



Late blight

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The Fungus That Conquered Europe

Americans may think of the disease that destroyed Ireland's potato crops, late blight, as a European phenomenon, but its devastations actually started with them. The origin of the fungal organism responsible, *Phytophthora infestans*, has been traced to a valley in the highlands of central Mexico, and the first recorded instances of the disease are in the United States, with the sudden and mysterious destruction of potato crops around Philadelphia and New York in early 1843. Within months, winds spread the rapidly reproducing airborne spores of the disease, and by 1845 it had destroyed potato crops from Illinois east to Nova Scotia, and from Virginia north to Ontario.

It then crossed the Atlantic with a shipment of seed potatoes ordered by Belgian farmers. They had been hoping that fresh stock would improve their yields. Unhappily, it brought the seeds of devastation. The warm damp spring of 1845 enabled late blight to become an epidemic. By mid-July, the disease had spread throughout Belgium and into the Netherlands. It went on to infect an area from northern Spain to the southern tips of Norway and Sweden, and east to Northern Italy. It moved inexorably through the British Isles and reached Connemara, on Ireland's west coast, in mid-October. The ruin of Europe's potato crops was complete.

Nothing like it had been known before. Neither the Vandal hordes nor the bubonic plague had penetrated Europe so deeply and so fast. The failure of the crop was a disaster for every farmer, market gardener and family in Europe that relied on potatoes. Few were unaffected; in Ireland, a population that in 250 years had grown from one million to more than eight million, solely because of the po-

tato's unrivaled quality as a staple food, was threatened with starvation.

The first intimations of Ireland's looming calamity reached the British government in August 1845. Although Britain was responsible for the social and economic inequities which had made Ireland so susceptible, the government of the day deserves some credit for its efforts to avert mass starvation. There were political as well as logistical difficulties.

The Conservative prime minister, Sir Robert Peel, without seeking the approval of either cabinet or Parliament, authorized the banker Sir Thomas Baring to secretly buy £100,000 of American maize for shipment to Ireland. But before any official relief program could proceed there was a political obstacle to overcome: Britain's Corn Laws, which imposed exorbitant duties on imported grain to ensure that it could never be cheaper than home-grown produce.

To Peel it was obvious that the Corn Laws would have to go, but his electorate of large landowners was vehemently opposed to their abolition. The Duke of Wellington, leader of the House of Lords, complained that Ireland's "rotten potatoes have done it all they put Peel in his damned fright." Peel drew heavily on the news from Ireland as he urged Parliament to vote for abolition:

"Are you to hesitate in averting famine which may come, because it possibly may not come? Are you to look to and depend upon chance in such an extremity? Or, good God! are you to sit in cabinet, and consider and calculate how much diarrhea, and bloody flux, and dysentery, a people can bear before it becomes necessary for you to provide them with food?" The bill abolishing the Corn Laws was passed in May 1846 in the

House of Commons, with two-thirds of Peel's party voting against it and the entire opposition voting in favor. A month later, Peel was out of office.

As it turned out, far from Britain being flooded with cheap wheat, within weeks of the abolition the price of grain had reached heights rarely seen before. Speculation was rife, with dealers buying grain futures at two and three times the price of a few months before, draining the country's gold reserves and eventually threatening the stability of the Bank of England itself. Then, as fate would have it, the summer of 1847 brought news that Ireland's potato crop, though small, was doing well. The grain harvests also promised to be exceptionally good. Prices tumbled just as the grain bought months before at inflated rates began arriving in the ports.

Dealers who had gambled on high prices now found themselves unable to recoup their investments. Twenty major grain trading companies were brought down in September with total liabilities approaching £10 million. An additional 99 trading and related firms collapsed in October as the crisis spread, bringing down 11 country banks and three of the biggest in Liverpool.

The London banks, though, survived and went on to prosperity, for Ireland's famine, by ending the Corn Laws, prompted the beginning of the free trade that established the success of Britain's industrial economy. Still, the banking crisis had such an impact on the British mind-set that it is the benchmark against which commentators compare subsequent banking problems.

*By John Reader
(New York Times 2008/03/17)*

LATE BLIGHT

Late blight is one of the world's most devastating plant diseases and has been responsible for many devastating epidemics, including the epidemic in Ireland, which led to the great potato famine of 1845-1846.

This epidemic resulted in the deaths of an estimated 1.5 million people out of a total population of eight million, and the emigration of another 1.5 million, mainly to North America. Late blight causes yield loss in almost all countries where potatoes are grown, but is particularly damaging in areas with frequent moist, cool weather. Late blight is a polycyclic disease, and both above and subsoil plant parts are affected. When conditions are conducive, late blight can destroy a potato field in two weeks. Worldwide, late blight on potatoes and tomatoes causes an estimated \$6 billion yield loss annually.

Late blight was reported for the first time in South Africa in 1913 and is a problem

where potatoes are grown under cool, moist conditions. The plantings most affected are in the cool areas of KwaZulu-Natal, and in winter in the Sandveld. However, when other regions such as Mpumalanga, the Northern Cape, Eastern Free State and Western Free State receive rain in late summer/ autumn, late blight can be a problem.

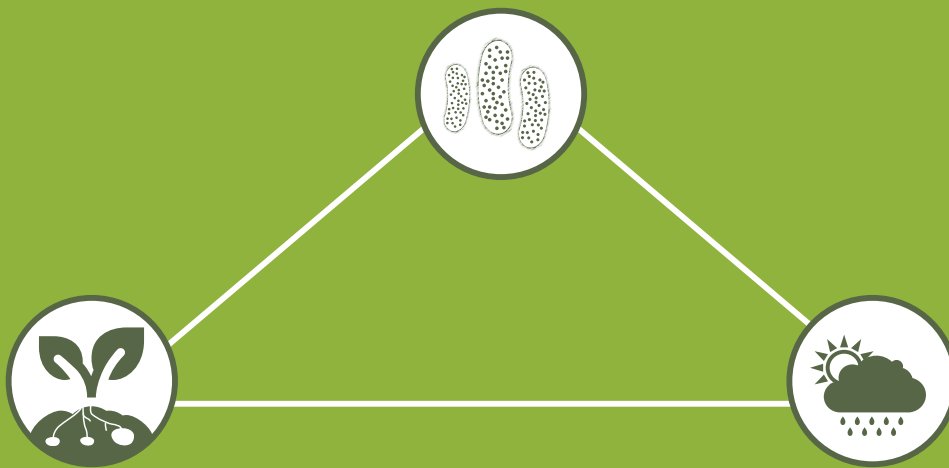
Late blight is caused by *Phytophthora infestans* (literally translated: the plant destroyer). By using modern technology the origin of this pathogen has recently been proven to be the Andean region of South America where the potato also originated. The pathogen spread from Mexico to North America and from there to Europe and the rest of the world.



DISEASE DEVELOPMENT

Pathogen

- *P. infestans* is an aggressive, multi-cyclic pathogen.
- Sporangia can be produced every 3-4 days under favourable conditions.
- Ability to rapidly build up resistance to fungicides.
- Spores germinate in free water on plant surfaces.
- Spores can penetrate plant cells, even in the absence of wounds.



HOST PLANT

- All plant parts can be infected.
- Popular local cultivars are not resistant, but some are less susceptible.

ENVIRONMENT

- Cool, cloudy conditions with high humidity for >48 h are conducive to late blight.
- Wind can disperse spores over long distances.
- Vegetative spores do not survive for long periods in soil.

MANAGING THE RISK OF LATE BLIGHT

PLANTING

RISK	MANAGEMENT
Climate favourable for disease development	<ul style="list-style-type: none"> • Potatoes planted during midsummer will probably mature during autumn when heavy dew is common. Choose the correct planting time to avoid such conditions. • If late blight is a common problem in the area, space rows more widely to improve ventilation and drying of plants

CHOICE OF FIELD

RISK	MANAGEMENT
Plant debris and cull heaps near the field	<ul style="list-style-type: none"> • Plant debris serves as a source of inoculum and must be removed or ploughed in deeply after harvesting to reduce the inoculum level. • Remove leftover seed potatoes from the field. • Avoid heaps of cull potatoes near potato fields.
Hosts of late blight growing near the field	<ul style="list-style-type: none"> • Volunteer potatoes should be controlled to keep the inoculum level in the region as low as possible. • Avoid planting potatoes near tomatoes.
Late blight hotspots	<ul style="list-style-type: none"> • Small areas with a micro-climate conducive to late blight in the field can serve as inoculum that can start an outbreak of late blight. • Do not plant too close to tall trees as shade delays drying of plants. • Make sure to spray the edges of the field properly. • Do not plant too close to structures such as electricity pylons, as they can create areas difficult to spray. • Avoid planting in places in the field where water collects.

CULTIVAR CHOICE

RISK	MANAGEMENT
Susceptible cultivars	Where possible, plant cultivars that are known to be less susceptible to <i>P. infestans</i> .

MANAGING THE RISK OF LATE BLIGHT

SEED POTATOES

RISK	MANAGEMENT
Infected seed potatoes	<ul style="list-style-type: none"> Plant only certified seed potatoes and maintain open communication with the seed supplier. Obtain the inspection report and inspect for the occurrence of late blight on seed tubers. If possible, do not plant seed produced during a blighty season. If no other seed is available, start with the spraying programme as early as emergence if the climatic conditions become favourable for late blight.

CROP MAINTENANCE

RISK	MANAGEMENT
Injudicious irrigation	<ul style="list-style-type: none"> Do not over-irrigate during cool times as this helps to create conditions favourable for late blight. Irrigate to allow enough time for plants to dry before sunset.
Climate favourable for disease development	<ul style="list-style-type: none"> Know the climatic conditions favourable for late blight. Consider the use of a disease forecasting service. Be vigilant during times of the year when conditions are normally favourable for late blight.
Dense plant canopy	<ul style="list-style-type: none"> A dense canopy helps to create a micro-climate favourable for late blight. Do not over-fertilise with nitrogen, so as to keep the top growth less dense. Reduce plant population if late blight is a common problem.
Spraying programme is not effective	<ul style="list-style-type: none"> A spraying programme must aim to prevent late blight outbreaks. Start an effective spraying programme before an outbreak of late blight. Ensure that the spraying programme is effective (see p. 6). Be sure to follow a programme designed to avoid the build-up of resistance.
Regrowth	<ul style="list-style-type: none"> Regrowth after kill-off will serve as a source of inoculum before harvest or before the next season. Make sure to kill off top growth completely. Control volunteer plants.

MANAGING THE RISK OF LATE BLIGHT

HARVESTING

RISK	MANAGEMENT
Harvesting under wet conditions	Do not harvest when the soil is wet, so as to prevent any inoculum in the soil from adhering to tubers.

POST-HARVEST TILLAGE

RISK	MANAGEMENT
Volunteer potatoes	<ul style="list-style-type: none"> • Plough in plant debris. • Control volunteer potatoes, as they will serve as a continuous source of inoculum.

THE PATHOGEN (*Phytophthora infestans*)

P. infestans reproduces asexually and sexually. Asexual reproduction is when a sporangium germinates by releasing zoospores (indirect) or by the formation of a germ tube (direct).

Sexual reproduction occurs when two mating types (mating type A1 and mating type A2) pair, forming oospores. Research on the late blight population was done by the Agricultural Research Council in the mid-1990s and again in 2007-2009.

Fortunately, all isolates in Southern Africa are of the A1 mating type and reproduction is therefore asexual. Sexual reproduction can result in the formation of new genotypes that can be more aggressive and/or resistant to fungicides. Oospores provide the means for long-term survival due to their thick, resistant cell walls. Oospores can serve as an inoculum to start an infection and as a source of pathological variability due to sexual recombination. Biosecurity measures should be strictly applied in order to prevent the A2 mating type from entering the country for as long as possible.

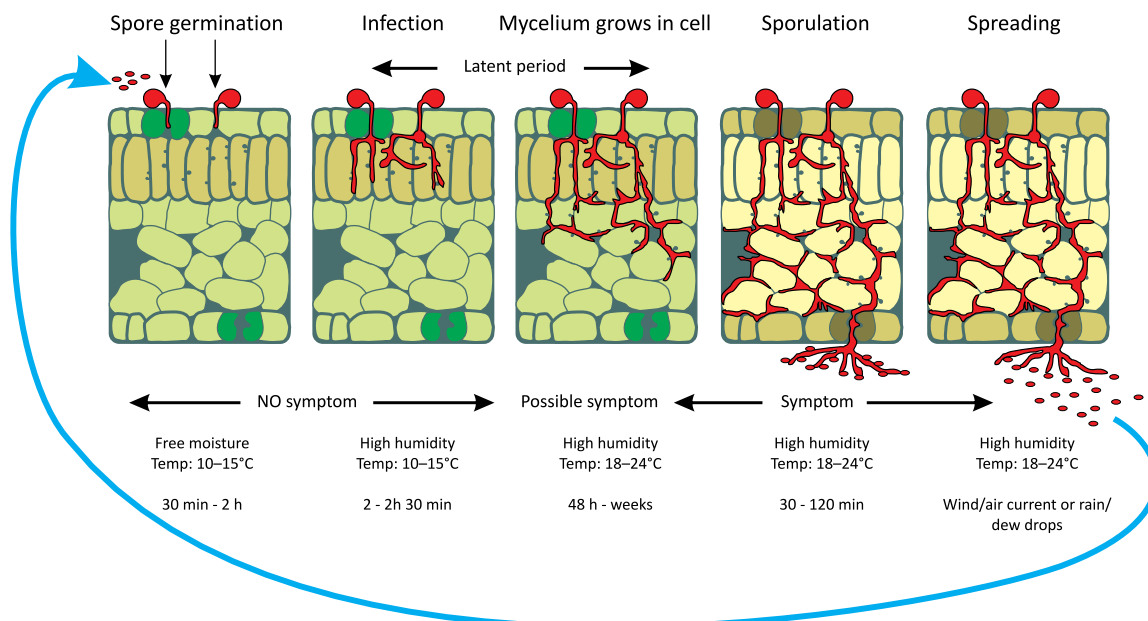
DISEASE DEVELOPMENT

Conditions conducive to disease development

- A 48-hour period with 15-24°C during the day, and $\pm 10^{\circ}\text{C}$ during the night.
- At temperatures of $<10^{\circ}\text{C}$, each sporangium can form eight zoospores.
- Germination of sporangia requires free moisture on the plant created by cool, cloudy days, frequent rainfall and/or overhead irrigation.
- Sporulation (multiplication): Relative humidity $>90\%$.
- After exposure to sunlight and dry air for one hour, 90% of exposed sporangia are killed.
- Several days of hot, dry weather will limit further disease development as sporulation is restricted. If these conditions persist, the mycelium may die off in the dry diseased leaves. However, the pathogen can remain viable in stem lesions. If cool, humid weather returns, disease development can resume.

Disease development

Disease development proceeds extremely quickly under conditions conducive to disease development. In each lesion, 900 000 sporangia or up to 2.4 million zoospores can be formed within only a few days. Under optimal conditions, symptoms of infection of leaflets are visible within three days.



SPREADING OF LATE BLIGHT

Wind

Air currents and wind with moisture (rain or irrigation) can spread spores from diseased plants in the field to healthy plants. Wind can disperse spores very quickly over very long distances.

Seed potatoes

The higher the incidence of late blight on seed potatoes, the greater the risk of spreading the disease in the next crop. As a result of South Africa's generally dry climate, infection of tubers is not that common. The South African Seed Potato Certification Scheme allows a tolerance of 0.1 % for Class 1, and 0.2 % for Standard Class for Generation 1 to 6.



How fast can late blight spread?

Example: The late blight epidemic in the 1840s.

Before 1843: *P. infestans* spread from the Toluca Valley in Mexico to North America.

1843: Late blight in the north-eastern states of America.

1844: Infected tubers carried by ship across the Atlantic to Europe.

June 1845: Late blight first noticed in Belgium. Spores spread by wind to the Netherlands, northern France, the southern coast of England and Dublin in Ireland.

August 1845: Late blight reported from western Germany, southern Denmark and the rest of England.

September 1845: Late blight spread to the rest of Germany and Ireland, and the southern parts of Scotland, Norway and Sweden.

1846: Tubers of the 1845 harvest, were planted for the 1846 season in Ireland and Scotland. The yield of 1846 harvest was not enough to plant as seed for the 1847 season.

Alternative hosts

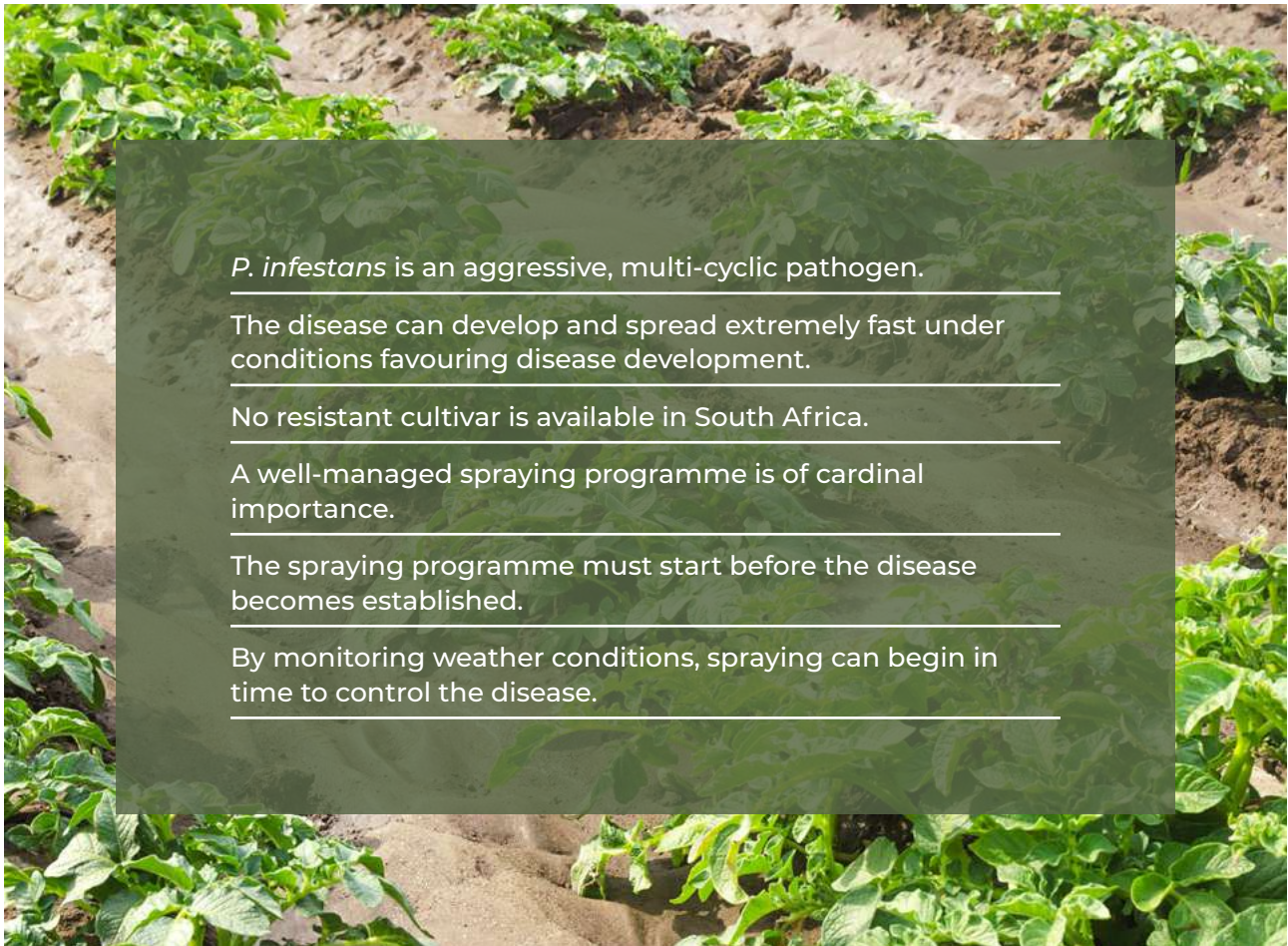
Tomatoes and petunias should not be grown in the vicinity of potato fields, also not in home gardens.

Cull heaps and volunteers

Control these potatoes before they sprout to prevent a source of inoculum near potato fields.



PRINCIPLES OF LATE BLIGHT CONTROL



P. infestans is an aggressive, multi-cyclic pathogen.

The disease can develop and spread extremely fast under conditions favouring disease development.

No resistant cultivar is available in South Africa.

A well-managed spraying programme is of cardinal importance.

The spraying programme must start before the disease becomes established.

By monitoring weather conditions, spraying can begin in time to control the disease.

Late blight-resistant cultivars?

Resistance breeding has proven to be a moving target for conventional breeding programmes because resistance to late blight is determined by more than one gene. In addition, the population of *P. infestans* changes continuously to overcome resistance in potatoes. Modern gene technologies have been used to develop cultivars with more than one gene resistant to *P. infestans*. However, as gene technology is not widely accepted, these cultivars have not been commercialised in South Africa.

If possible, establish a site separate from commercial plantings where cultivars can be evaluated by not spraying. Repeat the trials for more than one year.

Disease forecasting models

The purpose of these models is to accurately forecast periods conducive to late blight so that fungicides can be sprayed before the disease becomes established in a field.

Models incorporate the weather forecast for the next few days, information about available fungicides and quantities sprayed, into a risk model. A recommendation is sent to the farmer via cell phone. Various models are available in South Africa. Adjust spraying programmes based to the information received. Preventative spraying will help to manage the disease.

Tuber infection

During rain and overhead irrigation, spores can be washed from infected stems and leaves into the soil to infect tubers.

The risk of tuber infection is high when cracks in the soil are not covered by ridging, or when wind rocks the stems to create gaps between the stems and soil. Make sure top growth is properly dead and with no blighted regrowth before harvest.

Make sure the skin has set properly to reduce wounds through which spores can infect tubers, and do not harvest during wet weather.



Fungicides

A good fungicide spraying programme is a key element in an effective late blight management strategy, provided that:

- **Spraying is done in time.** Watch the weather and spray when conditions favourable for late blight are expected. Once late blight has established itself in a field, management is challenging even with curative and anti-sporulant fungicides.
- **All plant parts are adequately covered.** Spraying equipment must be in good order in respect of nozzles, pressure, nozzle height above the canopy and water volume, to ensure complete plant cover. The spray volume and spraying frequency must be adjusted as the plant cover increases.
- **Spraying is done at the right time of day.** Do not spray when the wind is blowing, when it is very hot, or when rain is expected within six hours. Do not spray when plants are still wet after rain or dew.
- **All plants are sprayed.** Ensure that crop borders as well as between spray routes, are sprayed. Unsprayed plants will serve as an inoculant.
- The spray mixture provides rain **fastness and persistence of the fungicide action.**
- **Resistance is avoided** by incorporating fungicides with different modes of action. The mode of action of each product is indicated on the label.

Resistance to fungicides

Metalaxyl is a very effective systemic fungicide. However, through over-use and lack of rotation with fungicides with other modes of action, *P. infestans* has developed resistance to metalaxyl. In South Africa resistance was first detected in the mid-1990s. In 2005 *P. infestans* was still resistant to metalaxyl.

The result is the loss of an excellent product to control late blight in South Africa.



Mode of action

Preventative products must be present on the plant before infection. Generally, all fungicides are preventative.

Curative fungicides are active on *P. infestans* immediately after infection, but before symptoms develop.

Anti-sporulant products decrease sporangia formation and/or decrease the viability of the spores.

Mobility

Contact fungicides do not enter the plant. They form a protective layer on the surface of plants and the active substance remains on the surface of the plant. No curative effect; some protect tubers.

Translaminar products enter the plant, have limited mobility and offer protection throughout leaves. These products have curative and anti-sporulant effects. Some are also effective to protect new growth and tubers.

Systemic fungicides are taken up by plants and are translocated within the plant, also to the growing tips and leaves. Curative action.



Fungicides differ in their effectiveness on different plant parts

Leaves can be measured by field tests.

New growth will be protected by using a systemic fungicide.

Stems can be attacked. Make sure to include a contact or systemic product.

Tubers - The fungicides should be used at the end of the season.

Systemic fungicides are effective on more than one plant part.

Rain fastness

Some contact fungicides are easily washed-off the plant by rain or dew drops, whereas others are not washed-off.

Translaminar and systemic fungicides do not wash off once they have been absorbed by plant tissue.

LATE BLIGHT AND GREY MOULD LESIONS ON TUBERS CAN BE CONFUSED

Tubers infected with *Botrytis cinerea* develop wrinkled lesions, which are usually covered with a dark-grey mass of conidia (A).

Late blight infected tubers initially show shallow, light reddishbrown, dry lesions (B).

Grey mould, caused by *Botrytis cinerea*, and late blight caused by *Phytophthora infestans*, are diseases that both develop under cool, damp conditions. Grey mould does not occur as commonly as late blight; therefore the symptoms can be confused.

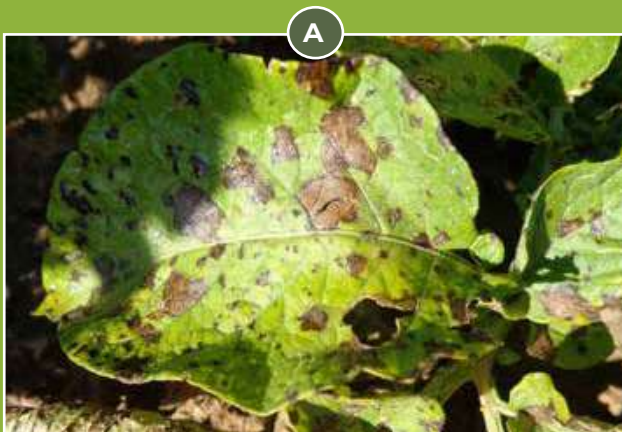


Photo A and B: ARC-VOP

DISTINGUISH BETWEEN EARLY BLIGHT AND LATE BLIGHT

Early blight (A) is caused by *Alternaria solani*, and late blight (B) by *Phytophthora infestans*. The diseases are easily distinguished from each other because early

blight blemishes show concentric circles while this is absent in late blight blemishes. Late blight blemishes are surrounded by chlorotic tissue, whereas this is absent in early blight.



LATE BLIGHT LESIONS ON LEAVES CAN BE CONFUSED WITH GREY MOULD LESIONS

Lesions caused by *P. infestans* (A and B) can be confused with grey mould lesions caused by *Botrytis cinerea* (C and D).

Grey mould lesions are watery and mould spores are grey, whereas those of late blight are white and appear on the underside of leaves.



Photo A: G. Hill, B,C and D: ARC-VOP

LATE BLIGHT ON STEMS CAN BE CONFUSED WITH BLACKLEG AND GREY MOULD

Late blight lesions caused by *Phytophthora infestans* (A) are not slimy like those of blackleg caused by *Pectobacterium* spp. (B).

Stem lesions caused by *Botrytis cinerea* (C) can show grey spore masses in contrast to white spore masses of *Phytophthora infestans*.



Photo A and C: ARC-VOP

LATE BLIGHT SYMPTOMS

Leaves.

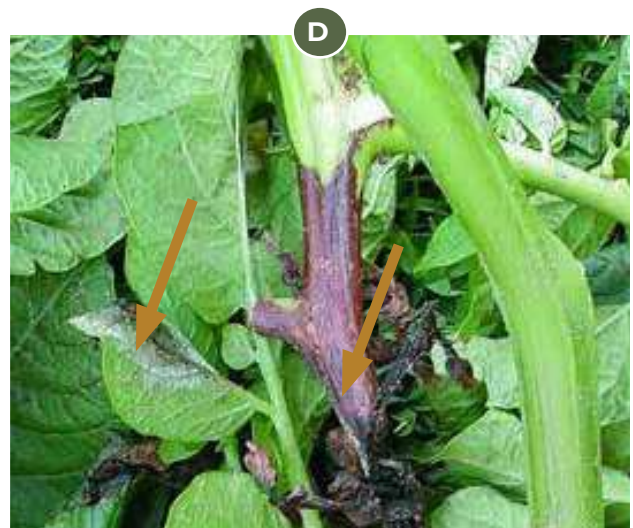
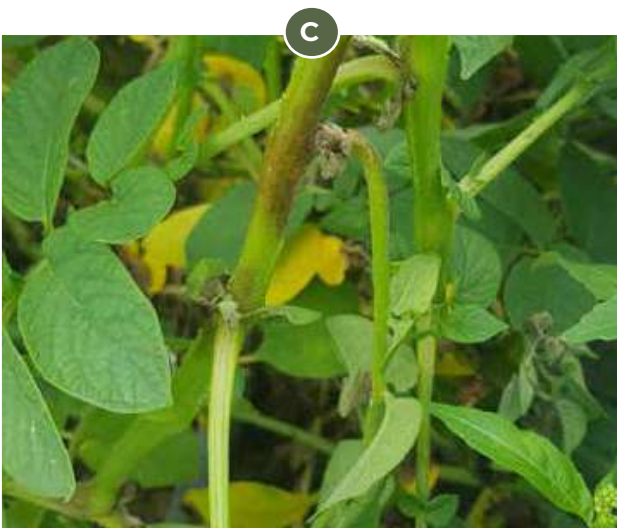
The first symptoms of late blight in the field are small, green to yellowish-brown, circular to irregularly shaped water-soaked spots which usually appear on the lower leaves first, often where dew drops accumulate (A). During cool, moist weather, these spots expand rapidly into large, dark brown or black lesions (B). When infected leaves are examined in the early morning or during cool, damp weather, a white fungal growth may be seen on the abaxial (lower) leaf surface (D: ↓). In dry weather, infected leaf tissues quickly dry up and the white fungal growth disappears. As many lesions accumulate and unite, entire leaves can become blighted and be killed within a few days.

Stems.

Late blight is characterised by brown to black lesions (C) on the stems and petioles. Stem lesions are difficult to detect early in their development. They are not slimy and can kill the stem or petiole when moist weather persists. Note white mycelium (D: ↓).

Tuber symptoms.

Initially, shallow, light reddish-brown, dry lesions develop. They may expand further during storage and are often followed by bacterial soft rot, which rapidly destroys the tuber (p10).





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Photo B: G. Hill; D: ARC-VOP



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