


The Irish Potato Famine Fungus, *Phytophthora infestans* (Mont.) de Bary

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The importance of the genus *Phytophthora*, both to humanity and to the development of the science of plant pathology, has been obvious ever since *P. infestans* devastated the potato crop in Western Europe in 1845. Its greatest impact was the potato blight epidemic in Ireland (Gregory 1983). In 1845 and again in 1848 a third of the potato crop was destroyed by blight, losses at the extremes of previous European experience. Even more disastrously, three-quarters of the crop failed in 1846. In all, one million people died of famine-related diseases (Clarkson 1989) and up to 1.5 million more emigrated (Alexopoulos, Mims, & Blackwell 1996).

After the initial outbreak of the disease there was a major search for the underlying cause which led to a controversy with one group attributing it to natural causes, such as the weather, and the other group saying it was caused by a fungus (Dowley 1997). Charles Montagne, a retired French army doctor, first described the fungus to a meeting of theSociety Philomatique in Paris on August 30th, 1945, naming it *Botrytis infestans* (Dowley 1997, Alexopoulos et al. 1996).

The German scientist Anton de Bary first coined the name *Phytophthora* (ôplant destroyerö) in 1876, when he described the potato late blight fungus, *Phytophthora infestans*, as the type species for the new genus (Zentmyer 1983). He unveiled the full life cycle of the fungus (Dowley 1997) and was the first person to conduct extensive, controlled experiments with the fungus in potato (Alexopoulos et al. 1996). The science of plant pathology was born and the fungus got its final title of *Phytophthora infestans* (Mont.) de Bary (Dowley 1997).

The fungus, Phytophthora infestans, belongs to the Kingdom Stramenopila, Phylum Oomycota, Class Oomycetes, Order Perenosporales, and Family Pythiaceae (Alexopoulos et al. 1996). Family Pythiaceae includes aquatic, amphibious, and terrestrial fungi, most of the last causing serious diseases of economic plants (Alexopoulos *et al.* 1996). *P. infestans* is parasitic on members of the Solanaceae (Von Arx 1987), its three major hosts being the potato (*Solanum tuberosum* L.), tomato (*Lycopersicon esculentum* Mill.), and the pear melon (*Solanum muricatum* Ait.) (Abad & Abad 1997). This species is characterized

by coenocytic mycelium and the production of biflagellate, motile zoospores (Dowley 1997). The sporangia are formed under humid conditions mainly during the night and are dispersed under dry conditions during the day by wind. They germinate under humid conditions e.g. in a dew droplet. The zoospores enter the host plant through the stomata and cause new infections (Von Arx 1987).

P. infestans is heterothallic and can reproduce sexually in the presence of the opposite mating type. Sexual reproduction follows fertilization of an oogonium by an antheridium resulting in the production of an oospore (Dowley 1997). The complicated life cycle, with very distinct and strikingly different spore forms ranging from motile zoospores to thick-walled oospores, makes control of diseases caused by *Phytophthora* difficult and challenging (Zentmyer 1983).

The potato blight struck the whole of Europe in the late 1840s.The blight seems to have arrived from the United States in 1844 with a shipment of seed potatoes offloaded at Ostende in Belgium. No serious damage was caused that year but the disease spread rapidly throughout the continent in the latter half of 1845 and again in 1846. Although yields everywhere were adversely affected there was no potato famine in Europe, certainly nothing on the same scale as the Irish catastrophe (Solar 1997).

The impact of the blight on European potato crops was most severe and most widespread in 1846. The blight had a longer term impact on European agriculture. Its intermittent out breaks reduced average potato yields and made potato growing a much riskier activity. The longer-term effects can be seen in prices. The prices of potatoes relative to those of cereals were, on average, 50-100 per cent higher in the late 1840s and 1850s than in the 1830s and early 1840s. The blight was a large, negative and persistant productivity shock that reduced the returns of potato growing (Solar 1997).

Losses from this disease in potatoes are of two kinds: losses caused by foliage infection which leads to premature death of the plant and consequently reduction in tuber yield; and those caused by tuber infection and loss through rotting of infected tubers in fields and stores (Singh, Roy, & Bhattacharyya 1993). It appears on leaves as pale green, irregular spots. In the beginning the spots are more localized on the tips and margins of the leaves. The spots enlarge rapidly in moist weather with the central tissue turning necrotic and dark brown or black. Often the spots have a purplish tinge. A white mildew ring forms around the dead areas on the under side of the leaves (Singh *et al.* 1993).

Light brown lesions, which elongate and enlarge, develop on stems and petioles. Under favorable conditions, the whole vine may be blackened and killed. The disease spreads to the entire crop in a few days causing death. The diseased and decaying plants give off a fetid odor that becomes more pronounced in severely affected plants (Singh *et al.* 1993). Tubers become infected while in the soil by rain borne spores from blighted foliage initially showing a shallow, reddish-brown dry rot that spreads from the surface through the flesh (Singh *et al.* 1993).

Reproduction in *P. infestans* is primarily asexual, sexual reproduction being mainly restricted to Mexico. *P. infestans* is heterothallic and requires two mating types, A1 and A2 for sexual reproduction. Prior to the 1980's the A2 mating type was restricted to Mexico. This region is considered the center of origin of

this fungus and both mating types occurred in approximately equal frequency. The first reports of the A2 mating type outside Mexico were from Switzerland in 1984 and from U. K. in 1985. Since then it has been reported from the Netherlands, Israel, Japan, Egypt, and India (Singh *et al.* 1993).

Goodwin, Cohen, & Fry (1994) concluded that the initial migration of *P. infestans* in the 1840s was from Mexico to the United States and that a single genetic individual was transported to Europe and subsequently to the rest of the world. If this hypothesis is correct, then the Irish potato famine was caused by a single clonal genotype of *P. infestans*. It appears that the migration of this genotype occurred in at least three stages. In the first migration a number of different genotypes, probably from a single source population, were transported from Mexico to the United States, most likely in infected tubers of native Mexican *Solanum* species. By 1845, these genotypes had spread throughout the eastern United States and Canada. Probably only one of these genotypes was transported to Europe, where late blight disease appeared beginning in 1845. Once into Europe, this genotype could easily have been spread panglobally, because Europe has been the source of seed potatoes for most of the world (Goodwin et al. 1994).

A second theory proposes a three-step migration process, first from Mexico into South America, and subsequently from there to North America and Europe. Historical evidence points to an ancient introduction (at least several centuries ago) of late blight into the Andean regions of South America from its original home in central Mexico (Andrivon 1996).

Abad and Abad (1997) present a third explanation. Strong evidence exists in the historical literature that the disease has been endemic in Peru and other Andean countries for centuries. There is little evidence that the potato was grown in Mexico prior to the Spanish conquest. Potatoes were not grown widely in Mexico until 1949. The first record of late blight on cultivated potatoes in Mexico was in 1908 by Gandara. Thus, the introduction of the fungus into Europe and the United States in the 1840s in cultivated potatoes from Mexico is highly improbable if not impossible (Abad & Abad 1997).

Although it is clear that central Mexico is a center of diversity for the fungus, it is not yet clear whether the center of origin of *P. infestans* is located in the Andes of South America or in central Mexico (Abad & Abad 1997).

The composition of *P. infestans* in each country outside Mexico may include direct decendants of pioneers consisting of the A1 and/or A2 mating type and offspring of pioneer decendants whose sex had been changed at various asexual generations through natural courses. The composition may also include newcomers that may be the A1 and/or A2 mating type (Ko 1994).

It is conceivable that both the A1 and A2 mating types of *P. infestrans* have coexisted in a number of countries throughout the world since the beginning of the 20th century. This may be used to explain the detection of both mating types in most countries surveyed since the resumption of research on this subject in 1984 (Ko 1994).

Resistance to late blight in potatoes was spotted in 1845-1847 when some of the genotypes survived despite the severe epidemic of late blight. During breeding programs it was found that *Solanum dimissum*, a hexaploid wild species, could confer resistance to *P. infestans* which was simply inherited and promised to give complete freedom from disease in the field (Singh *et al.* 1993). By the mid-twentieth century, late blight was kept to generally tolerable levels by agricultural practices that included planting healthy seed tubers, eliminating other sources of the fungus, treating potato with fungicides, and using moderately resistant potato varieties (Fry & Goodwin 1997).

Phytophthora infestans is again creating a major plant health problem. Migrations of virulent and fungicide-resistant strains in the past two decades have caused a worldwide resurgence of the potato (and tomato) late blight disease (Fry & Goodwin 1997). Epidemics in the United States and Canada during the early 1990s were locally devastating, sometimes causing total crop loss and severe economic hardship for many potato and tomato growers. It has been difficult to develop potato and tomato varieties with stable resistance to late blight because although specific resistance genes are known, they are overcome rapidly by mutants in local fungus populations (Fry & Goodwin 1997).

In the Columbia Basin of Washington and Oregon the population of *P. infestans* quickly changed between 1992 and 1995, from a population comprised almost exclusively of the US-1 genotype to a population represented by new or recombinant genotypes (Miller, Hamm & Johnson 1997). The mean number of fungicide applications per field varied from 5.1 to 6.3 for early- and mid-season potatoes, and from 8.2 to 12.3 for late-season potatoes in 1995. In 1994, a year when late blight was not severe, the mean number of fungicide applications per field made to early- and mid-season potatoes was 2.0 and late-season potatoes received a mean of 2.5 applications. Harvest yields were 4 to 6% less in 1995 than in 1994. The cost of managing the disease was estimated at $30 million (Johnson et al. 1997).

In 1995 and 1996, severe late blight epidemics occurred in wild *Solanum* species near Quito, Equador. Of 52 isolataes collected in 1995 and 1996 seven were of the A2 mating type. Extensive and systematic sampling of commercial potato and tomato in Equador have failed to reveal the presence of the A2 mating type. Apparently the A2 mating type reported for the first time in Equador is only associated with wild *Solanum* spp. (Oyarzun, Ordones, & Forbes, 1997).

Future research on the origin of *P. infestans* could improve the understanding of the evolution of this fungus, and perhaps generate new ideas to facilitate control of this destructive pathogen that caused one of the most devastating plant disease epidemics in human history and is still a threat to potato production (Abad & Abad 1997). So far *P. infestans* has outclassed plant breeders and plant pathologists. It has evolved and adapted faster than new varieties are bred (Singh *et al.* 1993).

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