

Pectobacterium atrosepticum (van Hall) Garden *et al.* (*Pa*) (syn. *Erwinia carotovora* subsp. *atroseptica*), *Pectobacterium carotovorum* subsp. *carotovorum* (Jones) Hauben *et al.* (*Pcc*) (syn. *Erwinia carotovora* subsp. *carotovora*), *Dickeya* spp. (including *D. dianthicola*, *D. dadantii*, *D. zaeae*) (*Dsp*) (syn. *Erwinia chrysanthemi*)

BLACKLEG AND BACTERIAL SOFT ROT, HARD OR PIT ROT

Symptoms

HAULM: All three species may cause non-emergence through rotting of the mother tuber or seed piece.

With *Pa*, if emergence does occur, the blackleg symptom is first detectable as a stunting of growth relative to neighbouring plants. Affected stems become restricted in growth with inward rolling of topmost leaves, the foliage begins to yellow (13) and the haulm progressively wilts. Not every stem from a seed tuber may exhibit symptoms. Above ground, a soft slimy and often black lesion develops on the stem (14) developing progressively upwards. It is this lesion that gives the disease its name of blackleg.

Occasionally *Pa* and *Pcc* bacteria can splash up from soil or basal blackleg lesions and invade stems, petioles or leaves at a damage point, often where leaves join the stem, and cause an aerial blackleg symptom (15). Above the lesion the foliage yellows, wilts and dies progressively. The stem is soft and slimy at the lesion, exuding bacteria. If the stem is sectioned at the leading edge of the lesion, the vascular tissue and pith show brown discoloration or blackening (16, 17).

Dsp causes wilting and desiccation but not the soft slimy black lesions of *Pa* or *Pcc*. Browning of the vascular tissue in the stem develops into a necrotic lesion and internal desiccation occurs. Wilting and foliage symptoms tend to occur later than with *Pa* or *Pcc* and the disease has been called slow wilt.

ROOTS: No distinct symptoms normally visible.

STOLONS: No distinct symptoms normally visible.

TUBERS: With *Pa* and *Dsp*, bacterial invasion of the stem extends from the mother tuber up the stem. Bacteria can pass along stolons from the stem to developing tubers. If bacterial numbers are sufficiently high a black, soft lesion can develop at the point of tuber



13 Yellowing of foliage – early blackleg symptoms.



14 Typical blackleg caused by *Pectobacterium atrosepticum*.



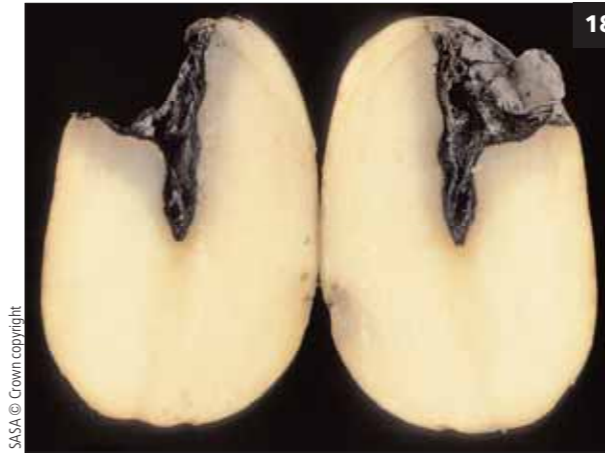
15 Aerial stem lesion.



16 Sections of diseased stem showing stem base lesion and vascular discoloration caused by *Pectobacterium atrosepticum*, compared to a healthy stem.



17 Sections of diseased stem showing stem base lesion and vascular discoloration caused by *Dickeya* spp., compared to a healthy stem.



18 Invasion and rotting of the stem end of tubers after movement of bacteria along stolon.



19 Bacterial soft rot caused by *Pa* or *Pcc*.

attachment, which starts small but can develop and rot the whole tuber (18).

Tubers can develop a bacterial soft rot in the ground or during storage. If they carry a high burden of bacterial numbers of *Pa*, *Pcc* or *Dsp*, or if bacteria have invaded wounds, a progressive soft rot may develop. Where no wounds are present, infection of tuber tissue begins around a lenticel. Such lesions look circular and brown when viewed externally. The pectolytic enzymes produced by the bacteria break down the pectin binding cells together. Initially, infected tissue in the lesion is granular and cream coloured (19). Infected tissue is sharply delineated from healthy tissue (20). Subsequently, the infected tissue turns black. In advanced states of rotting, liquid containing bacteria exudes from tubers and onto adjacent tubers in store,



20 Tuber exterior with bacterial soft rot.

21



21 Pit rot lesions.

initiating further rotting. As bacterial soft rot proceeds in a tuber, invasion by secondary fungi and bacteria often occurs. Once this happens, confirmation that blackleg bacteria are the primary cause can be difficult. Occasionally, rotting can be contained within the skin of a tuber, the fluid only leaking out if damage occurs. Early limited infection by *Erwinia* is often odourless but a characteristic of bacterial soft rot, particularly once secondary organisms invade, is a pungent odour.

During lesion development arising from lenticels, if external conditions become dry and unfavourable for the disease, the lesion may be halted and a wound periderm forms beneath the lesion preventing its progression. This is bacterial hard rot or pit rot (21). The external diameter and depth of hard rot lesions vary from 1–2mm to 4–5mm.

Status of the disease

These bacteria species may cause disease wherever potatoes are grown, although climatic conditions dictate which species predominates. *Pa* is most important in cool wet climates such as northern Europe. *Dsp* has a wide host range but is found primarily in lowland warm to hot climates. *Pa* and *Dsp* are the principal causes of blackleg symptoms in the field. *Pcc* exists in all climatic zones and has a very wide host range. It is the principal pathogen associated with soft rotting in tubers.

Under favourable conditions, blackleg symptoms and/or soft rot can be extremely serious. Pre-emergence rotting causes non-emergence which, if extensive, will affect yield seriously. Blackleg can affect certification of

seed in some countries (e.g. the UK) and by creating uneven plant stands can affect tuber size distribution. Soft rotting, if left unchecked, can reduce a stock of potatoes to a liquid mass as the rotting generates heat thus creating ideal conditions for further rotting.

Life cycle and biology

BLACKLEG: Seed tubers and seed pieces are the primary source of inoculum for *Pa* and *Dsp*. *Pcc* may also be found on seed tubers but is adapted to survival in soil. Investigations of the build up of contamination on seed through generations of seed production have shown that the pathogens can be introduced to a healthy stock in a number of ways. These include from the soil (*Pcc* and *Dsp* mainly), from rain, by insects from cull piles, by mechanical transmission during seed cutting and in aerosols after haulm pulverization in wet climates. Contaminated seed can break down when bacterial levels reach a threshold. Investigations in Europe have shown that seed with contamination by *Pa* of log 10³ per tuber or above can result in significant blackleg, although soil conditions play a large part in development of the disease. By contrast, blackleg from *Dsp* can develop from initial low levels of tuber contamination. When soil conditions are cool and wet, seed-tuber or seed-piece breakdown by *Pa* and *Pcc* can be rapid. The breakdown results in release of bacteria into the soil where multiplication may occur in the rhizosphere of certain weeds. The bacteria (particularly *Pa* and *Dsp*) can invade stems from the mother seed tuber, which can develop blackleg symptoms. The development of blackleg depends on the time at which the mother tuber rots. Rotting soon after planting leads to non-emergence, while rotting late in crop development may result in little or no blackleg symptoms developing. High levels of nitrogen can delay blackleg expression. Infection of seed by *Fusarium* spp. can predispose it to *Pectobacterium* soft rot and blackleg development.

Bacteria from rotting seed or, to a lesser extent, blackleg stems can contaminate daughter tubers, water aiding dispersal of the bacteria through the soil. Survival in the soil depends greatly on soil conditions. If the period prior to harvest is warm and dry bacterial contamination of daughter tubers can be limited. Conversely, wet conditions in the period leading to harvest can result in high levels of tuber contamination. In general, bacterial contamination of tubers increases the later the harvest.

At harvest, blackleg bacteria can be found on the tuber surface, within wounds or within lenticels. In wet conditions, lenticels can invert and allow bacteria easy entry. Rapid drying after harvest will normally lead to death of surface bacteria but those in lenticels are protected from the storage environment, declining in numbers only slowly if unfavourable conditions persist. Numbers of blackleg bacteria in lenticels can increase if favourable conditions for bacterial growth occur. These include warm storage temperatures and the presence of surface moisture through condensation. At grading, rotting tubers can spread the bacteria on the machinery to many other tubers.

SOFT ROT: Invasion of tubers by bacteria can occur in a number of ways. If *Erwinia* numbers are high, rotting can develop in wounds and through lenticels where conditions favour the bacteria. High temperatures (15–25°C) and the presence of free water are conducive conditions. *Pa* and *Pcc* are facultative anaerobes, and the presence of free water for a period of time can induce anaerobic conditions at the tuber surface and enhance infection. At temperatures of 6°C or below, growth of these bacteria is very slow and rotting inhibited. *Erwinia* often invade lesions made by other pathogens including *Fusarium* spp., *Phoma exigua* var. *foveata*, and occasionally *Streptomyces scabies* and *Spongospora subterranea*. Other bacteria such as *Pseudomonas* spp., *Bacillus* spp. and *Clostridium* spp. can cause soft rotting but these are mostly favoured only at very high temperatures. Immature skins on tubers, wounding and high nitrogen fertilization predispose tubers to soft rot.

Control

Reduce contamination of seed tubers

- This is achieved by using limited generation seed, harvesting early in dry conditions, and by minimizing damage by correct harvester setting and lifting tubers with a good skin set.

Minimize disease spread

- Remove mother tubers and rotting tubers at harvest. Do not plant diseased or damaged tubers, especially those with damage to sprouts. Plant when conditions are favourable for rapid growth.
- Select well-drained fields and use recommended rates of fertilizer. Rogue out infected plants (seed crops). Avoid waterlogging by irrigation. Do not pulverize haulm during wet conditions.

Rapid desiccation of seed crops (e.g. with sulphuric acid) is advantageous.

Good storage

- Dry crops immediately after harvest, dry cure and reduce tuber temperature steadily thereafter. Avoid condensation and CO₂ build up during storage by effective ventilation. Pick off rotted tubers early in the grading process, clean the grader between stocks and especially after grading a stock containing bacterial soft rot. Warm tubers before grading to at least 8°C to minimize damage.
- Maintain good hygiene by cleaning and disinfecting stores, machinery, boxes, seed cutting equipment and trays between seasons. With tubers washed before sale, use clean wash water or treat water with a suitable disinfectant to reduce bacteria and dry tubers rapidly after washing.

STUART WALE

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Ralstonia solanacearum (Smith) Yabuuchi *et al.*
(syn. *Pseudomonas solanacearum*, *Burkholderia solanacearum*)

BROWN ROT (BACTERIAL WILT, SOUTHERN BACTERIAL WILT)

Symptoms

HAULM: In the growing crop, the first symptoms are wilting of younger leaves during the heat of the day. Initially, this may occur in only one stem. The wilting may recover at night, but the wilting is progressive, eventually becoming permanent and leading to stunting, yellowing and haulm death. Stems may show brown streaks externally from soil level upward. When cut, stems exude a grey-brown bacterial ooze from the vascular tissue.

ROOTS: No distinct symptoms are normally visible.

STOLONS: Discoloration along the stolon may be visible.

TUBERS: In tubers, an early symptom is necrosis of the vascular ring (22). The area of necrosis can extend from the vascular ring into the parenchymatous tissue. When cut, a milky fluid exudes from the vascular ring (23). Infection by some strains of *R. solanacearum* does not result in vascular browning. Bacteria can exude from eyes (24), especially at the rose end and the stolon attachment, resulting in soil particles adhering to the tuber. Not all tubers show symptoms; some can be infected latently.

Status of the disease

The bacterium is widely distributed in the tropics, the sub-tropics and warm temperate regions and can be significant in limiting potato production. Yield losses up to 75% have been recorded in tropical countries. It has a wide host range, including the Solanaceae and a number of important crops including tobacco, pepper, groundnut and banana. Certain weeds can act as host reservoirs of infection. *R. solanacearum* has been classified into five races based on host range and five biovars based on chemical tests. Race 1 is mainly found in tropical and sub-tropical areas including parts of North America and Africa. Race 3, biovar 2 has a narrower host range including potatoes, woody nightshade (*Solanum dulcamara*) and black nightshade



22 Necrosis of the vascular ring.

(*Solanum nigrum*) and is adapted to lower temperatures. It is responsible for brown rot outbreaks in Europe and North Africa. Some countries remain free of the pathogen and impose quarantine measures to prevent importing it.

Life cycle and biology

Seed-borne infection is the most important source of the pathogen, but infection can occur via the soil especially in warmer climates. Seed-cutting knives can spread the bacterium from infected tubers to the cut surfaces of healthy tuber pieces. The bacterium can persist in crop debris and on weed hosts and survive in the soil for a period of time. However, in temperate climates, survival in soil more than two years after harvest of an infected crop is unlikely, provided there are no groundkeepers. Where soil is contaminated, infection can occur by invasion of the roots at root emergence points or at wound points (e.g. caused by nematode activity). The pathogen moves through the vascular system, multiplies and blocks xylem vessels through extracellular polysaccharide production and aggregation of bacteria, thus causing wilting. The bacterium also passes along stolons to daughter tubers. In warmer climates and in wet conditions, the pathogen multiplies faster and the development of symptoms is rapid. In cool climates (soil temperatures below 15°C) it may take several years for the disease to manifest itself during multiplication, and it can also be latent and symptomless. The pathogen



23 Cut tuber showing necrotic vascular ring and milky exudates from ring.

can cause brown rot in a wide range of soil types and levels of acidity. In cool temperate climates, *R. solanacearum* has been found to persist and multiply on the roots of *Solanum dulcamara*, in or on the edge of watercourses. Irrigation using water from these sources can spread the bacterium to uninfected potato crops.

Control

Differential resistance (tolerance) to *R. solanacearum* has been identified. However, whilst symptoms may be suppressed, a large population of the pathogen may build up on resistant cultivars. This has implications for the spread of the disease. Long rotations, dense cover crops and effective weed control to prevent survival of the bacterium on weed hosts or volunteers is important. However, the principal control measure is to plant healthy, uncontaminated seed. To achieve this, routine testing of seed stocks for the presence of *R. solanacearum* is carried out in some seed-producing countries. In Europe, this follows EPPO guidelines and consists of testing 200 tubers per 25 tonne seed lot. Various methods are employed to test seed lots including serology, PCR and plating on to selective media. Legislation, quarantine measures and certification schemes linked to seed and watercourse testing are used to ensure freedom from brown rot. Disinfection of cutting knives is important to prevent spread within a seed lot.

STUART WALE



24 Exudation from eyes of tuber infected by *Ralstonia solanacearum*.

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Streptomyces scabiei (Thaxt.) Waksman & Henrici
(syn. *S. scabies*)

COMMON SCAB

Whilst *S. scabiei* is considered the most widespread and common species, a further nine species have been associated with common scab: *S. acidiscabiei*, *S. caviscabiei*, *S. europaeiscabiei*, *S. luridiscabiei*, *S. niveiscabiei*, *S. reticuliscabiei*, *S. stelliscabiei*, and *S. turgidiscabiei*.

Symptoms

HAULM, ROOTS, AND STOLONS: Disease symptoms are normally not seen.

TUBERS: There are three basic common scab types – raised, pitted and superficial. There is some correlation with the causal *Streptomyces* spp., but there is also some correlation with cultivar and environmental conditions. For example, a species that causes one symptom in one cultivar may cause a different symptom in another or in the same cultivar grown under different conditions. The disease caused by *S. scabiei* is usually characterized by corky erumpent or pitted lesions on the surface of the tubers (25, 26). Lesions are tan to brown and roughly circular in shape, although in severe cases they may coalesce and cover much of the surface area. Other *Streptomyces* species may cause similar symptoms.

Pitted scab lesions are raised but often deeply pitted and crater like. Deep pitted scab has been associated with *S. caviscabiei*. Symptoms of superficial lesions include netted scab and russet scab, which are often confused with each other. Netted scab (27) in Europe can be caused both by *S. reticuliscabiei* and *S. europaeiscabiei*. Superficial russetting symptoms accompanied by necrosis of the root system have been attributed to species of *Streptomyces* such as *S. reticuliscabiei* and appear to have different etiology.

Status of the disease

Potato scab occurs in potato production soils throughout the world and reduces the quality of processing, table and seed potatoes because of the unsightliness of infected tubers and the tuber-borne nature of the disease. Increased peeling costs, diminished marketability and increased seed grade-out are the major economic effects. Total yields are seldom reduced.



25 Common scab lesions.

Life cycle and biology

Streptomyces species are classified as aerobic bacteria yet they have some characteristics, including filamentous morphology, resembling fungi and hence are termed actinomycetes. Aerial mycelia are usually mouse grey in colour. Sporulating scab lesions may be observed sometimes on tubers. In culture, a characteristic earthy smell is emitted. *S. scabiei* produces phytotoxins called thaxtomins, which elicit scab symptoms. Thaxtomins are likely to play a role in pathogenicity. The organism is tuber-borne and is also a well-adapted saprophyte that persists in soil on decaying organic matter and manure. (*S. acidiscabiei* causes similar symptoms but has different morphological and physiological characteristics.) Infection occurs mainly through immature lenticels making the tubers most susceptible for six to eight weeks following tuber initiation, since they rapidly enlarge. Infection of the stolons and fibrous roots may also occur. The optimum temperature for the growth of *S. scabiei* is 30°C. Soil properties influence the extent of symptom development. The disease is usually most severe in dry soils with a pH of 5.2–7.0, although *S. acidiscabiei* has caused scab in soils with a pH of 4.5. High soil moisture inhibits growth and offers a means of control. Common scab does not spread in storage.

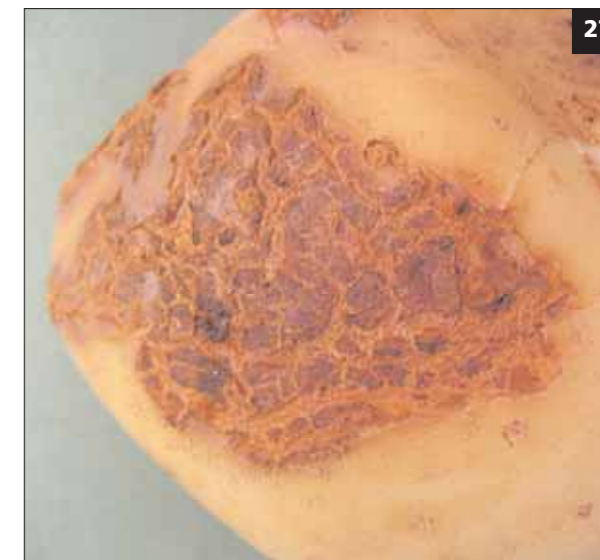


26 Common scab lesions on red tubers.

Control

Differences exist in the susceptibility of potato cultivars to scab, but as yet no cultivars are totally resistant. Under conditions that are highly conducive to common scab development, even the more resistant cultivars may develop symptoms. Potato-breeding programmes around the world seek new sources of resistance in relatives of the cultivated potato to combine with agronomically acceptable characteristics. Lowering soil pH with acid-producing fertilizers or sulphur applications has reduced the levels of scab in some cases, but this may negatively influence fertilizer absorption and yield. Soils with lower pH may also limit the choice of rotation crops. Over-liming of fields is to be avoided. Increasing the interval between potato crops may reduce the soil population but is unlikely to eliminate the organism. Irrigation to maintain high soil moisture during tuber formation has effectively controlled scab development in the UK. Soil and seed treatments are costly, not particularly reliable and may not be available or acceptable in all production areas.

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27 Netted scab lesions.

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