



Phytophthora: a blight on Ireland

Late blight of potatoes caused by *Phytophthora infestans* had an enormous socioeconomic impact on 19th century Ireland. According to **Gareth Griffith**, the outbreak also heralded a landmark in the development of microbiology, especially in the areas of plant pathology and crop protection.

As the world's fourth most important food crop, the potato is a major part of the Western diet. It first became known to Europeans after the conquest of the Andean Aztecs by the Spanish in the early 16th century. The route whereby the potato reached Ireland is unclear. Reports that Sir Walter Raleigh introduced the potato through his extensive estates in County Cork or that it arrived via the fleeing Spanish Armada are unsubstantiated, though there was extensive trade between Ireland and Spain in the 16th century. Spanish seafarers were certainly quick to recognize that potatoes were well-suited for ship's stores, providing a useful source of fresh food and vitamins. With increasing transatlantic sea travel at this time, it is likely that there were numerous introductions to Europe.

In Ireland, the high rainfall and mild winters in the west were conducive to

the cultivation of potatoes and from the early 18th century much of the population was dependent on this crop, especially the high-yielding 'Lumper' variety. Apparently, adult males consumed over 6 kg per day. A further contributory factor to the success of the new crop was the small size of land holdings in Ireland. Most families were forced to live off small plots, often on marginal soils; potato yields were greater than for other crops and the plants were generally less susceptible to disease. The availability of potatoes was probably a major contributory factor to the continued growth of the population in Ireland which exceeded 8 million by 1841.

Arrival of late blight

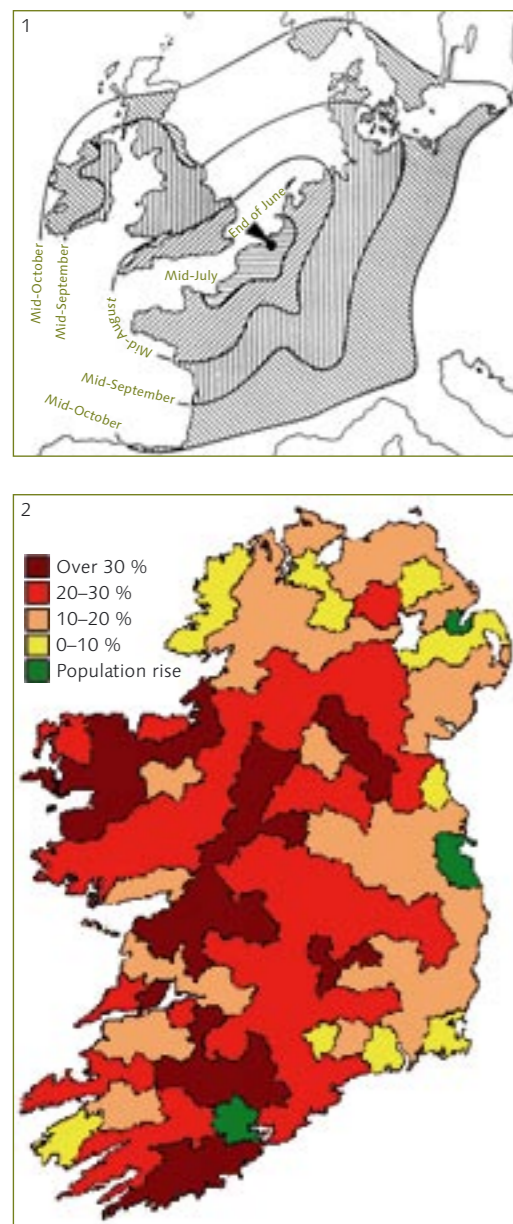
The pandemic of late blight (originally called potato murrain or gangrène humide) has its earliest confirmed origins on the US east coast in 1843, probably due to the spread of the pathogen in tubers on the trade routes from Southern/Central America. Irish immigrants had introduced potato cultivation to the USA in the 1790s and the crop was widely grown along the east coast. The next jump, and the one that secured the infamy of this pathogen, was across the Atlantic in 1845. Potato disease was first reported in Belgium in May and air-borne dispersal of the sporangia permitted its rapid spread, so that it reached Ireland in July, arriving in western Ireland by September (Fig. 1). Though

◀ Far left. The distinctive sporangia of *Phytophthora infestans* which were observed by Berkeley and others to emerge 'out of the mouths of stomata' of infected leaves. G.W. Griffith & A. Edwards

▲ Centre and right. The symptoms of late blight on leaves and tubers. The small black lesions enlarge and coalesce, leading to defoliation. Sporangia washed by rainfall from leaves infect the tubers which develop a brown marbled appearance during storage. Garden World Images / D. Bevan (leaf) & USDA Photo Library (tuber)

crops in many parts of Europe were badly infected by the new disease, the 1845 crop in Ireland was better than average. Unfortunately, during storage in clamps, tubers infected in the field developed blight symptoms and blackened, making them inedible and providing ample inoculum for the 1846 season. Severe food shortages in early 1846 were exacerbated by a total crop failure later that year.

As in more recent famines, the greatest damage was caused by failures to recognize the seriousness of the problem and to mobilize chains of supply to bring grain to the areas most heavily dependent on potatoes. The insensitivity of landlords was also shocking, with widespread eviction due to unpaid rents. In the small town of Kilrush, Co. Clare, there were 7,000 evictions in the second half of 1848. Much blame was also laid at the door of the government in London and specifically its tardiness in repealing the much-hated, anti-free-trade Corn Laws which had maintained high wheat



▲ Fig. 1. The spread of *P. infestans* through north-west Europe in the summer of 1845. Reprinted by permission from Macmillan Publishers Ltd: Nature, London (Bourke, P.M.A., *Emergence of potato blight, 1843–6*, 203, pp. 805–808), © 1964

▲ Fig. 2. Depopulation of Ireland caused by the famines. Public domain – taken from Edwards, R.D. & Williams, T.D. (1956) *The Great Famine: Studies in Irish History 1845–1852* (Dublin: Brown & Nolan)

prices by preventing imports. According to the Nobel prize-winning economist Amartya Sen, the mortality rate in Ireland in the 1840s was higher than in any other recorded famine. The Irish nationalist and politician John Mitchel went as far as to write ‘the Almighty sent the potato blight, but the English created the Famine’. The resulting mass mortality and emigration – it is estimated that 1 million people died and a similar number emigrated between 1845 and 1849 – had a profound effect on the history, not only of Ireland, but also of the industrializing areas of the UK and the US east coast. The depopulation of Ireland, which began in 1845 as a result of the famine (Fig. 2), led to the disappearance of the cottier (crofter) class of peasant and continued for 150 years, with 4.5 million emigrating between 1851 and 1921. It is only very recently that the population of Ireland has begun to grow again.

The origins of plant pathology

The causes of the potato famine were the subject of much speculation as soon as the disease appeared. The prevailing view at the time was that all diseases were caused by ‘bad air’ or ‘miasma’, with some authors blaming deterioration of potato breeding stock, damp weather or an origin in outer space. The idea that plant diseases were due to fungi was rather heretical, and microbial growth in diseased tissues was generally viewed as a consequence rather than a cause of disease. The ‘fungalist’ view of plant disease had long been propounded, notably by Edouard Prévost (in 1807 for the wheat bunt *Tilletia*), Agostino Bassini (in 1835 for muscardine disease of silkworm by *Beauveria bassiana*) and von Martius (in 1842 for ‘dry rot’ of potato by *Fusarium coeruleum*), but was not accepted by the scientific establishment. In July 1845, as late blight began to take its toll, the French cleric Edouard van den Hecke described the sporulation of a fungus from blighted leaves, giving it the name *Botrytis*. Several other eminent mycologists went into print in support

of this idea, notably Charles Morren in Belgium and Camille Montagne in France. With remarkable prophetic ability, in August 1845 Morren suggested the use of copper sulfate/lime to protect seed potatoes and destruction of diseased tissues, strategies similar to those which became the mainstays of control of late blight until the 1930s, although it is unclear where his ideas originated. Meanwhile Montagne christened the fungus *Botrytis infestans*.

The Rev. Miles Joseph Berkeley, a Northamptonshire parson and prominent mycologist, who had been in contact with the continental ‘fungalists’, first observed the disease in early September and rapidly ascribed to the fungalist theory. However, the scientific establishment in Europe remained unpersuaded and the fungalists were widely pilloried. So vehement was this opposition in the later 1840s that only Morren refused to moderate his opinion. Montagne even suggested that his specific epithet *infestans* should be changed to *fallax*. Berkeley’s behaviour at this time suggests a degree of fence-sitting. Despite bravely writing ‘I believe the fungal theory to be the correct one’, in 1846, he skilfully avoided much of the resulting flak, being, in the words of Austin Bourke, more of a ‘believer than a missionary’. The debate rumbled on until 1861 when Anton de Bary published his papers on the life cycle of the pathogen, eventually renaming it *Phytophthora infestans* in 1876. Although its name has remained stable for over a century, *P. infestans* and its numerous pathogenic relatives now reside in the phylum Oomycota, in the Kingdom Stramenopiles (heterokonts), and thus in fact are only very distantly related to the members of Kingdom Fungi. Despite many similarities in gross morphology with Fungi (hyphal growth, etc.), the oomycetes are now recognized to possess several distinctive ultrastructural features.”

From a 21st century perspective, this whole debate about the origin of a disease so consistently and obviously associated with the distinctive repro-

ductive structures of *P. infestans* might seem odd. Had these events occurred a few decades later, with due regard to Koch’s postulates, the matter might have been settled more quickly and poor Morren would have been vindicated in his own lifetime (he died young in 1858). Berkeley, though older, lived to a ripe age and is with justification known as the father of English mycology.

Modern migrations of *P. infestans*

The taxonomy of fungi and other multicellular eukaryotes is based on the morphology of the sexual reproductive structures. In renaming *P. infestans* without having ever found its oospores, De Bary predicted where these might be found and what they would look like. Despite several conflicting reports in the late 19th century of the discovery of oospores in *P. infestans*, it was only when isolates were obtained from the Central Highlands of Mexico, the area of greatest diversity and presumed to be the evolutionary origin of the fungus, that oospores were found. It was realized that only the A1 mating type had originally escaped from Mexico and that outside Mexico the fungus relied totally on asexual reproduction. It remains a matter of debate whether *P. infestans* was transmitted directly from Mexico to the US or whether there was an intermediate migration to the Andes, followed by transport in the new steamships carrying guano from Peru to the US and Europe.

A further twist in the potato blight story came in 1976 when a drought in Europe led to poor potato crops and the need to import potatoes from abroad, including Mexico. Over the next 20 years numerous papers documented the discovery of the A2 mating type in various European countries. Use of molecular markers has demonstrated that the genetically uniform ‘old’ genotypes (the ‘Ib’ mitochondrial haplotype) prevalent up to the 1970s were progressively superseded over the next 15 years by a more diverse range of ‘new’ genotypes. The presence of both mating types opened the possibility of sexual reproduction, allowing not only the generation of additional diversity among pathogen populations, but also the formation of thick-walled oospores which could remain dormant in soil for prolonged periods. As with all plant pathogens, severe selection pressure for pathogen evolution is imposed by farmers (assisted by scientists). In the case of late blight this was due to both the breeding of progressively more resistant cultivars and the introduction of highly effective systemic phenylamide fungicides in the late 1970s. ‘Old’ genotypes were highly susceptible and resistance arose amongst the new genotypes, though the extent to which sexual reproduction plays a role in the modern evolution of the pathogen is still uncertain. Recent genetic analysis of the pathogen from herbarium specimens collected in the 1850s has revealed these to be of the ‘Ia’ rather than the ‘Ib’ haplotype, as had been widely assumed. Thus it seems that at least one pan-global migration of *P. infestans*, probably during the early 20th century, has gone unnoticed.

Late blight is still the most important disease of potatoes and commercial production is not viable without fungicides. Fungicide mixtures and targeted application based on meteorological data (blight forecasts) are used to great effect, but the delisting of many products under the EU Pesticide Directive and environmental concerns (some farmers spray their crops 10–20 times in a season) provides impetus for potato breeding and more effective fungicide application. Copper-based fungicides were widely used for late blight control between 1885 and 1935 and are still used for organic potato production.

Other *Phytophthora* diseases

The genus *Phytophthora* contains over 60 species, all of which are plant pathogens, with many more likely to be found. Unlike *P. infestans* which infects foliar tissues and is wind-borne due to its dehiscent (detachable) sporangia, most *Phytophthora* spp. are soil-borne root pathogens. Other members of the genus currently causing serious problems around the world have mysterious names such as Jarrah dieback of Eucalyptus, Black Pod of Cacao and Sudden Oak Death. It is ironic that free trade, as enforced by the WTO and for which the repeal of the Corn Laws in 1846 was a key step in the process, leading to the current global market for plant produce, leaves us at greater risk of suffering at the hands of introduced plant diseases.

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