Phytophthora infestans

Introduction

Late blight of potato is one of the most destructive of plant diseases. It was the cause of the great Irish famine of 1845-7 that claimed the lives of about one million people and forced the emigration of another 1.5 million, mainly to North America. The elucidation of its disease cycle and etiology by Anton de Bary, published in 1863, at the same time as Louis Pasteur's germ theory, contributed significantly to repudiating the idea of spontaneous generation. De Bary's incisive research served to establish the science of plant pathology.

Plant pathologists recognize late blight as a special disease not only because of its historical significance to their profession but to the distinctive, pungent odour which emanates from a field of potato in the 'grip' of disease that is rapidly developing but not yet in the unmistakable blight stage. Potato farmers associate the smell with total crop loss and severe financial hardship.

Late blight is equally destructive on tomato and this crop can be intimately involved in the epidemiology of the disease on potato.

Identity

Authority : (Mont.) de Bary

Classification

- Kingdom : Stramenopila
- Phylum : Oomycota
- Order : Peronosporales
- Family : Pythiaceae
- Genus : *Phytophthora*
- Species : *infestans*
- Synonyms : *Botrytis infestans* , *Botrytis devastatrix* , *Botrytis solani* , *Peronospora infestans*
- Common names : Potato Late Blight, late blight, blight, potato murrain
- Role : Pest

Over the last few decades there have been significant changes in fungal systematics.

There is now general acceptance for a system of phylogenetic classification based on evolutionary relationships.

In the new classification the former oomycetes are placed in the kingdom, Stramenopila and the Phylum, Oomycota. Alexopoulos *et. al.,* (1996) list the distinguishing characteristics of the Oomycota as follows:

- Asexual reproduction by means of biflagellate zoospores with a longer tinsel flagellum directed forward and shorter whiplash flagellum directed backward
- Various features of zoospore ultrastructure
- The production of a diploid thallus in which meiosis occurs in the developing gametangia Oogomous reproduction by gametangial contact that results in the production of a thick-walled sexual spore termed an oospore
- Cell walls composed primarily of β- glucans but also containing the amino acid hydroxyproline as well as a small amount of cellulose
- Mitochondria with tubular cristae

- Various biochemical and molecular characteristics

Signs & Symptoms

Under favourable environmental conditions ($\leq 20^{\circ}C$, moist, with RH of 95-100%) the first symptoms are small irregular, light green to greyish lesions on leaflets, rachis, petiole and stem, that are not delimited and expand rapidly to form general black blighting and death of affected parts (Fig.1). Close examination of the upper surface of early leaf lesions reveals an area outside the greyish zone that is pale green and merges into it. On the lower surface a white mildew is visible in the area where the two parts of the lesion merge. The mildew consists of the sporangiophores and sporangia of the fungus, the asexual stage that is responsible for the rapid spread of the disease (Fig. 1.). If the temperature reaches $30^{\circ}C$, with reduced humidity, the pale area becomes less evident, the spore-bearing structures disappear and the advance of the disease is arrested. Symptoms and fungal structures reappear if humid, wet weather returns.
Potato tubers can be infected in the field, at harvest or in storage. The earliest symptom is a brown to purple discolouration of the epidermis, later becoming a brownish, dry rot extending about 5-15mm into the tuber. In storage bins the dry rot changes to a slimy, wet decay, having an offensive odour, resulting from invasion by secondary fungi and bacteria. The fungus is often found sporulating on the surface of tubers, if atmospheric conditions are favourable.

Morphology

The mycelium is hyaline, branched, coenocytic and produces indeterminate, sympodially-branched sporangiophores distinguishable from the somatic hyphae. The thin-walled, lemon-shaped, hyaline sporangium (21-38 x 12-23 µm), having an apical papilla, is borne at the tip of the branch and, as it matures, the tip of the branch swells and continues to elongate, resulting in the sporangium being turned laterally. A sporulating hypha is characterized by periodic swelling that marks the points at which sporangia had been attached. Depending on prevailing conditions, a sporangium may germinate directly to form a germ tube or indirectly to form 8-10 swimming zoospores. The latter have two different types of flagella, which are of taxonomic significance. Most strains are heterothallic and production of the sexual spore (oospore) requires two compatibility groups (mating types). Reproductive structures are antheridia and oogonia from opposite mating types. During the development of these structures, the antheridium is punctured by the oogonium, which grows through it and matures into a round body above the antheridium – an arrangement termed amphigynous. The oospore (25-35 µm) has a thickened wall that renders it resistant to unfavourable conditions. It germinates to form a zoosporangium.

Biology & Epidemiology

P. infestans perennates as mycelium in infected tubers a) left in the field after harvest, b) in cull piles close to production areas, c) in seed pieces, d) in tomato fruits produced in close proximity to potato farms, e) in wild *Solanum* spp. or f) in soil. In the tropics potato is grown continuously, so that disease can be initiated in newly planted fields by air-borne sporangia.
Mycelium in tubers invades the sprouts, emerging above ground in them and sporulates to form the primary inoculum (Fig.3.). The conditions favouring sporangium production, dissemination

and infection determine the extent of the epiphytotic. Optimum temperature and RH for sporangium formation are 18-22°C and 100% , minimum RH is 91 % and the temperature range is 3-26°C. The optimum temperature range for zoospore formation is
12-15°C and for the formation of germ tubes from zoospores it is 21-24°C. Sporangia produce germ tubes most rapidly at 25°C. Thus, cool, moist nights favour the most rapid production and germination of inoculum. Optimal development after infection requires somewhat warmer temperatures. In such conditions sporangial production can occur within 14 days of infection, which indicates why late blight is used so frequently to exemplify the polcyclic type of pathogen.
The sporangium falling on susceptible host tissue germinates to produce about 8 biflagellate zoospores at cooler temperatures (12-15°C) or directly produces germ tubes in slightly warmer conditions (20-27°C). Zoospores require a film of water in which they migrate over the plant surface. Entry into host tissue is either through stomata or directly into the epidermis. The ramifying mycelium in the host is both inter- and intracellular, displaying necrotrophic properties of rapid cell destruction that cause the devastating blight.
Tuber infection arises from sporangia being washed down from aerial plant parts. Zoospores germinate and enter through lenticels and wounds, the mycelium being intercellular and feeding on tuber cells via variously- shaped haustoria.

The possible role of the *P. infestans* oospore

P. infestans has two mating types, termed A1 and A2, that can produce the sexual, resting or oospore. In order for the oospore to be produced in nature, both A1 and A2 would have to infect the same plant or tuber. There is general acceptance that the Toluca Valley in Mexico is the centre of diversity of both *P. infestans* and *Solanum*. Grunwald et. al. (2001) have found a large diversity of multi-locus genotypes even within single fields and detected 1:1 frequencies of A1 and A2 mating types.
The experience in potato-producing areas of the world has been that oospores are rarely produced and have no role in the disease cycle of *P. infestans*. For a long while only the A1 mating type was widely distributed, except in Mexico and Bolivia. In 1978, the A2 mating type was discovered in Great Britain and, since then, it has been commonly found in most of Europe. Several recent studies indicate an important role of oospores in the epidemiology of potato late blight. Certainly, the increasing spread of the A2 mating type could lead to greater genetic diversity in populations of *P.infestans*, which would, in turn, challenge existing management procedures.

Dispersal/Vectors

The sporangiophores emerge through stomata and through lenticels in tubers. The sporangia detach when they are mature and are dispersed by rain splash and wind, the latter being the means of longer-range dissemination. Infected tubers are an important means of dispersal, both locally and over long distances.

Management

Plant Quarantine

As with any crop that is vegetatively propagated, there is great risk in using any but the highest quality, disease-free planting material. This requires controlling the entry of seed potato through appropriate quarantine regulations. An indigenous certification programme is the most desirable approach, but requires virus indexing capabilities that may be difficult to institute. Only certified seed of the most resistant varieties, known to perform well in the area, should be planted. Planting is normally scheduled to permit maximum crop growth before the expected date of the first blight- favourable weather.

Sanitation

Sources of perennating (overwintering) mycelium- dumps, cull heaps, volunteer potato plants and nearby tomato plants need to be destroyed.

Avoid conditions favouring late blight

a) Select fields that are well drained and, at planting, avoid areas that would be difficult to spray by air -areas next to windbreaks, houses, power lines or around irrigation towers.

b) If irrigation is used, ensure that the above areas are not excessively wet, since they tend to remain wet for longer periods than the open field. Overly wet areas are more favourable for blight development. Timing irrigation cycles to allow plants to dry before nightfall reduces the chances of active fungal sporulation.

c) Control the application of nitrogen to avoid unnecessarily heavy top growth that would extend the period in which the RH within the canopy exceeds 90 %.

d) Store seed pieces at < 7°C and cut just before the tuber sprout in order to reduce the possibility of contamination between different seed lots. Seed stores should be carefully cleaned and all equipment disinfected.

e) Become familiar with the weed hosts in the area and eliminate them before planting. General weed control within the crop will improve airflow through the canopy and assist in reducing humidity.

f) Carefully monitor the crop for early symptoms of late blight, concentrating on areas known to remain damp for longer periods. Obtain diagnosis from extension personnel, if there is uncertainty over symptom recognition. Check for sections that were not properly covered by fungicide application, e.g., areas below power lines and upwind from windbreaks.

g) Make use of any forecasting service that is provided and keep records of daily weather reports and weekly projections.

h) Prevent tuber infection, by maintaining soil on plant hills (done in a period of sunny weather) and, at least two weeks before harvest, by killing the vines with an appropriate herbicide. Scheduling harvest operations to avoid damp conditions reduces the possibility of tuber infection.

Fungicide Application

The use of fungicides is recommended-even though resistant/ tolerant varieties are available and planting tolerant varieties is advisable, since they retard the development of blight and, consequently, reduce the need for chemical management. There is also the risk of infection by a race(s) of the pathogen to which the varieties in use are not resistant. In light of the more universal distribution of A1 and A2 mating types, the rate of emergence of new pathogenic strains is likely to increase.

In a number of countries efficiency in the use of fungicides is improved through the establishment of late blight warning systems. The following are among the better known:

1. Beaumont period - was developed in the UK and describes a period of 48-hr duration during which the temperature remains above 10°C and the RH does not fall below 75%.
2. Smith period - is defined as one in which the minimum temperature remains at or above 10°C for 48 hr, during which the RH remains at 90% or higher for at least 11 hr. Under such

conditions the fungus is able to produce sporangia and to reinfect neighbouring plants. The practical application of the period may vary, depending on the stage of crop growth and extent of infection.

3. BLITECAST - a computerised system developed in the USA in which weekly recordings of temperature, RH and rainfall are made by potato farmers in their fields and telephoned into a central computer programmed with data similar to the Beaumont and Smith parameters (MacKenzie, 1981). The computer generates weekly severity values derived from daily risk scores based on the weather information. A blight risk estimate and fungicide recommendation are provided (Fig. 4).

4. Metpole - used in Denmark utilizes powerful microcomputers, linked to a weather station providing field data on rainfall, air and soil temperature, RH, wind speed, surface wetness and radiation, that permit more accurate risk assessment (Hansen, 1993).

The early use of Bordeaux mixture and other neutral coppers was followed by a period dominated by the dithiocarbamates. In the era of systemic fungicides having activity against the oomycota, metalaxyl and furalaxyl came into wide use. The appearance of resistance in populations of *P.infestans* has led to the reintroduction of protectants such as mancozeb, cupric hydroxide and chlorothalonil employed either alternately or in mixtures with the acylalanine systemics. These strategies have reduced the frequency of resistant strains and enhanced the degree of fungicide management. Exposure of the systemics to the fungus is reduced through the coordination of fungicide application with blight forecasting systems. There has been the additional benefit of these strategies being less stressful on the environment.

Resistant varieties

The earliest attempts at breeding resistant varieties used *Solanum tuberosum* in which a number of minor resistance genes were discovered. In the 1940s and 1950s four major resistance genes (R1 to R4) found in *S. demissum* were incorporated into a number of commercial varieties. However, the fungus developed physiologic races that overcame the resistance of the four R genes. Most present day varieties are susceptible to *P. infestans*, though in differing degrees. Varieties resulting from crosses of *S. tuberosum* with wild species have shown broad resistance to all known races of the pathogen for a period of time, only to succumb to some hitherto unknown race. Until such time that varieties expressing more durable horizontal resistance are developed, the use of existing varieties in fully integrated management programmes may lead to reduced costs of and dependence on fungicide application. Due to the wide range of potato varieties that are developed in various locations worldwide and the notorious variability of the pathogen, varietal selection for any particular area needs to be based on thorough evaluation.

Host Notes

White potato (*Solanum tuberosum*), tomato *solanums (Lycopersicon) esculentum* and many in the Solanaceae.

Distribution

Late blight is an important disease wherever potato is grown and environmental conditions favouring development of the disease exist. Distribution is worldwide, whether in the tropical highlands of Mexico, Peru or Bolivia, in cooler areas of Russia and Canada, in France, the United Kingdom, USA, Israel or India- the pathogen, *Phytophthora infestans*, is a major adversary to potato farmers.

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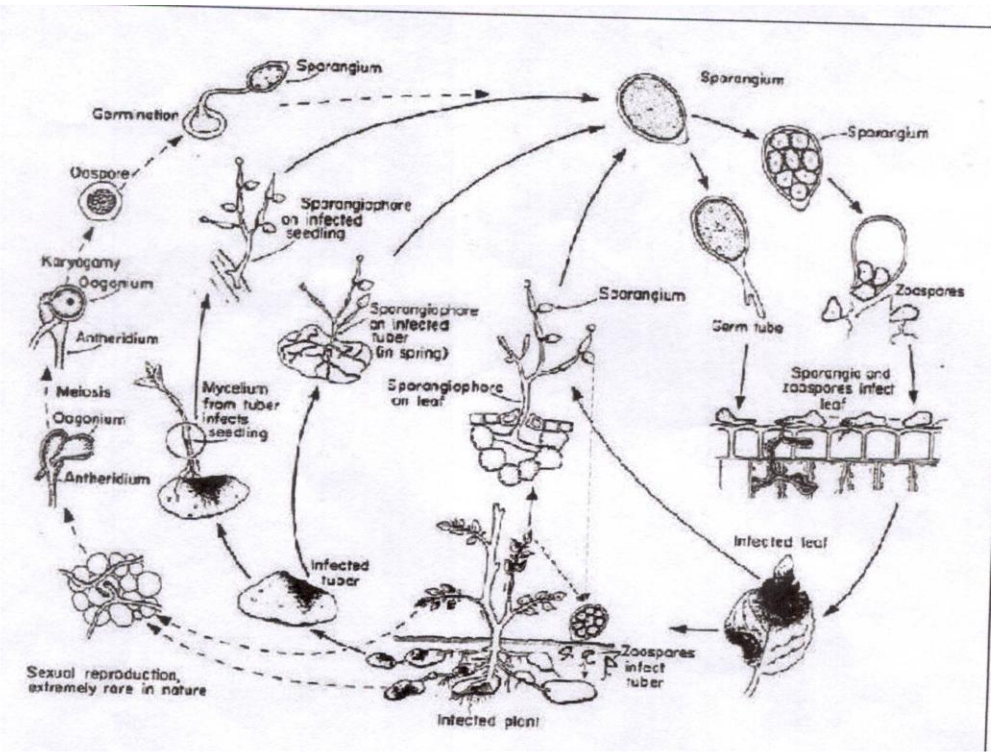
Web Resource -

http://helios.bto.ed.ac.uk/bto/microbes/blight.htm
http://www.ipm.ucdavis.edu/PMG/r607101211.html

Fig. 1: Potato late blight leaf lesion showing white mildew of sporangiophores and sporangia.

Fig. 2: Potato field in advanced stage of blight caused by ***Phytophthora infestans***.



Sporangium
Germination
Oospore
Karyogamy
Oogonium
Antheridium
Meiosis
Oogonium
Antheridium
Sporangiophore on infected seedling
Sporangiophore on infected tuber (in spring)
Mycelium from tuber infects seedling
Infected tuber
Sporangium
Sporangiophore on leaf
Sporangium
Sporangium
Germ tube
Zoospores
Sporangia and zoospores infect leaf
Infected leaf
Zoospores infect tuber
Infected plant
Sexual reproduction, extremely rare in nature

Fig.3: Potato Late Blight
Disease cycle of ***Phytophthora infestans***

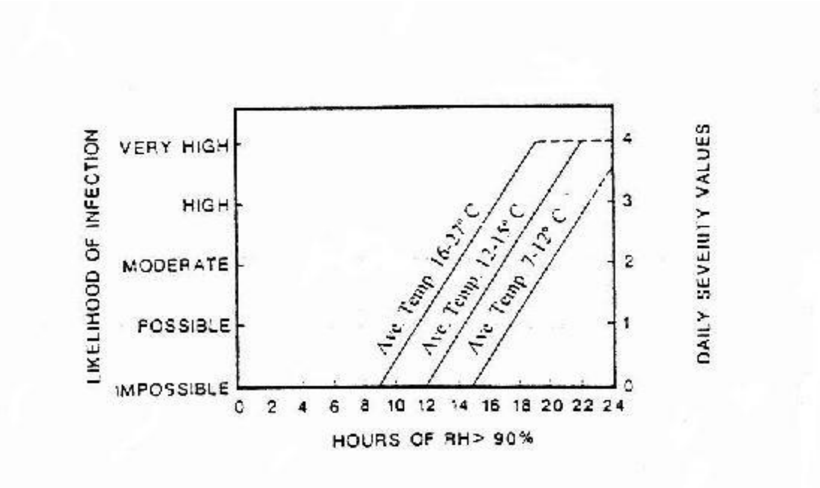


Fig. 4: Daily severity values, calculated from relative humidity/ temperature relationship, with corresponding likelihood of infection by ***P. infestans*** in BLITECAST system.