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The return of *Phytophthora infestans*, a potato pathogen that just won't quit

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Summary

Since the early 1980s and continuing through the end of the 20th century, potato late blight caused by *Phytophthora infestans* has become noticeably more problematic throughout the world. Exotic strains of the pathogen are largely responsible for the increased problems. The new strains were initially detected in Europe, but subsequently they have been detected in Asia, the Middle East, South America and North America. Populations in the Middle East and South America may represent secondary migrations from Europe. Several independent migrations have occurred such that migrant populations in North America are very different from those in Europe. Also, population structures of *P. infestans* are different in different worldwide locations. In some locations the migrant strains are resistant to metalaxyl, but in other locations either migrant or indigenous strains may be resistant. In most locations, the migrant strains are more aggressive than the previous indigenous strains.

Introduction

Phytophthora infestans (Mont.) de Bary is an oomycete plant pathogen that causes one of the most fearsome of plant diseases - potato (*Solanum tuberosum* L.) late blight. All parts of the plant are susceptible - leaves, stems and tubers. The disease was first problematic in the early 1840s in the northeastern United States (Stevens, 1933), and subsequently caused the plant disease that led to the Irish Potato Famine (Bourke, 1993). The disease decreased potato production in Ireland to ca. 25% of its previous level and thus caused mass starvation. In addition to deaths by starvation, the population of Ireland was reduced by emigration, and an emigration mentality in Ireland has been a century-long legacy of the disease.

Initial success in controlling the pathogen

During the 150 years following the European introduction of *P. infestans*, efforts to suppress the disease gradually reduced the impact of the disease. Notable factors included the discovery of Bordeaux mixture as a protectant fungicide, identification of cultivars with field resistance, discovery of organic fungicides that were more effective and less phytotoxic than Bordeaux mixture, development of late blight forecast systems and discovery of systemic fungicides that had curative efficacy. Thus by the late 1970s, the disease was less important than it had been for the previous century.

The pathogen strikes back

This situation was altered in Europe in the early 1980s. The first indication of change was the occurrence of metalaxyl-resistant strains that caused disease control failures and significant yield loss. Initially it was thought that this fungicide resistance had been selected in the indigenous population of *P. infestans* in Europe. However, subsequently it has been demonstrated that a new, diverse population of *P. infestans* had been introduced into Europe, and the first suggestion that such an introduction had occurred was signalled by the discovery of A2 mating types of *P. infestans* (There are two mating types of *P. infestans*; previously it was thought that there were only A1 mating types in Europe).

It is now well established that a new, diverse population of *P. infestans* has been introduced into Europe from its center of diversity, central Mexico. The new population is more aggressive than the previous population (Day & Shattock, 1997) and has displaced the previous population (Fry et al., 1993). The new population has now been distributed from Europe to other continents (Forbes et al., 1998; Fry & Goodwin, 1997b).

Exotic strains of *P. infestans* have also been introduced into the United States and Canada (Fry & Goodwin, 1997a). However, the introductions into the United States occurred later than into Europe and, because of the previous experience in Europe, American scientists were forewarned and were therefore able to detect quickly exotic strains. The exotic strains in the United States also came from Mexico, but from a different location, and contain some different characteristics. The introductions into the United States were primarily of single genotypes so that the structure of *P. infestans* populations in the United States remains very simple, with only a few genotypes with widespread distribution. However, as in Europe the exotic strains have displaced the previous indigenous strains.

Analysis of the renewed success of the pathogen

Why have exotic strains displaced the previous indigenous strains and what is the significance of the potential for sexual recombination? It appears that the benefits of sexual reproduction are well illustrated in the biology of *P. infestans*. Sexual reproduction is thought to provide a mechanism for eliminating deleterious mutations that can accumulate in an asexual lineage, and it also provides a mechanism for producing particularly fit genotypes. Recently introduced strains have come from central Mexico where *P. infestans* is sufficiently sexual so that most loci have alleles in Hardy-Weinberg equilibrium (Goodwin et al., 1992). The clonal lineage that dominated most other populations until recently (US-1) is thought to have been asexual for 150 years (Goodwin et al., 1994). There have been repeated demonstrations that this lineage is less aggressive a pathogen than the recently introduced strains (Day & Shattock, 1997; Kato et al., 1997; Lambert & Currier, 1997; Miller et al., 1998). In the United States, some of the new strains require significantly more fungicide for adequate suppression of late blight. We have previously predicted that an additional 25% may be required (Kato et al., 1997). In the USA and Canada the exotic strains were introduced as metalaxyl-resistant lineages, and this trait contributes considerably to the fitness of *P. infestans* in agro-ecosystems. Additionally, there is recent circumstantial evidence that the US-11 lineage, recently problematic on potatoes and tomatoes in western USA and now moving into eastern USA, was generated by a sexual recombination event in western USA.

Finally, and somewhat specific to *P. infestans*, the sexual spore form (oospore) may provide a mechanism for this organism to overwinter in the absence of its host. Some scientists believe that oospores may even initiate earlier epidemics than mycelium associated with seed tubers. However, the accuracy of that hypothesis awaits rigorous testing.

What have we learned?

Perhaps because of the recent diversification of pathogen populations worldwide, some of our understanding of the biology of this pathogen is being challenged. For example, our ideas about hosts of *P. infestans* have been modified. In the United States, plants from which *P. infestans* recently has been observed as a significant pathogen include hairy nightshade (*S. sarachioides*), *Petunia hybrida*, and bittersweet (*S. dulcamara*). It has even been demonstrated that silencing of a single gene in *P. infestans* enabled it to colonize *Nicotiana benthamiana* (Kamoun et al., 1998). The implication to late blight management in potatoes is that there may be a larger number of alternate hosts than previously thought. Finally, the ability of diverse strains to produce oospores in the absence of the alternate mating type is also greater than previously understood (Smart et al., 1998). The implication to late blight management is that oospores might contribute to the epidemiology of late blight more significantly than previously considered. Finally, it has recently been demonstrated that different genotypes of the pathogen can vary from each other in terms of responses to environmental parameters (Mizubuti & Fry, 1998). The implication for management is that forecasts based on only one genotype may be slightly misleading when applied to other genotypes.

Conclusion

The new strains differ from the previous monomorphic populations and there will be greater diversity in the biology of this organism (oospores, response to environmental variables, pathogenicity) than in the past.

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