Phytophthora – an abiding threat to our crops

Jim Duncan

Late blight caused the Irish Potato Famine in the 1840s, but as Jim Duncan describes, the dangers from this plant pathogen to food crops today are still significant.

ABOVE:
Close-up of typical blighted leaves.
PHOTO COURTESY SCOTTISH CROP RESEARCH INSTITUTE

BELOW RIGHT:
Detachable sporangia of *P. infestans* viewed under microscope. Bar, 20 µm.
PHOTO COURTESY SCOTTISH CROP RESEARCH INSTITUTE

The Irish Potato Famine in the mid-1840s is still the most vivid example of the damage that can be wrought on plants and human society by the depredations of a plant pathogen. The almost complete destruction of the potato crop in a country that had come to depend on it as the chief staple, and inadequate responses to the subsequent food crisis by government at all levels, led directly to the deaths of over a million people and the emigration of many more. Between 1841 and 1861, the population of Ireland fell from 8.2 million to 5.8 million. The famine also occasioned fundamental shifts in Irish nationalism and politics that echo to this day.

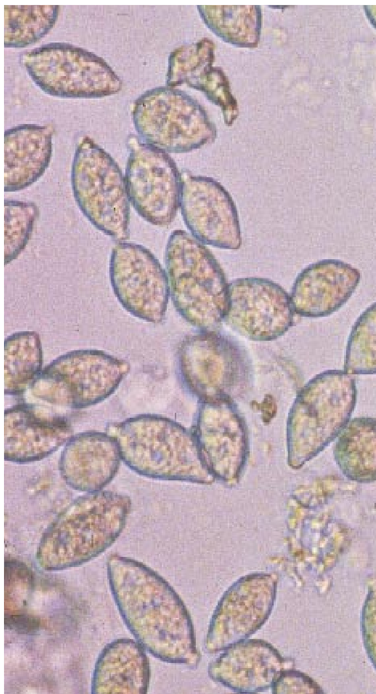
Late blight of potato, as the disease is known, has remained in Europe ever since. Moreover, just as import of infected potatoes probably brought the disease to Europe in the 1840s, exports of infected seed potatoes from Europe led to further spread to all other parts of the world, including the Andes of S. America, the original home of the 'Irish' potato. Ironically, the disease does not appear to have originated in the Andes but in the mountains of central Mexico, home to many wild potato species.

Late blight is caused by the 'fungus' *Phytophthora infestans*. Although in everyday parlance *Phytophthora* is a 'fungus', it does not actually belong to the Kingdom *Fungi*, to which the majority of fungi are consigned. Rather it belongs in the Kingdom *Straminipilia* along with various groups such as the brown and golden brown algae. There are around 60 *Phytophthora* species, most of which are of considerable economic or environmental importance. Fairly typical is black pod of cocoa caused by *P. palmivora*, *P. capsici* and *P. megakarya*, which together caused an estimated loss of US$300 million in 1982 and more recently have been behind scares about shortages of chocolate. Large areas of rare, world heritage forest ecosystems in Western Australia have been killed by *P. cinnamomi* (Jarrah dieback). The fungus attacks numerous species in the forest, killing many of the unique herbaceous understorey plants, shrubs such as the spectacular banksias, and the dominant eucalypt *Eucalyptus marginata*. Many more examples could be quoted for the range of plants attacked by *Phytophthora* is enormous. Some species have very broad host ranges, although others have very narrow ones.

Nevertheless, *P. infestans* is undoubtedly the best known and most investigated *Phytophthora* species and it deserves to be! Even today, with modern potato varieties having some resistance to the disease, and effective fungicides, the costs of losses to potato late blight and of controlling it are enormous. Estimates vary considerably but a common figure is US$3 billion per annum worldwide. In an average year, farmers in Europe will spray up to eight times to control blight at a cost of £150 per hectare; in the disease-favouring climate of the tropical highlands this can rise to as many as 30 sprays a year. And *P. infestans* is not confined to the potato: it can infect many relatives of the potato, including tomato and aubergine. On a recent trip to Ecuador I saw spectacular damage to plantations of the tree tomato, so severe that one grower had dug up and burned all his plants.

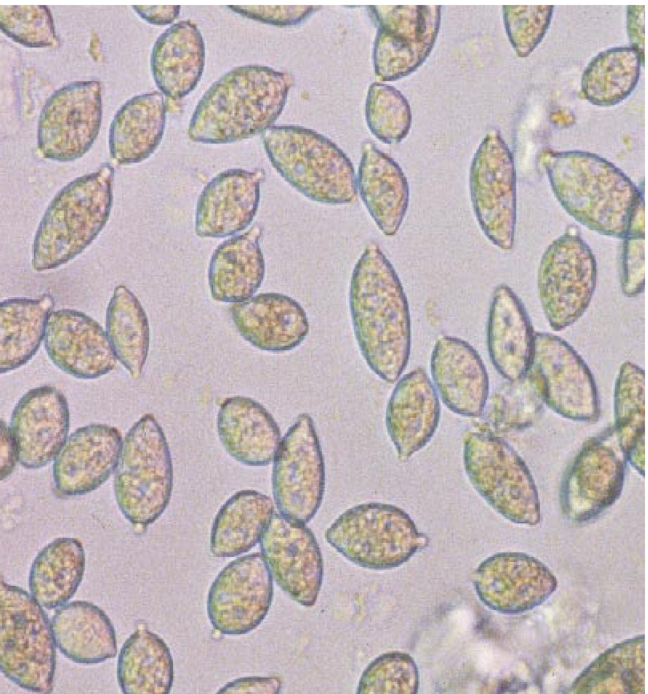
Late blight until 1980

From the late 1840s until the early 1980s, farmers learned to live with late blight. The discovery of Bordeaux mixture by Millardet in France in the 1880s heralded a new era of control by chemicals, for although developed for the control of grape downy mildew, it was effective against late blight. In the 1930s, discovery of the dithiocarbamates gave the first effective organic fungicides. Later, plant pathologists were able to develop forecasting systems to tell farmers when to begin spraying with fungicides, from knowledge that successful infection was critically dependent on the presence of free water on the foliage, and on high humidity around the leaves and moderate temperatures for a period thereafter.



Some of the early potato varieties that survived the first onslaughts of disease in the 1840s proved to have some resistance and breeders used these to develop new, more resistant varieties. The protection offered by resistance was far from complete but it was useful. A dramatic breakthrough came when breeders turned to some wild species from Mexico as sources of resistance, which they were able to introgress into *Solanum tuberosum*. The results were spectacular: the resulting material was immune to late blight. Alas, it proved a false dawn. When new immune varieties were finally released to commercial cultivation, the fungus quickly adapted to overcome the resistance, and they became as susceptible as more conventional material. Later, scientists around the world, most notably Dr William Black of the Scottish Plant Breeding Station at Pentlandfield near Edinburgh (now part of SCRI in Dundee), worked out that the wild species from Mexico had 'race-specific' resistance. It transpired that the fungus exists as a series of races and the most common race in the early part of this century could not overcome the race-specific resistance introduced from Mexico. But when the breeders introduced a variety with a new race-specific resistance, a race emerged within a few years that could overcome it: a biological arms race. Eventually, breeders abandoned breeding for this form of resistance, partly because control by fungicide was by then very good and relatively cheap, and partly because they had decided to try to breed instead for durable field resistance. This is not based on a single gene but on many genes acting in concert. It is not race-specific and should not be overcome. On the other hand it is not usually as complete as race-specific resistance when the latter is effective, and developing it is a long haul for the breeder because of the number of genes involved.

While all this was going on, much more had been learned about the biology of the fungus. First, American and Mexican scientists had discovered that at its origins in central Mexico, the fungus is pathogenic to the same wild species used in early resistance breeding in Europe. In Mexico the fungus exists as two mating types, A1 and A2, both of which are needed for sexual reproduction. The ratio of A1 and A2 was about 50:50, strongly suggesting that sexual reproduction was important in the Mexican life cycle. The product of sex is a thick-walled spore, the oospore, which unlike all other structures formed by the fungus can survive well in soil, probably for many years. Thus in Mexico each year, the epidemic was begun from oospores in soil and not from dormant infections in seed tubers. The disease now had a soilborne dimension.



ABOVE:
Two views of a field of susceptible Bintje unprotected by fungicides. The upper photograph was taken in early August and some blight is visible. The lower photograph was taken 10 days later.
PHOTO COURTESY SCOTTISH CROP RESEARCH INSTITUTE

Late blight today

At this point in the story only the A1 strain had been found outside of Mexico: in other countries the fungus had no sex life, and no soilborne dimension. There the position would have remained till today but for the summer of 1976, which was was hot and dry across most of Europe. The largely unirrigated potato crop failed leading to shortages and high prices. Consequently, import restrictions were relaxed to allow imports of potatoes from other countries, including large tonnages from Mexico. With them came many new strains of late blight, including the other mating type A2. In retrospect, what existed before 1976 outside Mexico had been a unique situation. Genetic fingerprinting has shown that then, all non-Mexican isolates of the fungus had a single fingerprint: the fungus was to all intents and purposes a single 'clone' throughout the world but for Mexico. Apparently, the same clone had devastated the potato crop throughout Europe in 1845/46 and done so much damage since.

It took until 1984 for the world to become aware of the changed situation. Hans Hohl in Switzerland reported that while carrying out a routine laboratory teaching exercise with undergraduates, he had discovered that some isolates of *P. infestans* collected from his garden were A2 mating type. At more or less the same time, reports started circulating of earlier and more severe attacks of late blight, stimulating a period of intense research.

The new population turned out to have many different fingerprints, and various proportions of A2 strains, depending on where the samples were collected. It also appeared to be more aggressive, causing larger lesions with more sporulation than the original population, although there is still some debate about this. What is not in dispute is that the new population displaced the old population throughout most of Eurasia, beginning in the Netherlands in the 1980s and gradually spreading eastwards through the 1990s to reach Korea and Japan. Similar changes in North American populations have occurred over roughly the same period of time, but with the added complication that there probably have been several introductions, some of them on tomato.

Dutch workers have shown that the new population is undergoing sex and producing oospores. This may lead to earlier and more intense epidemics as oospores infect shoots before they emerge from the soil. In addition, fields will remain infested between crops as oospores can survive for years in soil. It may be necessary, for example, to lengthen the period between crops in a rotation if oospore inoculum becomes a greater problem.

The changes in blight populations have not only led to increased research on the pathogen, they have renewed interest in breeding for resistance. Needless to say an increase in diversity has led to an increase in the number and complexity of races and breeding for race-specific resistance would be a waste of time. This is where the alternative strategy initiated by Bill Black back in the early 1960s has begun to pay off. Some of the varieties bred at the Scottish Crop Research Institute have high scores for resistance, i.e. scores of 7 or 8 on a scale of 1–9. There is no indication that this resistance is race-specific. Some have already been grown in organic systems and have performed very well without the protection afforded by fungicides.

● The developing world and GILB

When the risk of new populations became widely apparent in the early 1990s, the International Potato Centre in Lima, Peru (CIP) took a keen interest. CIP has done a tremendous job promoting the potato throughout the tropical highlands of the world. From the early sixties until today, production of this popular, nutritious and relatively simple to grow crop in the developing world has expanded from about 6% to just over 30% of the world total.

Not unnaturally, CIP saw the emergence of new blight populations as a particular threat to farmers and peasants growing potatoes in the developing world, given the expense of fungicide control. CIP therefore led the formation in 1996 of the Global Initiative on Late Blight (GILB). This is a 10 year programme of research and development that aims to produce cultivars suitable for growing in the tropics, with high levels of durable blight resistance. One of the first results is a multi-site trial in 10 countries from the tropics to high latitudes. Fourteen varieties with varying levels of resistance, half tropical and half from developed countries, have been grown in each country and ranked for their resistance against a wide diversity of local strains. It is pleasing to report that the varieties ranked more or less the same for late blight resistance regardless of the blight population and the environment at each site, strongly suggesting that what appears durable in the laboratory may also be durable in the field. This is only the first step in attempts to introduce and popularize blight-resistant potatoes which do not require fungicide treatment, but it is a promising one.

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