried out in MTT, Agrifood Research Finland. Most of the Finnish isolates and up to 75 isolates from each of the other countries were tested for sensitivity to fungicides and a subset of these for virulence (Table 1).

Mating type determination

The mating type of the isolates was determined by pairing them with Dutch reference isolates 90209 (A1) and 88055 (A2) obtained from Cyanamid Forschung GmbH, Germany in separate plates of rye agar (pea agar in Norway) described by Gallegly & Galindo (1958). After 2–4 weeks incubation the presence/absence of oospores was recorded under the light microscope.

Fungicide resistance tests

The sensitivity to metalaxyl and propamocarb-HCl of the isolates was assessed by a floating leaf disc method (Sozzi *et al.*, 1992; Hermansen *et al.*, 2000). Six leaf discs (cv. Bintje) were floated abaxial side up in Petri Plates (50 mm diameter) each containing 7 mL distilled water, metalaxyl-M (Novartis experimental compound (metalaxyl-M), CGA 329351) at concentrations of 1·0, 10·0 and 100·0 mg L^{-1} a.i., or propamocarb-HCl (Previcur N, Batch number 03445549, Schering AG) at concentrations of 10, 100 and 1000 mg L^{-1} a.i. Sporangia were harvested from the leaflets in distilled water. Leaf discs were inoculated with a 20 μL droplet of the sporangial suspension (1×10^4–2×10^4 sporangia mL^{-1}). After seven days incubation on greenhouse benches at 15–18°C the area covered with sporangiophores was estimated as percentage of total area of the leaf disc. The test was repeated if less than four out of six leaf discs per plate containing distilled water produced sporulating lesions. Isolates sporulating on the discs floating on water containing 100 mg L^{-1} metalaxyl-M were rated resistant, those on 1 or 10 mg L^{-1} were rated intermediate and those that sporulated only on water were rated sensitive. The highest concentration of propamocarb-HCl where sporangiophores were observed on the discs was considered to be the concentration which that isolate could tolerate.

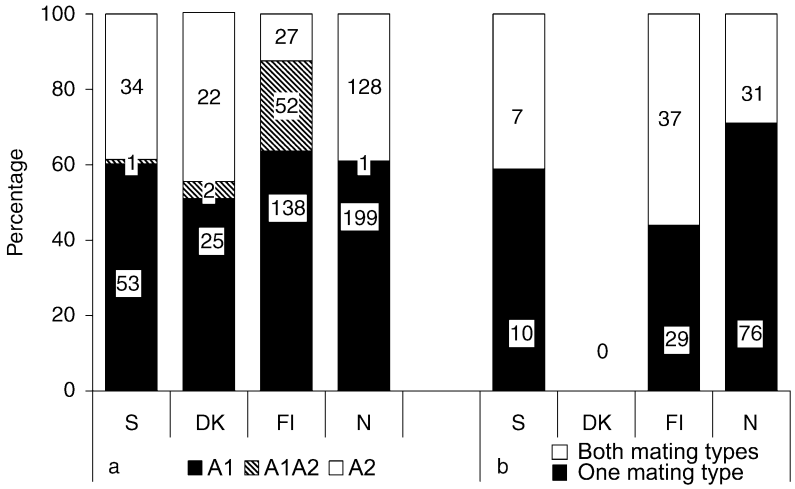

Figure 1 (a) Percentages of mating types (A1, A2 or A1 and A2) among all *Phytophthora infestans* isolates in 2003 in Sweden (S), Denmark (DK), Finland (FI) and Norway (N). (b) Proportion of fields with only one or both mating types present, when more than one isolate per field was tested. Figures in the bars indicate number of fields.

Assessment of virulence spectrum

Black's R-gene differential set including single R-gene clones R1-R11 and the universally susceptible clone R0 (provided by Scottish Agricultural Science Agency (SASA), Edinburgh, UK), was used to determine the virulence (host specific pathogenicity) profile of the *P. infestans* isolates. Plants were propagated *in vitro* and planted as microplants in the greenhouse under natural day light supplemented with artificial light (Airam HgMT-D 400W, 16 h photoperiod) in 16–18°C. Fully or nearly fully expanded leaflets were picked from plants at 7–9 weeks. Inoculation and incubation of the Petri dishes was performed as in the fungicide tests above. After seven days incubation the interaction was considered compatible if sporangiophores were clearly visible to the naked eye. A test was repeated if less than four out of six leaf discs produced sporulating lesions on the susceptible clone (R0). Mean number of virulence factors per isolate (C_i) and pathotype (C_p) were calculated as described by Andrivon (1994).

Statistical analysis

Logistic regression was used to derive odds ratios with 95% confidence intervals for all studied response variables as a function of country. The rationale for using logistic regression and odds ratios has been discussed elsewhere (Lehtinen *et al.*, 2007). Sweden was selected as the reference country because it is situated between the other countries studied. Suppose x is a vector of indicator variables (country), and p is the predicted response probability to be modelled. The linear logistic model used was thus

$$\text{logit}(p) = \alpha + \beta' x$$

where α is the intercept parameter and β is the vector of regression coefficients. The analyses were performed by the SAS/LOGISTIC procedure in SAS/STAT version 9 (SAS Institute Inc., Cary, NC, USA). The statistical significance of the grouping by country was tested with likelihood ratio tests, and 95% confidence intervals were calculated for the odds ratios of the different outcomes (Yuen, 2006).

Results

Mating types

The proportion of A1 mating type was nearly the same (51–64%) in all countries (Fig. 1a). In contrast the proportion of A2 was significantly smaller in Finland (Table 2) because of the large number of isolates that produced oospores with both tester isolates. In the other countries, isolates capable of mating with both mating type testers were rare. Both mating types were present in 29–56% of the fields where more than one isolate was tested, indicating strong potential for sexual reproduction (Fig. 1b). The proportion of fields with both mating types varied considerably between the countries (Fig. 1b), being highest in Finland and lowest in Norway. This variation was significant (Table 2).

Sensitivity to metalaxyl and propamocarb-HCl

On average 6% of all tested isolates were resistant to metalaxyl (Fig. 2). The highest frequency of resistant isolates was found from Sweden (13%) and Norway (12%), while in Finland only 2% of the isolates were resistant. The difference between Sweden and Finland was also statistically significant (Table 2). Interestingly, no isolates with intermediate resistance were found from Sweden where resistance was most common.

There was no association between metalaxyl sensitivity and mating type over all countries and the proportion of metalaxyl resistant isolates was the same among A1 and A2 isolates. It was decided not to investigate the association within the countries due to low number of resistant isolates per country (max. 10). However, in Norway eight of nine metalaxyl resistant isolates were A1 mating type.

Prevalence of A2 mating type over A1	Odds ratio (95% CI)[a]	*P*-value[b]
S	1·00	< 0·001
DK	1·37 (0·67–2·81)	
FI	0·30 (0·17–0·55)*	
N	1·00 (0·62–1·63)	
Occurrence of both mating types in the same field		
S	1·00	< 0·001
DK	nt[c]	
FI	1·97 (0·64–6·08)	
N	0·59 (0·19–1·78)	
Prevalence of metalaxyl resistant isolates		
S	1·00	< 0·005
DK	0·36 (0·09–1·36)	
FI	0·16 (0·05–0·45)*	
N	0·87 (0·33–2·29)	
Prevalence of isolates tolerating at most 10 mg L^{-1} of propamocarb-HCl		
S	1·00	0·04
DK	0·81 (0·33–2·00)	
FI	0·44 (0·22–0·86)*	
N	0·44 (0·20–0·96)*	

Table 2 Odds ratios for prevalence of A2 mating type of *Phytophthora infestans*, occurrence of both mating types in the same field, prevalence of metalaxyl resistance, and prevalence of isolates tolerating at most 10 mg L^{-1} of propamocarb-HCl in Denmark (DK), Finland (FI) and Norway (N) in relation to Sweden (S)

[a]95% confidence intervals are based on the Wald estimate of the variance of the comparison of the named country with Sweden, and are significant at a *P* value of 5% if this confidence interval does not contain 1 (marked with an asterisk).
[b]*P*-value for a likelihood ratio test that compares all countries simultaneously. This test can indicate that there is a statistically significant difference among the countries even if the confidence interval estimates indicate that there is no country which differs significantly from Sweden. In this case the significant difference will occur at least between countries with smallest and largest odds ratio.
[c]Not tested, because only one isolated was collected per field in Denmark.

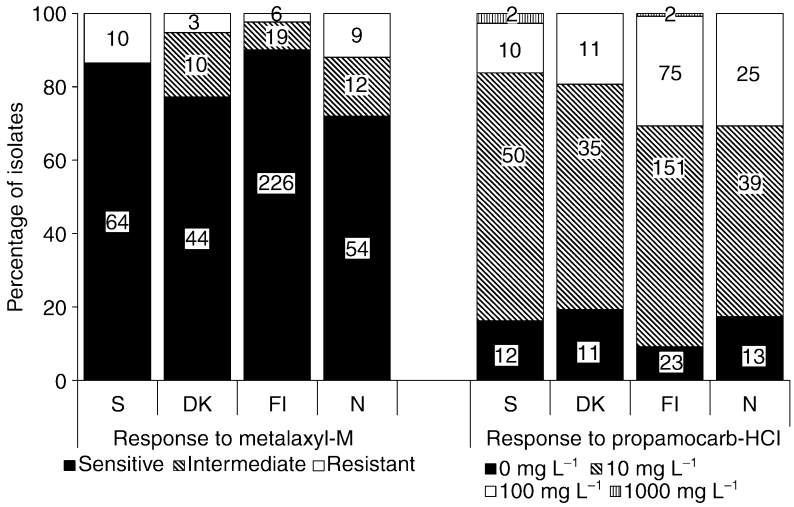

Figure 2 Response to metalaxyl (sensitive, intermediate or resistant) and propamocarb-HCl (0, 10, 100 or 1000 mg L^{-1}) among the *Phytophthora infestans* isolates collected from Sweden (S), Denmark (DK), Finland (FI) and Norway (N). Figures in bars indicate number of isolates.

Differences in resistance towards propamocarb-HCl were small between Nordic countries (Fig. 2). Only four isolates (two from Sweden and two from Finland) were able to sporulate in the presence of propamocarb-HCl at a concentration of 1000 mg L^{-1}.

Virulence

Virulence factors clearly segregated into three classes: common virulence factors with frequencies of 86–100% of isolates, rare with mean frequency 10–30%, and absent. Virulence to R9 was not found (Fig. 3). Pathotype 1,3,4,7,10,11 was the most common in all countries except Sweden (Table 3). The most common pathotype in Sweden was 1,2,3,4,7,10,11 which was also the second common pathotype in Finland. However, this pathotype was rare in Denmark and absent in Norway. The rare virulence factors were only found in complex pathotypes. The number of virulence factors per isolate or pathotype was both 6·6. There were no marked

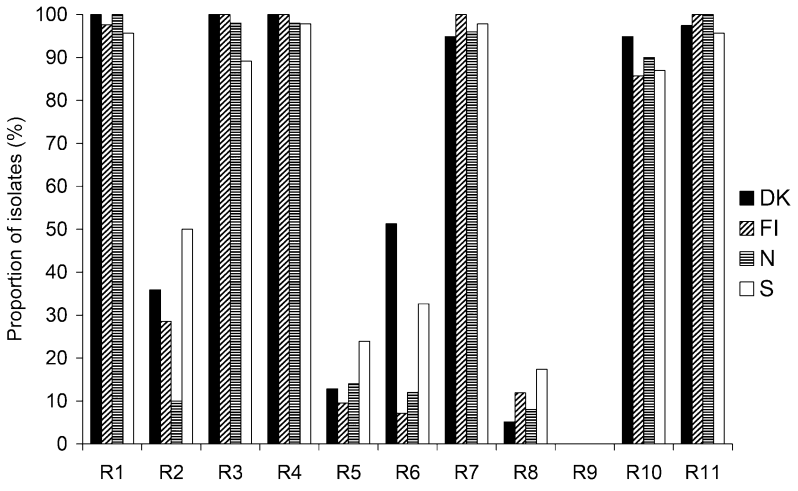

Figure 3 Percentage of *Phytophthora infestans* isolates capable of overcoming eleven major resistance (R) genes in Denmark (DK), Finland (FI), Norway (N) and Sweden (S).

differences in pathotype complexity between countries (Table 4).

Discussion

The main motivation for studying mating types of the Nordic isolates of *P. infestans* was to verify if the potential for sexual reproduction is present in the Nordic populations. The common occurrence of both mating types in the fields and the nearly even mating type ratio suggests the presence of sexual reproduction. Actual frequency of fields with both mating types present was certainly higher than observed, since an average of only three isolates per field were analysed for mating type and in 85% of the fields less than four isolates were analysed. The data from 2003 indicate that the potential for sexual reproduction was much greater in all four Nordic countries than in most of the European countries that have been studied (Gisi & Cohen, 1996; Lebreton & Andrivon, 1998; Knapova & Gisi, 2002; Cooke *et al*., 2003; Day *et al*., 2004; Cooke *et al*., 2006) and were similar to the Netherlands (Zwankhuizen *et al*., 2000). When more than one isolate was collected from each field in Norway and Finland in the 1990s, 36–64% of the fields had both mating types present in the two countries (Hermansen *et al*., 2000; Lehtinen *et al*., 2007). This supports data from previous studies conducted in Norway, Sweden and Finland indicating that oospores are formed in the fields, survive in soil to the next season in Nordic environmental conditions, and are still capable of causing infections the following season (Andersson *et al*., 1998; Hermansen *et al*., 2000; Lehtinen & Hannukkala, 2004; Widmark *et al*., 2007). Oospores can remain viable in the soil for four years (Andersson *et al*., 1998; Turkensteen *et al*., 2000). Hannukkala *et al*. (2007) studied the time of onset of epidemics, comparing potato crops where the previous crop had also been potato with those that had a different crop. They found that a previous crop of potato would advance the epidemic by an average of nine days. These data are also consistent with a soil-borne source of inoculum.

Table 3 Number of *Phytophthora infestans* isolates possessing particular pathotypes in Denmark (DK), Finland (FI), Norway (N) and Sweden (S)

Pathotype	DK	FI	N	SE	Total
R1,3,4,7,10,11	15	18	30	5	68
R1,2,3,4,7,10,11	2	9		10	21
R1,2,3,4,6,7,10,11	7	1	2	4	14
R1,3,4,6,7,10,11	6		1	3	10
R1,3,4,7,11		3	3	3	9
R1,3,4,5,7,10,11		3	4	1	8
R1,3,4,7,8,10,11		3	3		6
R1,2,3,4,5,6,7,10,11	3		2	1	6
R1,4,7,10,11				3	3
R1,3,4,5,6,7,8,10,11			1	2	3
R1,4,7,11			1	1	2
R1,3,4,6,7,8,10,11	1	1			2
R1,3,4,5,6,7,10,11				2	2
R1,3,4,11	1		1		2
R1,2,3,4,7,8,10,11		1		1	2
R1,2,3,4,5,7,8,10,11				2	2
R1,2,3,4,5,6,7,8,10,11	1			1	2
R1,2,3,4,10,11			1	1	2
R1,3,7,10,11			1		1
R1,3,6,7,10,11				1	1
R1,3,4,7,10	1				1
R1,3,4,6,7,8				1	1
R1,3,4,6,7,11	1				1
R1,3,4,5,7,11		1			1
R1,2,4,5,7,10,11				1	1
R1,2,3,4,6,7,11		1			1
R1,2,3,4,5,7,10,11				1	1
R1,2,3,4,5,6,10,11	1				1
R,3,4,7,11		1			1
R,3,4,7				1	1
R,2,3,4,7,8,10,11				1	1
Total	39	42	50	46	177

In Finland the prevalence of A2 was significantly smaller ($P < 0{\cdot}001$) in 2003 than in 2000 as indicated by logistic regression. In 2000, A2 isolates were more common than had ever previously been observed in Finland.

Table 4 Pathotype complexity of four Nordic populations of *Phytophthora infestans* measured as number of virulence factors per isolate (C_i) or pathotype (C_p)

Country	C_i	C_p
S	6·87	6·90
DK	6·92	6·27
FI	6·40	6·64
N	6·26	6·42
All	6·60	6·61

Isolates capable of mating with both tester isolates were rare in all countries except in Finland where their proportion was 24%. Before 1998self-fertile isolates were observed only occasionally (Hermansen *et al*., 2000), but since then their proportion has been over 10% (Lehtinen *et al*., 2007). Fyfe & Shaw (1992) have shown that the self-fertile isolates they studied were in most cases mixtures of A1 and A2 hyphae. In another study, most of the A2 isolates were capable of producing oospores in single individual cultures depending on the growth media used (Smart *et al*., 2000). In this study, the isolates were taken from single lesions, but single spore or hyphal tip cultures were not produced. If the observed self-fertile isolates were mixtures, then this must have been due to mixtures in the original lesion, or it is the result of contamination.

In the early and mid 1990s approximately 60% of the isolates were resistant to metalaxyl in Norway and Finland (Hermansen *et al*., 2000). From 1997 to 2000 metalaxyl resistance decreased from 40% to 17% in Finland (Lehtinen *et al*., 2007). In the present study the proportion of metalaxyl resistant isolates decreased to 2–13% in the four Nordic countries. The difference between results for 1997–2000 and 2003 in Finland was statistically significant as indicated by logistic regression ($P < 0{\cdot}001$). One likely reason for the reduction is lowered selection pressure due to decreased use of metalaxyl. The proportion of metalaxyl products has remained under 10% of all fungicides used against blight since 1993 in Finland (reviewed in Hannukkala *et al*., 2007) while in Sweden the proportion has been approximately 15%. In Norway the use of metalaxyl-M was limited and it was recently withdrawn. In Denmark it is not registered for commercial use. In other European countries the proportion of metalaxyl resistant isolates has been higher during the 1990s and early 2000s than in any Nordic countries in 2003 (reviewed in Gisi & Cohen, 1996; Cooke *et al*., 2003; Day *et al*., 2004). In Ireland the proportion of metalaxyl resistant isolates during 1995–1996 was similar to the Nordic countries (Carlisle *et al*., 2001; Griffin *et al*., 2002), but it was clearly higher thereafter in Northern Ireland (Cooke *et al*., 2006).

During the 1990s metalaxyl resistance was clearly associated with the A1 mating type in many European countries including Norway and Finland (Gisi & Cohen, 1996; Hermansen *et al*., 2000; Day *et al*., 2004; Cooke *et al*., 2006; Lehtinen *et al*., 2007). In 2003 this was not evident any more as the proportion of metalaxyl resistant isolates was the same among A1 and A2 isolates when looking at all the countries together. The result was expected because sexual reproduction (if present) should break any associations unless the genes for resistance and mating type are closely linked. In Norway metalaxyl resistance remains associated with the A1 mating type, but only a small number of resistant isolates were recorded. Interestingly, occurrence of both mating types in the same field was also less frequent in Norway than in Finland and Sweden. Thus sexual reproduction, to the extent that it takes place, may be less frequent in Norway compared to the other countries, and may have been inadequate to break the association between metalaxyl resistance and mating type in Norway.

Propamocarb-HCl sensitivity remained unchanged in Finland when compared to the situation in 1997–2000 (Lehtinen *et al*., 2007). Due to the infrequent (less than 10%) use of products containing propamocarb-HCl the selection pressure has been quite low in all Nordic countries (reviewed by Hannukkala *et al*., 2007). Therefore the risk of accumulation of propamocarb-HCl resistance in the Nordic population is low, although four isolates from Sweden and Finland were capable of sporulation when exposed to 1000 mg L^{-1} propamocarb-HCl. Bardsley *et al*. (1998) noticed that sporangia formed on leaf discs floated on 500 mg L^{-1} of propamocarb-HCl were not capable of infecting potato leaves, but infectivity of the resistant Finnish and Swedish sporangia was not investigated.

Isolates of *P. infestans* virulent to R1, R3, R4, R7, R10 and R11 dominated the populations in all four countries, similar to the 1990s in Finland and Norway (Hermansen *et al*., 2000), Finland (Lehtinen *et al*., 2007), France (reviewed in Pilet *et al*., 2005), France and Switzerland (Knapova & Gisi, 2002), Scotland (Cooke *et al*., 2003) and 1999–2001 in Morocco (Achbani *et al*., 2005). Frequency of virulence to R2 increased more than 20% in Finland when compared to earlier studies (Hermansen *et al*., 2000; Lehtinen *et al*., 2007). The pathotype possessing virulence factors to these six R-genes was clearly the most common one in all studied Nordic countries except in Sweden, although the most common Swedish isolate contained virulence to these six R-genes in combination with virulence to R2. Rare virulence factors appeared in complex pathotypes which has also been typical for other surveys. In Denmark and Sweden virulence to R2 and especially R6 were more common than in Norway and Finland. In Sweden, the use of the cv. Escort possessing R1, R2, R3 and R10 may have caused accumulation of virulence to R2 in the *P. infestans* population there. Interestingly none of the isolates possessed virulence to R9. This is probably due to a lack of selection pressure because it is understood that R9 has never been introduced into commercial cultivars. It was also interesting that the mean number of virulence factors per isolate increased from 5·3 and 5·8 in Norway and Finland, respectively, in the early 1990s to approximately 6·3 in 2003.

It is likely that sexual reproduction takes place in the *P. infestans* population in Nordic countries. This is supported by the presence of both mating types in all countries studied, and in a number of fields where multiple samples were taken. Resistance to both metalaxyl and propamocarb-HCl can be found, although the prevalence of metalaxyl resistance has markedly decreased compared to earlier studies. Virulence factors corresponding to most known R-genes are present, except for virulence to R9. While the populations in the different countries are not identical, they resemble each other in that both mating types are present, and fungicide resistance levels and the number of virulence factors are similar. This phenotypic variation is consistent with regular sexual reproduction within this pathogen population and this should be considered in future disease control strategies.

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