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Impact of new populations of *Phytophthora infestans* on integrated late blight management

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Summary

A recent migration of a variable population of *P. infestans* has largely displaced the clonal A1 population in Western Europe. Sexual reproduction in European late blight populations is now possible and has been reported. The increased levels of aggressiveness form an important epidemiological feature of this new blight population. The impact of 'new blight' on crop protection strategies based on late blight resistant cultivars and fungicides is discussed.

Introduction

The oomycete *Phytophthora infestans* (Mont.) de Bary, the cause of late blight in potatoes and tomatoes, is considered to be among the most important pathogens of potato crops worldwide (Hooker, 1981). The pathogen is feared by farmers around the globe due to its ability to quickly destroy entire fields of potatoes and tomatoes. The pathogen affects foliage and stems, reducing the photosynthetic capacity of the crop and therefore leading to tuber yield reduction. In addition, *P. infestans* can infect fruits and tubers, which adds to total losses in marketable yield. These days, crop losses due to late blight have been estimated to account for 10 to 15 percent of the total global annual potato production (Anonymous, 1996). The economic value of the crop lost, plus the costs of crop protection amount to 3 billion US $ annually (Duncan, 1999).

In the developed world, control of potato late blight is heavily dependent on the use of fungicides. Despite frequent fungicide use, late blight epidemics have proven to be increasingly more difficult to control (Turkensteen *et al.*, 1997; Schepers, 2000).

Resurgence of the late blight pathogen

The increased problem with controlling potato late blight coincides with the displacement of the US-1 clonal lineage by a new, more variable *P. infestans* population in many parts of the world (Spielman *et al.*, 1991). New populations are marked by more aggressive genotypes of the pathogen (Day & Shattock, 1997; Lambert & Currier, 1997, Turkensteen *et al.*, 1997). In regions where both mating types have been found, evidence is accumulating that sexual reproduction takes place (Drenth *et al.*, 1994; Andersson *et al.*, 1998). In sexual populations, both sexual (oospores) and asexual (i.e. mycelium in infected tubers) propagules serve as inoculum sources, whereas asexual populations are totally dependent on asexually produced inoculum. Prior to the 1980s, a single A1 clonal lineage of *P. infestans,* designated US-1, was spread throughout the world, whilst the occurrence of the A2 mating type was confined to an area of the highlands of central Mexico (Niederhauser, 1956). Oospores in field crops (Gallegly & Galindo, 1958) were first reported from the Toluca Valley of central Mexico, and evidence indicates that the highlands of central Mexico are indeed the centre of origin of *P. infestans* (Fry & Spielman, 1991; Goodwin *et al.*, 1992). Populations of *P. infestans* outside central Mexico were restricted to asexual reproduction and survived during crop free periods by existing as mycelium inside potato tubers. During the 1980s, potato late blight became more difficult to control in Europe and. resistance to the fungicide metalaxyl developed rapidly. (Davidse *et al.*, 1981). It is plausible to suggest that the displacement of the US 1 population by 'new' isolates may have been accelerated by the concomitant introduction of phenylamides in Europe as tolerance to phenylamides (including metalaxyl) is more common amongst 'new' isolates.

The presence of A2 mating type strains in Europe was first reported in Switzerland (Hohl & Iselin, 1984), and was soon followed by a UK report on the presence of A2 mating type strains in imported ware potatoes from Egypt (Shaw *et al.*, 1985). These observations led to a revival of late blight research in Western Europe. Population genetic studies using allozymes (Spielman *et al.*, 1991) and DNA fingerprinting revealed the presence of a new, genetically

variable population of *P. infestans* in Western Europe. In the United Kingdom, it appeared that a genotypically diverse population had displaced the old clonal population of *P. infestans* during the 1970s and early 1980s (Shattock *et al.*, 1990; Cooke *et al.*, 1995). In contrast to reports from other European countries, the A1 mating type remained the predominant type among samples of *P. infestans* obtained from potato and tomato collected in England, Wales and Northern Ireland. The A2 mating type was identified in 3-10% of the samples collected, and no evidence for an overall increase in the frequency of the A2 mating type over this period was observed. As a consequence, dumps and infected seed still act as principal infection sources for late blight, caused by the A1 mating type, possibly supplemented by oospores, which may act as an additional infection source in both commercial potato fields and home gardens. The relative contribution of oospores to initial inoculum appears to be limited by the low frequencies of A2 mating type strains observed. In a recent survey during the 1995-1997 growing seasons, Cooke and co-workers (in prep.) reported a mixture of A1 and A2 mating type strains in 8.4% (Scottish farm sites) and 35.3% (home gardens) of the locations sampled. Like the present situation in the UK, tuber related inoculum sources appear to be important for initiating early late blight epidemics in the Netherlands (Table 1), even when high frequencies of A2 isolates are present in field crops and volunteer plants (Turkensteen, unpublished).

Table 1. Sources of early outbreaks of *Phytophthora infestans* in three different potato growing areas in the Netherlands, June 2000

Region	Source				
	Infected mother tuber	Dump	Distant source	Volunteer potatoes	Unknown (incl. oospores)
North-East (starch potato area)	8	2	0	0	0
South-East (ware potatoes)	2	0	5	2	1
South-West (seed & ware potatoes)	3	0	4	0	0
Total	13	2	9	2	1

The results in Table 1 show that thirteen out of twenty seven (48%) early late blight epidemics recorded in the Netherlands in 2000, were caused by infected seed. Dumps did

not appear to have a strong role in causing epidemics in 2000, which can be attributed to an active campaign for elimination of potato dumps by the Dutch farmers association.

Impact of 'new' populations

Farmers' experience of controlling late blight suggests that blight epidemics tend to start earlier in the growing season and the onset appears less predictable than in the past. It was found that 'new' isolates are more aggressive than 'old' isolates when infection frequency, latent period, sporulation and tuber infection were measured under controlled conditions (Day & Shattock, 1997; Flier *et al.*, 1998; Flier & Turkensteen, 1999). It is conceivable that the presence of aggressive strains will lead to shorter infection cycles and a more rapid epidemic development of the disease. In moncyclic tests, the difference between the individual components for aggressiveness in the old and the new population are strikingly in favour of the new population. The combined effect of the components of increased aggressiveness on polycyclic late blight epidemics is dramatic. Comparison of infection efficiencies and sporulation capacity of isolates representing the old and the new population of *P. infestans* in the Netherlands shows that isolates of the newly established population are able to infect potatoes at temperatures ranging from 3 to 27 ℃ while old population isolates caused infections from 8 to 23 ℃ (Flier *et al.*, unpublished). Recent results (Flier *et al.*, in preparation) show that isolates of the new population are marked by more rapid spore germination and host penetration, leading to shorter critical leaf wetness-periods. Under normal field conditions, isolates need only a few hours of leaf wetness (approx. 4 hours at 15 ℃) to penetrate potato leaves instead of the 8 hours that was widely considered to be the minimum time needed for germination and infection. In 1999, we successfully inoculated a field crop under extremely high temperatures (max/min: 34°C/27°C) and observed a latent period of approximately 2.5 days under field conditions. In 2000 and 2001, comparable latent periods were observed (Flier, unpublished). Whether observations like this should be regarded as rare incidents or to represent the current performance of *P. infestans* is still under debate, yet evidence supporting the hypothesis of increased levels of pathogenic fitness is accumulating.

The increased chance of infection at sub-optimal temperatures, in combination with shorter leaf wetness periods will increase the number of critical infection periods during the growing season, whilst shorter latent periods boost the speed of the epidemic. The window of

opportunity for action by the potato grower is narrowing and it has become extremely difficult to achieve a proper fungicide application timings. This grim view of the negative impact of 'new blight' on late blight control is supported by recent figures on fungicide use in the Netherlands. To date, the number of fungicide applications to control late blight in potatoes range from an average of 7 to more than 20 applications per season (Schepers, 2000), which is approximately 40% higher than fungicide use in the late 1970s.

Stability of late blight resistance

With the growing public demand for environmentally acceptable crop protection methods, breeding for durable resistance against late blight has been a focus for most modern potato breeding programmes (Colon *et al.*, 1995; Inglis *et al.*, 1996; Peters *et al.*, 1999). Incorporation of host resistance in integrated late blight disease management could result in significant reductions in fungicide use, whilst maintaining present yield and quality standards (Inglis *et al.*, 1996). The importance of minimising yield losses due to potato late blight by exploiting host resistance has been recognized for more than a century. In the early days of breeding for late blight resistance, complete resistance of potatoes to late blight was highly valued and the first complete resistant potato cultivars appeared in the 1930s (Müller & Black, 1952). During the 1950s and 1960s, breeding efforts to select for more durable forms of late blight resistance were initiated (Toxopeus, 1964; Hermsen & Ramanna 1973). These forms of resistance, often referred to as partial resistance, field resistance or quantitative resistance (Turkensteen, 1993; Colon *et al.*, 1995) are thought to be polygenic, non-race-specific and therefore effective against all *P. infestans* genotypes by reducing the rate of the epidemic (van der Plank 1968; Parlevliet & Zadoks, 1977). Partial resistance is thought to provide long-lasting protection against late blight (Turkensteen, 1993). The need for potato cultivars with high levels of stable late blight resistance was highlighted with the increase of organic potato production during the 1990s and the presence of a more aggressive sexual reproducing *P. infestans* population.

Recent work (Flier *et al.*, 2001) has shown differential interactions in tuber blight attack between potato cultivars and *P. infestans* isolates, manifested by changed resistance ranking of cultivars after exposure to several different *P. infestans* strains. Unpublished data support evidence for substantial differences in expression of foliar blight resistance depending on the

strain of the pathogen. The observed levels of partial resistance in foliage and tubers did not correlate well with foliar and tuber blight resistance ratings as presented in the Dutch national list of recommended potato varieties (Flier, 2001). It is concluded that cultivar-by-isolate interactions are important in determining the outcome of interactions between partially resistant potato cultivars and *P. infestans* strains. The presence of specificity in interactions between *P. infestans* and partially resistant potato cultivars may affect the stability and the durability of partial resistance against late blight in potatoes.

The road ahead

Late blight management has become more complicated following the introduction of 'new blight' in Europe. The pathogen has become more aggressive, and epidemics can start early in the season, even at crop emergence. In the past, missing one or two critical periods for late blight development did not lead to a severe blight situation, but such risks can no longer be taken. In response to this situation, an integrated approach to late blight management is advocated in which cultivars with stable forms of resistance, effective fungicides that combine low levels of active ingredient with superior persistence on leaves, and accurate timing of fungicide applications are implemented in late blight decision support systems (DSS). These integrated late blight management tools will enable potato growers to choose and apply the most effective fungicide at a suitable timing, whilst at the same time complying with the current impetus to optimise fungicide inputs. In addition, decision support systems offer the opportunity to safely explore the use of reduced fungicide rates in combination with more resistant cultivars (Fry, 1975; Clayton & Shattock, 1995).

In conclusion, potato growers, breeders and plant pathologists alike are facing a pathogen that is becoming more adaptable, more variable and more aggressive. Late blight has also become less predictable for the farmer. An integrated strategy for late blight control based on sophisticated decision support systems will enable potato growers to exploit stable forms of host resistance, dynamic fungicide use and cultural practices in an effort to protect their crops whilst minimising fungicide inputs for late blight control.

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P. infestans oospores in the Netherlands: occurrence and effects of cultivars and fungicides

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Introduction

In the Netherlands, a genotypically diverse, sexually reproducing *P. infestans* population has displaced the old, clonally reproducing, population during the 1980s and early 1990s (Drenth *et al.*, 1993). A1 and A2 mating types were detected in infected potato crops (Frinking *et al.*, 1987) and new complex races and virulence factors were found (Drenth *et al.*, 1994). Functional oospores were found in naturally infected commercial potato and tomato crops and in home gardens (Turkensteen *et al.*, 1996). Oospores are able to survive Dutch winter conditions (Drenth *et al.*, 1995) and are thought to be common in the Netherlands. Specific measures to control or prevent oospore formation are not available.

This paper describes a survey for the occurrence of oospores in the four major potato-producing regions in the Netherlands and experiments on the effects of fungicides and potato cultivars on oospore formation.

Materials and methods

Oospore survey

A survey was conducted in the north-eastern (NE), central (CE), south-eastern (SE) and south-western (SW) potato production areas in the Netherlands. Sandy soils dominate the