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Authentication

We declare that this work was done under our supervision according to the procedures described herein and that the report represents a true and accurate record of the results obtained.

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Grower Summary

Headline

- The symptoms, distribution, biology, epidemiology and control of five main bacterial pathogens of lettuce has been reviewed citing 233 references. These are: *Xanthomonas axonopodis* pv. *vitians*, *Pseudomonas cichorii*, *Pseudomonas fluorescens/marginalis*, *Pectobacterium carotovorum*, *Sphingomonas suberifaciens*.
- There is considerable overlap in the disease symptoms caused by the first four, these are variously characterised as rots, head rots, spots and blights; thus identification based solely on symptoms without laboratory confirmation is unreliable.
- *Sphingomonas* causes a corky root disease, with vague symptoms on the leaves/head. The majority of work has focussed on identifying the causal bacteria, with relatively little work on either epidemiology or practical control.

Background and objectives

Bacterial diseases have been causing sporadic problems in outdoor and protected lettuce for a number of years. Most recently there have been severe problems in outdoor crisphead lettuce with losses of £0.5 million estimated for a single grower in a single season. There are several bacterial species which may cause disease on lettuce, but the causal organism(s) of much of the disease seen in the UK has not been established with any certainty; symptoms of the most recent outbreaks are consistent with varnish spot, caused by *Pseudomonas cichorii*. Given the uncertainties about the primary cause and the taxonomic difficulties with soft-rotting fluorescent pseudomonads, this proposal represents the first phase of what is envisaged as a three-stage project. A proposal to improve understanding of the causes of bacterial problems in (outdoor) lettuce was submitted in March 2007 and comprised both practical laboratory work to identify the primary disease causing organisms and a survey of the existing literature. This project addressed the literature review component as requested by Field Vegetable Panel, and aimed to identify information of relevance to UK growers and conditions. This will be used as a basis for a follow-on experimental project.

Disease names

Due to the overlap in symptoms attributed to four of the five main bacterial pathogens of lettuce, the following table (Table 1) lists the various disease names/major symptoms in lettuce which have been attributed to bacteria; the main body of the review is then organised according to pathogens rather than disease name or symptoms.

Table 1. Lettuce diseases/symptoms caused by bacteria and the pathogens that cause them.

Disease name	Pathogen(s)
Bacterial leaf spot	<i>Xanthomonas axonopodis</i> pv. <i>vitians</i>
Bacterial wilt	<i>Pseudomonas marginalis/fluorescens</i>
Butt rot (field)	<i>Pectobacterium carotovorum</i>
Butt rot (glasshouse)	<i>Pseudomonas marginalis</i>
Corky root	<i>Sphingomonas suberifaciens</i>
Dry rot	<i>Xanthomonas axonopodis</i> pv. <i>vitians</i>
Head rot	<i>Pseudomonas cichorii</i> , <i>Pseudomonas marginalis/fluorescens</i> , <i>Pectobacterium carotovorum</i> , or <i>Xanthomonas axonopodis</i> pv. <i>vitians</i>
Jelly butt	<i>Pectobacterium carotovorum</i>
Marginal leaf blight	<i>Pseudomonas marginalis/fluorescens</i>
Kansas disease	<i>Pseudomonas marginalis/fluorescens</i>
Midrib rot	<i>Pseudomonas marginalis/fluorescens</i> or <i>Ps. cichorii</i>
Pink rib	<i>Pseudomonas marginalis/fluorescens</i>
Soft rot	<i>Pectobacterium carotovorum</i> or <i>Pseudomonas fluorescens/marginalis</i>
South Carolina disease	<i>Xanthomonas axonopodis</i> pv. <i>vitians</i>
Stem rot	<i>Pseudomonas cichorii</i>
Varnish spot	<i>Pseudomonas cichorii</i>
Virginia disease	<i>Xanthomonas axonopodis</i> pv. <i>vitians</i>

Xanthomonas axonopodis* pv. *vitians

Synonyms: *Bacterium vitians*, *Bacterium lactucae*, *Xanthomonas vitians*, *Xanthomonas lactucae*, *Xanthomonas campestris* pv. *vitians*, *Xanthomonas hortorum* pv. *vitians*

Diseases and Symptoms

Lettuce

Bacterial leaf spot, South Carolina disease, Virginia disease, head rot. Dark, brown to black, initially water-soaked, spots/lesions and larger V-shaped lesions on leaves. Larger areas may turn necrotic. Dark brown/black longitudinal lesions may also occur on the flowering stems and flower stalks.

Chicory & Endive

Not known to occur.

Distribution

USA, Canada, Japan, New Zealand, South Africa, Italy, Venezuela, Australia, Brazil, Germany, Hawaii, USSR, Zimbabwe, Turkey. Has also been isolated in the UK in 1995 and 1999 and Portugal in 1992 and 1994. Considered Non-Indigenous to the UK (but not EC).

Notes

Disease optimum around 23°C.

The pathogen is seedborne and can be detected in commercial seed lots. The spread of the disease around the world is most likely associated with the dissemination of infested seed. Most seed is probably 'contaminated' rather than internally infected.

Xav is a poor soil inhabitant, but may survive in soil in association with infected plant debris for up to four months following an infected crop.

Control

Use clean seed; however there are no standards for seed health or detection. Rotation. Avoid movement in fields where plants are wet. Use less susceptible cultivars (research is underway in the USA to develop resistant lines). Spray treatment with Serenade (biological) and copper may give significant reductions under conditions of mild disease pressure.

Sphingomonas suberifaciens

Synonyms: *Rhizomonas suberifaciens*

Diseases and Symptoms

Lettuce & Endive

Corky Root. yellowing, wilting, poor growth, reduced head size, initially yellow-brown root lesions, eventually the tap root becomes rough and cracked (i.e. corky).

Distribution

USA, Italy, England, Netherlands, Spain and Greece.

Control

Use resistant or less susceptible varieties. Resistant lines have been released by USDA's Agricultural Research Service. Use transplants rather than direct drilling to minimise period of exposure to the pathogen.

Pectobacterium carotovorum

Synonyms: *Bacillus carotovorus*, *Bacterium carotovorum*, *Erwinia carotovora*, *Erwinia carotovora* subsp. *carotovora*.

Diseases and Symptoms

Butt rot (field), *Jelly butt*. Outer leaves may show sudden wilting as plants approach maturity. The internal core of the stem shows a wet, slimy, jelly-like rot. Symptoms can be easily confused with lettuce drop caused by *Sclerotinia* fungi.

Soft rot. Brown to greenish-black, wet, slimy collapse and disintegration of affected tissues.

Distribution

Worldwide.

Notes

Pect. carotovorum is considered as an opportunistic pathogen and will cause soft rots in a wide range of plant species both in the field and post-harvest under suitable environmental conditions, and especially as a secondary invader of already damaged tissues. As it is a facultative anaerobe, disease is often associated with poor ventilation leading to condensation and surface wetness.

Pect. carotovorum is often considered to be ubiquitous and soil-borne. It is likely that it can survive in association with volunteers, in the rhizosphere of many weeds, in plant debris and crop residues remaining in the field.

Long distance dispersal of soft rot Pectobacteria has been shown to occur in aerosols generated by rain impact on diseased plants, overhead sprinkler irrigation and pulverization.

Control

Field

Avoid physical damage and excessive moisture, use tolerant cultivars. Crop rotation. Good hygiene.

Post harvest

Rapid cooling.

Pseudomonas fluorescens/marginalis

Synonyms: *Bacterium marginale*, *Phytomonas intybi*, *Pseudomonas intybi*, *Pseudomonas marginalis* pv. *marginalis*.

Diseases and Symptoms

Lettuce

Marginal Leaf blight, Kansas disease. Slight wilting, water-soaking, browning and necrosis of leaf margins. Initially, necrotic areas may be soft, later becoming dry and papery.

Bacterial wilt, butt rot (glasshouse). Heads may wilt or collapse with leaf colour changing from shiny to dull green. Soft-rot of core of the stem, becoming apparent as plants reach maturity.

Soft rot, head rot, leaf rot, midrib-rot (glasshouse). Brown to greenish-black, wet, slimy rot.

Pink rib. Post-harvest pink discolouration of the midrib tissues at the base of the outer leaves.

Chicory and Endive

Soft rot. Initially brown to black wet spots on the leaves that enlarge into larger areas. The disease may also progress through the veins, leaves may wither and die. Young leaves may stay healthy for some time, but finally rot from the base of the plant. In dry weather, disease progress may stop.

Distribution

Worldwide.

Notes

The taxonomy and nomenclature of this pathogen is confusing. The name *Ps. marginalis* is not used consistently in the literature; it is often used for any fluorescent Pseudomonad strain which produces soft-rot enzymes. Such strains could legitimately be called *Ps. fluorescens*, but not all strains of *Ps. fluorescens* are pathogenic and produce soft-rot enzymes.

Ps. marginalis/fluorescens are generally considered as opportunistic pathogens, requiring wounds for entry into plant tissues. Diseases are often associated with cooler conditions and high humidity/moisture levels. *Ps. marginalis/fluorescens* can cause soft rot on vegetables even at very low temperatures (0.4-1°C); and the pink rib symptoms seen in harvested lettuce may be the result of infection at low temperatures.

Bacteria identified as *Ps. marginalis/fluorescens* have been found in many habitats including the rhizosphere, soil and industrial waste sites, and are frequently reported as part of the microflora of harvested lettuce. *Ps. fluorescens* is well established as a soil and rhizosphere inhabiting bacterium, and some strains are used as biocontrol agents or plant growth promoting bacteria, but in most cases there is no pathogenicity data. *P. marginalis* may survive in the soil for up to 4 months depending on temperature and moisture.

Strains of soft-rotting *Ps. fluorescens* have been shown to be transmitted from seed to seedling and subsequently survive on symptomless lettuce leaves.

Control

In the crop

Avoid wet conditions and high humidity. Rotation and destruction of crop debris prior to planting. Use less susceptible cultivars.

In storage

Avoid physical damage, low storage temperatures (close to 1°C) and low humidity. Controlled atmosphere storage (with elevated carbon dioxide levels) may reduce storage rots by limiting growth.

Pseudomonas cichorii

Synonyms: *Phytomonas cichorii*, *Bacterium cichorii*, *Bacterium endiviae*, *Pseudomonas endiviae*, *Phytomonas endiviae*

Diseases and Symptoms

Lettuce

Varnish spot. Dark-brown shiny necrotic spots (i.e. varnish spots) on inner leaves, 2-3 layers down from the outside wrapper leaves. Areas along veins are most often affected. The outer leaves generally do not show any symptoms,

Head rot. General rot.

Midrib rot, stem rot (glasshouse butterhead). Dark greenish-black slimy rot along the midrib.

Chicory & Endive

Bacterial leaf spot, blight. Dry, dark grey-to-black lesions on leaves that expand to several cm in diameter.

Distribution

Worldwide.

Notes

Ps. cichorii has been reported as causing disease on cabbage, celery, tomato and chrysanthemum and a number of other crops, with over 40 species of vegetables and ornamentals listed as 'natural' hosts.

The prevalence of *Ps. cichorii* in lettuce is often associated with climatic conditions. In the UK, *Ps. cichorii* is likely to be favoured by warmer conditions than those which favour *Ps. marginalis/fluorescens*.

Ps. cichorii may survive in the soil in association with crop debris from a previously infected crop, but there is no evidence that *Ps. cichorii* is a soil inhabitant, or is able to survive in the soil free of plant debris. *Ps. cichorii* can survive as epiphyte on leaf surfaces in the absence of symptoms and has been detected on lettuce leaves prior to head formation. It has apparently been detected in irrigation water in California.

Control

Avoid the use of contaminated irrigation water. Rotation.

Financial benefits

No direct financial benefits have arisen from this project. It is anticipated that there will be a follow-on experimental project targeted at identifying the primary causal agents in the UK and opportunities for improved disease management.

Action points for growers

- Symptoms are not a reliable indicator of the casual bacterial pathogen, therefore it is important to send samples to a laboratory that specialises in bacterial pathogens for confirmation.
- *Xanthomonas axonopodis* pv. *vitians* is currently considered non-Indigenous in the UK (but not EC), and represents a significant threat to UK lettuce growers. Growers should be aware that, although seedborne, there is no current requirement for seed testing.

Science Section

Introduction

Bacterial diseases have been causing sporadic, but severe, problems on outdoor and protected lettuce crops for a number of years. Most recently, severe losses have occurred in outdoor crisphead crops with entire crops rendered un-marketable and losses estimated as up to £0.5 million by a single grower.

The outdoor UK lettuce crop has a value of over £70 million (Defra 2006), and given the production and market structure, losses of individual crops can have a major impact on continuity of supply and the profitability of individual growers, depending on market conditions.

There are potentially several bacterial diseases/pathogens which may affect lettuce: specific pathogens which are the primary cause of the disease symptoms or opportunistic invaders of tissues which have already been either physically damaged or affected by fungal pathogens.

Erwinia carotovora and fluorescent *Pseudomonas* spp. (*Ps. fluorescens*/*P. marginalis*) have most often been associated with butt-rot and soft-rot symptoms in lettuce; *Xanthomonas campestris* pv. *vitiens* causes leaf spots and head rot and *Pseudomonas cichorii* is considered the specific cause of the disease varnish spot. The symptoms most recently reported seem to be consistent with varnish spot caused by *Pseudomonas cichorii*.

Isolations from clinic samples in the 2007 growing season have indicated the presence of three distinct *Pseudomonas* types which appear to be pathogenic.

As a result of difficulties with the taxonomy of fluorescent *Pseudomonas* spp. it is possible that diagnosis together with statements about the 'ubiquitous' nature of the causal organism(s) are sometimes incorrect.

Given the uncertainties over the primary causal agent(s) and their biology, a proposal to improve understanding of the causes of bacterial problems in (outdoor) lettuce was submitted in March 2007. This proposal comprised both practical laboratory work to identify the primary disease causing organisms and a survey of the existing literature. This revised proposal concentrates on the literature review component as requested by Field Vegetables Panel.

Search strategy and scope

A variety of approaches were used to identify relevant scientific and popular literature. These included computerised searches using web-based search engines such as Google, Google Scholar, Yahoo, etc.; computerised searches of academic literature using ISI - Web of Science, Agricola, etc.; computerised searches of specific journal databases, e.g. Phytopathology, Plant Pathology. Inevitably all of the computerised search engines favour the recent literature, therefore older literature cited in more recent publications was also followed up manually.

A number of 'Grower guides' and 'Leaflets' were identified, but these often reproduced the same general information, therefore only those containing comments or significant information not contained elsewhere are reported.

Several of the bacterial pathogens of lettuce also cause disease on endive and chicory, information is also included for these crops where relevant.

As the aim was to obtain information of practical relevance to growers and production, literature dealing with molecular genetics of the pathogens was not pursued in any detail.

Disease names

In the American Phytopathological Society (APS) publication, Compendium of Lettuce Diseases (Davis *et al.*, 1997), five bacterial diseases are recorded: Bacterial Leaf spot, Corky Root, Marginal Leaf blight, Soft Rot, Varnish Spot, each of these diseases is ascribed to a different pathogen. Butt rot is also described by Ellis & Maude (Ellis & Maude, 2001), and throughout the literature soft rot and head rot diseases are attributed to several different pathogens. This overlap of symptoms (and hence disease names) ascribed to particular bacterial pathogens presented some difficulties in the writing of this review, therefore, to minimise confusion/repetition, the following table (Table 1) lists the various disease names/major symptoms in lettuce which have been attributed to bacteria, and the main body of the review is organised according to pathogens rather than disease name or symptoms.

Table 1. Lettuce diseases and symptoms caused by bacteria and the pathogens

Disease name	Pathogen(s)
Bacterial leaf spot	<i>Xanthomonas axonopodis</i> pv. <i>vitians</i>
Bacterial wilt	<i>Pseudomonas marginalis/fluorescens</i>
Butt rot (field)	<i>Pectobacterium carotovorum</i>
Butt rot (glasshouse)	<i>Pseudomonas marginalis</i>
Corky root	<i>Sphingomonas suberifaciens</i>
Dry rot	<i>Xanthomonas axonopodis</i> pv. <i>vitians</i>
Head rot	<i>Pseudomonas cichorii</i> , <i>Pseudomonas marginalis/fluorescens</i> , <i>Pectobacterium carotovorum</i> , <i>Xanthomonas axonopodis</i> pv. <i>vitians</i>
Jelly butt	<i>Pectobacterium carotovorum</i>
Marginal leaf blight	<i>Pseudomonas marginalis/fluorescens</i>
Kansas disease	<i>Pseudomonas marginalis/fluorescens</i>
Midrib rot	<i>Pseudomonas marginalis/fluorescens</i> or <i>Ps. cichorii</i>
Pink rib	<i>Pseudomonas marginalis/fluorescens</i>
Soft rot	<i>Pectobacterium carotovorum</i> or <i>Pseudomonas fluorescens/marginalis</i>
South Carolina disease	<i>Xanthomonas axonopodis</i> pv. <i>vitians</i>
Stem rot	<i>Pseudomonas cichorii</i>
Varnish spot	<i>Pseudomonas cichorii</i>
Virginia disease	<i>Xanthomonas axonopodis</i> pv. <i>vitians</i>

Xanthomonas axonopodis* pv. *vitians

This is probably the most extensively studied bacterial pathogen of lettuce, as a result of a number of major epidemics in the USA over the last 15-20 years, with estimated losses of several millions of US dollars (Robinson *et al.*, 2006).

Diseases

Lettuce

Bacterial leaf spot (BLS), South Carolina disease (Brown, 1918), Virginia disease (Brown, 1918), head rot (Burkholder, 1954), dry rot.

Endive

Not known to occur on endive (Pernezny & Raid, 2006).

Symptoms

Dark, brown to black, initially watersoaked, lesions develop on the leaves. The spots may have chlorotic (yellow) haloes. Lesions developing along the leaf margins may expand towards the leaf veins to result in larger V-shaped lesions (Sahin & Miller, 1997). Later, larger areas of the leaves may turn necrotic. Dark brown/black longitudinal lesions may also occur on the flowering stems and flower stalks (Sahin & Miller, 1997). Dry rotting and collapse of leaves (Harrison, 1963) and head rots have also been attributed to *Xanthomonas axonopodis* pv. *vitians* (Burkholder, 1954).

Taxonomy

Synonyms: *Bacterium vitians*, *Bacterium lactucae*, *Xanthomonas vitians*, *Xanthomonas lactucae*, *Xanthomonas campestris* pv. *vitians*, *Xanthomonas hortorum* pv. *vitians*

The pathogen has most commonly referred to as *Xanthomonas campestris* pv. *vitians* (Xcv), although a major revision of the genus *Xanthomonas* by Vauterin *et al.* (1995) saw strains of the pathogen divided into two species and renamed as *X. axonopodis* pv. *vitians* (Xav) or *X. hortorum* pv. *vitians*. However, there is still some uncertainty/dispute about the correct nomenclature, and a recent study (Barak & Gilbertson, 2003) did not support these revisions, both Xav and Xcv are currently used in the scientific literature.

History and Distribution

The disease was first reported in the USA in 1918 (Brown, 1918), and has also been reported in Canada (Toussaint, 1999), Japan (Ohata *et al.*, 1979), New Zealand (Boeswinkel, 1977), South Africa (Wallis & Joubert, 1972), Italy (Stefani *et al.*, 1994), Venezuela (Daboin & Tortolero, 1993), Australia (Harrison, 1963), Brazil, Germany, Hawaii, USSR, Zimbabwe (Bradbury, 1986), Turkey (Marlatt & Stewart, 1956). The pathogen has also been isolated in the UK in 1995 and 1999 (NCPPB catalogue) and Portugal in 1992 and 1994 (J.D. Taylor Pers. comm.).

Note that Xav is considered Non-Indigenous to the UK (NCPPB catalogue), but it is not specifically mentioned in any legislation and there are no specific requirements for testing of seeds or planting material entering the UK.

Description

Xav is a Gram-negative, obligately-aerobic, rod-shaped bacterium, motile by a single polar flagellum, and produces yellow mucoid growth on YDC agar. Most strains appear to be genetically homogeneous with a narrow host range limited to cultivated and wild lettuce (Barak & Gilbertson, 2003) although pepper (*Capsicum*) may also be an alternative host (Sahin & Miller, 1998; Robinson *et al.*, 2006).

Aetiology/Infection

Much of the earlier literature is inconsistent about the conditions required for disease development (Robinson, 2003; Robinson *et al.*, 2006), but a recent study indicates the optimum to be around 23°C (Robinson *et al.*, 2006). These authors, based in Florida, consider that this makes BLS of lettuce a “cool weather” disease; in the UK we might consider that such an optimum makes it a “warm weather” disease, and as such we might expect it to become more prevalent if temperatures rise as a result of global warming.

Xav may move systemically upwards in lettuce stems (Sahin & Miller, 1997) and may move within the vascular system of lettuce plants in the absence of symptoms (Barak *et al.*, 2002)

Epidemiology

The pathogen is seedborne (Ohata *et al.*, 1982; Umesh *et al.*, 1996; Sahin & Miller, 1997) and can be detected in commercial seed lots (Zoina & Volpe, 1994). The spread of the disease around the world is most likely associated with the dissemination of infested seed (Robinson *et al.*, 2006).

Most seed is probably 'contaminated' rather than internally infected; this can result from systemic movement of the pathogen in the plant in the absence of symptoms (Barak *et al.*, 2002); and also from contamination of seed with infected plant material at harvest. The pathogen may spread rapidly during glasshouse transplant production with overhead irrigation (Wellman-Desbiens *et al.*, 1999)

In common with many other bacterial plant pathogens, *Xav* is a poor soil inhabitant, but may survive in soil in association with infected plant debris for up to four months following a previously infected crop (Barak *et al.*, 2001). Thus, in areas where short rotations are practised, debris may be as (or more) important as seed as the primary source of inoculum.

Control

The use of clean seed is important for control, however, there are no standard methods for detection of the pathogen in seed, and no target seed health standards. Given the potential for rapid spread from a few primary infectors in glasshouse transplants (Wellman-Desbiens *et al.*, 1999), and by analogy with black rot on brassicas, significant field epidemics could occur in transplanted crops with even very low levels of seed infestation.

Several studies have examined seed treatments (Zoina & Volpe, 1994; Sahin & Miller, 1997; Carisse *et al.*, 2000; Pernezny *et al.*, 2002). Seed treatment with hypochlorite and other treatments may reduce (but not necessarily eliminate) the pathogen from seed (Zoina & Volpe, 1994; Sahin & Miller, 1997) and Carisse *et al.* (2000) concluded that 1% sodium hypochlorite for 5 or 15 min was the most effective treatment. Pernezny *et al.* (2002) found that treatment of lettuce seed with aqueous 3 to 5% hydrogen peroxide or with copper hydroxide/mancozeb effectively reduced or eradicated *X. campestris* pv. *vitiensis* from heavily infested lettuce seed. However, given that the numbers of seeds examined in these studies were relatively small: even when authors report so-called eradication, the potential for significant epidemic development may still exist, especially in transplanted crops.

Pernezny & Raid (2006) suggest avoiding movement in fields where plants are wet and not to follow an infected crop with another lettuce crop.

Some studies have demonstrated differences in the relative susceptibility between cultivars (Sahin & Miller, 1997; Carisse *et al.*, 2000). It has been suggested that Romaine types are the most susceptible and butterhead least (Pernezny & Raid, 2006), but reports are conflicting (Pernezny *et al.*, 1995). It would appear that some research is underway in the USA to develop resistant lines (Bull, 2005).

There are limited options for effective control in the field, although one US study (Bull & Koike, 2005) has suggested that spray treatment with Serenade (a biological control agent, *Bacillus subtilis*) and Cuprofix (basic copper sulphate) may give significant reductions under conditions of mild disease pressure.

Sphingomonas suberifaciens

Disease

Lettuce and Endive

Corky Root

Symptoms

Symptoms on the top part of plant result from a lack of roots and vary depending on the extent of root damage: yellowing, wilting, poor growth, and reduced head size, with 92% yield reductions reported in susceptible cultivars. On the roots, the disease is first seen as yellow-brown lesions, especially on the tap root, which then enlarge and become darker. Eventually the tap root becomes rough and cracked (i.e. corky). Smaller feeder roots are also destroyed (O'Brien & van Bruggen, 1992; Ryder, 1999; Pernezny & Raid, 2006).

Taxonomy and History

Synonyms: *Rhizomonas suberifaciens*

The disease was originally attributed to various environmental conditions until van Bruggen *et al.* (1988) demonstrated the infectious nature of the disease. They then characterised (van Bruggen *et al.*, 1989) and named the causal organism as *Rhizomonas suberifaciens* (van Bruggen *et al.*, 1990b). More recently it has been transferred to the genus *Sphingomonas* as the original nomenclature was incorrect (Young *et al.*, 1996).

Distribution

The disease has been reported in the USA and Italy (van Bruggen *et al.*, 1989) and in England, the Netherlands, Spain and Greece (van Bruggen & Jochimsen, 1992).

Description

Sphingomonas suberifaciens is a slow-growing, strictly-aerobic, Gram-negative rod-shaped bacterium. Due to its slow growth on common bacteriological media isolation may be difficult.

Aetiology/Infection

No information.

Epidemiology/Control

Little is known about the epidemiology of this disease. The pathogen is soil-borne and can survive/live in association with a number of crop species (van Bruggen *et al.*, 1990a). It may be a common rhizosphere inhabitant, but only lettuce and closely-related species (i.e. endive, common sow-thistle, prickly lettuce) become diseased (van Bruggen *et al.*, 1990a; Datnoff & Nagata, 2003). The disease is reported to be worse in fields where crops are grown consecutively (Koike & Davis, 2007a), and so increasing the interval between crops may contribute to control (Alvarez *et al.*, 1992).

Host resistance is considered the most effective way of managing this disease (Koike & Davis, 2007a) and resistant lines have now been released by USDA's Agricultural Research Service.

The use of transplants rather than direct drilling may be useful to minimise disease impact in infested soils (van Bruggen & Rubatzky, 1992), as this reduces the relative period of exposure to the pathogen.

Pectobacterium carotovorum

Diseases

Lettuce

Butt rot (field), Jelly butt, (Cox, 1955; Wehlburg & Meyer, 1966; Stone, 1966; Taylor *et al.*, 1983; Taylor *et al.*, 1985), Soft rot.

Chicory and endive

Soft rot

Symptoms

Butt rot, Jelly butt

Heads appear initially sound, then outer leaves may show sudden wilting as plants approach maturity. The internal parenchyma tissues (core) of the stem become wet, slimy and macerated, and may take on a jelly-like appearance. Symptoms can be easily confused with lettuce drop caused by *Sclerotinia* fungi.

Soft rot

Brown to greenish-black, wet, slimy collapse and disintegration of the affected tissues.

Taxonomy and History

Synonyms: *Bacillus carotovorus*, *Bacterium carotovorum*, *Erwinia carotovora*, *Erwinia carotovora* subsp. *carotovora*.

Pectobacterium carotovorum was first described as *Bacillus carotovorus* by Jones (1901). For most of the last century it has been known as *Erwinia carotovora*, but following recent changes to the nomenclature, it has reverted to one of its earlier names: *Pectobacterium carotovorum* (Young *et al.*, 2004). It was originally divided into several subspecies according to host specialisation and other characteristics; although several of these sub-species have now been elevated to the rank of species (Young *et al.*, 2004).

In lettuce field crops, butt rot was first reported as being caused by *Erwinia carotovora* in Florida (Cox, 1955), and subsequently in Arizona (Stone, 1966) and again in Florida (Wehlburg & Meyer, 1966). In the early 1980s, butt rot was reported in the UK as being caused by *E. carotovora* (Taylor *et al.*, 1983; Taylor *et al.*, 1985). Butt rot in outdoor lettuce is also attributed to *Erwinia* in the most recent assured produce guide (Anon., 2006).

Distribution

Worldwide.

Description

Pect. carotovorum is a Gram-negative, rod-shaped bacterium, motile by peritrichous flagellae. As a member of the Enterobacteriaceae (like *Escherichia coli*), it can grow both aerobically and anaerobically (i.e. both in the presence and absence of oxygen). A key characteristic is its ability to produce pectolytic enzymes (i.e. soft rot enzymes).

Aetiology/Infection

Pect. carotovorum is often considered as an opportunistic pathogen and will cause soft rots in a wide range of plant species both in the field and post-harvest under suitable environmental conditions, and especially as a secondary invader of already damaged

tissues. As it is a facultative anaerobe, disease is often associated with poor ventilation leading to condensation and surface wetness, which may inhibit respiration and promote anaerobiosis.

Taylor *et al.* (1983) reported that observations on butt rot by ADAS indicated that the disease was more common in block-raised plants, in crops with high levels of nitrogen, and in wet conditions. The only reported studies on lettuce in the UK were done at the National Vegetable Research Station (NVRS, Wellesbourne) in 1983 and 1984 (Taylor *et al.*, 1985). In these studies, block-raised transplants were inoculated with *Pect. carotovorum* prior to planting, but there was little subsequent disease development (none in 1983 and 2-4% in 1984). Some work was also done at the University of Leeds at around the same time, but there do not appear to be any published reports. In Japan, *Pect. carotovorum* (with *Ps. cichorii*) was the main cause of head rots in the spring-cropping lettuce type, but it decreased in the autumn- and winter-cropping types (Ohata *et al.*, 1979).

Although all lettuce types can be infected by inoculation, the disease was only seen in crisphead types in the field in Florida. It was suggested that leaf ruptures which occur when crisphead types approach maturity provide entry sites for the pathogen (Wehlburg & Meyer, 1966)

Epidemiology

Pect. carotovorum is often considered to be a ubiquitous. It is considered to have greater capacity for survival in the environment in the absence of a host than the related potato blackleg pathogen *Pect. atrosepticum* (Perombelon & Kelman, 1980).

Pect. carotovorum is often referred to as a soil-borne organism (e.g. O'Neill & Stokes, 2004), however, Goto (1990) highlights disagreements amongst a number of definitive studies, and numbers declined rapidly following inoculation into peat blocks containing lettuce transplants (Taylor *et al.*, 1985). Nevertheless, longevity of the bacteria in soil is considered to be primarily related to temperature and soil moisture; the population of antagonistic flora may also play an important role. Long term survival of Pectobacteria in the absence of plants on which a rhizosphere relation can be established is considered doubtful (Anon., 2000). It is likely that *Pect. carotovorum* can survive in association with volunteer plants of the affected crop, in the rhizosphere of many weeds, in plant debris and crop residue remaining in the field.

Long distance dispersal of soft rot Pectobacteria has been shown to occur in aerosols generated by rain impact on diseased plants, overhead sprinkler irrigation and pulverization (Perombelon & Kelman, 1980).

Pect. carotovorum is not considered to be seedborne on true seed (Anon., 2000) and transmission on lettuce seed could not be demonstrated (Roberts & Conway, 2001).

Control

Field

In Hawaii, weekly applications of copper reduced disease and several tolerant cultivars were identified (Cho, 1977). Crop rotation may be beneficial (Raid, 2004) and removal of trash after harvest may help to prevent carry over of the disease (Anon., 2006). Avoidance of physical damage and excessive moisture may also be useful (Raid, 2004).

Post harvest

Rapid removal of field heat through vacuum cooling, and refrigeration may contribute to minimising losses (Raid, 2004).

Pseudomonas fluorescens/marginalis

Diseases

Lettuce

Marginal leaf blight, Kansas disease (Brown, 1918), bacterial wilt (Cleary, 1960), butt-rot (glasshouse) (Elmhirst, 2006; Anon., 2007), soft rot, head rot (Burkholder, 1954; Tsuchiya *et al.*, 1979), leaf rot, midrib-rot (glasshouse) (Bleyaert *et al.*, 1999; Cottyn *et al.*, 2005); pink rib (Hall *et al.*, 1971).

Chicory and Endive

Soft rot (Friedman, 1952)

Symptoms

Lettuce

Marginal Leaf blight, Kansas disease. Slight wilting, water-soaking, browning and necrosis of leaf margins. Initially, necrotic areas may be soft, later becoming dry and papery (Brown, 1918)

Bacterial wilt, Butt rot (glasshouse). Externally heads may appear sound or may show wilting with leaf colour changing from shiny to dull green. Heads may collapse and are easily detached from the butt/roots. Soft-rot of the parenchyma tissues (internal core) of the stem, becoming apparent as plants reach maturity.

Soft rot, head rot, leaf rot, midrib-rot (glasshouse). Brown to greenish-black, wet, slimy collapse and disintegration of tissues.

Pink rib. Post-harvest pink discolouration of the midrib tissues at the base of the outer leaves (Hall *et al.*, 1971). However, many reports consider these symptoms to be a physiological disease.

Chicory and Endive

First symptoms are small, brown to black wet spots on the leaves that enlarge under humid weather conditions, turning into large, wet, brown to black necrotic lesions. In later stages, the disease may also progress through the veins, and leaves may wither and die. Young leaves may stay healthy for some time, but finally rot from the base of the plant. In dry weather, disease progress may stop (Anon., 2000).

Taxonomy and History

Synonyms: *Bacterium marginale*, *Phytomonas intybi*, *Pseudomonas intybi*, *Pseudomonas marginalis* pv. *marginalis*.

Ps. marginalis was first described as *Bacterium marginale* causing a marginal leaf blight (Kansas disease) on lettuce in the USA by Brown (1918), and in the UK by Paine & Branfoot (1924), and has since been associated with a range of soft-rot type of symptoms in lettuce. It was first described from chicory as *Phytomonas intybi* by Stevens (1925) It has also been recorded as causing disease on a wide range of host plants (Bradbury, 1986). Most recently in the UK *Ps. marginalis/fluorescens* has been reported as the primary cause of Spear rot in Broccoli (Roberts, 2001) and has been associated with browning and soft-rot of cut-salads (Roberts & Conway, 2001).

The taxonomy and nomenclature of this pathogen is confusing. The name *Ps. marginalis* has been commonly used for fluorescent soft rot pseudomonads belonging to LOPAT group IVa (Lelliot & Stead, 1987) or resembling *Ps. fluorescens* biovar 2 (*P. marginalis sensu stricto*) or for any fluorescent, oxidase positive soft rot pseudomonad (*P. marginalis sensu lato*). Janse *et al.* (1992) used fatty acid analysis and other tests to

investigate the taxonomy of strains originally identified as *P. marginalis* or *Ps. fluorescens* bv. 2 from different hosts and geographic origins. They concluded that the occurrence of soft rot activity in many diverse fluorescent, oxidase-positive pseudomonads did not justify the designation of soft rot strains that conform more or less to biovar 2 (i.e. *P. marginalis*) as a separate species. Subsequent work by Brosch *et al.* (1996) on ribotyping (rRNA restriction patterns) and SDS-PAGE of whole cell proteins (van Canneyt *et al.*, 1996), continues to support this conclusion.

Further adding to the confusion: *Ps. marginalis* has been sub-divided into three separate pathovars (*alfalfae*, *marginalis*, *pastinaceae*) (Young *et al.*, 1978), but the validity of this may be doubtful (Lelliot & Stead, 1987).

In many publications reporting soft rot diseases caused by *Ps. marginalis* or *fluorescens* it is not possible to determine if the pathogen conforms to *Ps. fluorescens* bv. 2 or some other form is involved, further adding to the taxonomic confusion.

It is important to note that whereas all strains identified/characterised as *P. marginalis* produce soft-rot enzymes (and hence are likely to be pathogenic at least to some extent), not all strains of *Ps. fluorescens* produce soft-rot enzymes (and hence may be non-pathogenic).

Distribution

Worldwide (Bradbury, 1986; Anon., 2000).

Description

Ps. marginalis/fluorescens is an aerobic, Gram-negative, rod-shaped bacterium, motile by polar flagellae, and produces fluorescent pigment on certain agar media. Strains characterised as belonging to 'LOPAT' group IVa (Lelliot *et al.*, 1966; Lelliot & Stead, 1987) are Levan positive, Oxidase positive, Potato rot positive, Arginine dihydrolase positive, Tobacco hypersensitivity negative (i.e. LOPAT + + + + -) and are usually identified as *Ps. marginalis*. Strains which do not produce Levan and are characterised as belonging to LOPAT group IVb (i.e. LOPAT - + + + -) are usually identified as *Ps. fluorescens*. Regardless of whether strains are identified as *Ps. marginalis* or *fluorescens*, the key characteristic is that, unlike *Ps. cichorii*, pathogenic strains produce pectolytic (soft-rot) enzymes and rot potatoes.

Aetiology/Infection

Ps. marginalis/fluorescens are generally considered as opportunistic pathogens, requiring wounds for entry into plant tissues. The soft-rot symptoms result from the maceration of tissues and break down of the middle lamellae and cell walls with pectic enzymes.

Diseases caused by *Ps. marginalis/fluorescens* are often associated with cooler conditions and high humidity/moisture levels. In lettuce they seem to be particularly associated with disease in protected crops. Thus, in Japan *Ps. marginalis* was prevalent in Autumn and Winter poly-tunnel crops (Ohata *et al.*, 1979), and is associated with butt rot and mid-rib rot in protected Winter crops in the UK (O'Neill, 2004; Anon., 2007), Belgium (Bleyaert *et al.*, 1999), and Canada (Elmhirst, 2006).

Ps. marginalis/fluorescens can grow and cause soft rot on vegetables even when stored at very low temperatures (0.4-1°C) (Brocklehurst & Lund, 1981); and the pink rib symptoms seen in harvested lettuce may be the result of infection by *Ps. marginalis* at low temperatures (Hall *et al.*, 1971).

As well as pectolytic enzymes, some strains of *Ps. marginalis/fluorescens* can produce a biosurfactant (natural wetting agent). This biosurfactant seems to play a critical role in

the development of spear rot of broccoli (Hildebrand, 1989; Roberts, 2001), and may also be important for disease development in lettuce.

Cleary (1960) reproduced symptoms with *Ps. marginalis*-like isolates by stabbing the stem, but not by soil inoculation. He suggested that the absence of abscission layer in lettuce may mean that invasion occurs via decaying cotyledons and older leaves in contact with wet soil.

Epidemiology

As a result of the taxonomic confusion, some care is needed in evaluating some of the published references to isolation of the pathogen; it is not always clear if the strains isolated are plant pathogenic or indeed would be pathogenic on lettuce.

Bacteria identified as *Ps. marginalis/fluorescens* have been found in many habitats including the rhizosphere, soil (Cuppels & Kelman, 1980), deep ground water (Jain *et al.*, 1997) and industrial waste sites. Bacteria identified as *Ps. fluorescens* are frequently reported as part of the microflora of harvested lettuce (Lund, 1983; Magnuson *et al.*, 1990; Wurr *et al.*, 2003). *Ps. fluorescens* is well established as a soil and rhizosphere inhabiting bacterium, and some strains are used as biocontrol agents or plant growth promoting bacteria, but in most cases there is no pathogenicity data.

P. marginalis has been reported to survive in the soil for a period of up to 4 months when the soil water content is 15-30% and at a temperature of 8°C, but at lower moisture levels and/or higher temperatures, survival is lower (Dealto & Surico, 1982). Curiously in this work, a soft-rotting strain survived better than a strain isolated from the rhizosphere. Thus, survival characteristics may be strain-specific rather than species-specific.

Strains of soft-rotting *Ps. fluorescens* (LOPAT Gp. IVb) have been shown to be transmitted from seed to seedling and subsequently survive on symptomless lettuce leaves (Roberts & Conway, 2001). It would seem that some strains of *Ps. fluorescens* are specifically adapted to attach to lettuce leaves (Takeuchi *et al.*, 2000).

Control

In the crop

The Assured Produce Protocol for protected lettuce (Anon., 2007) recommends that as the disease is favoured by wet conditions and high humidity, these should be avoided as far as possible.

Raid (2004) suggests that although considered ubiquitous, inoculum levels in soil may be reduced by crop rotation and destruction of crop debris prior to planting.

Considerable differences were recorded in the rate of disease development when lettuce cultivars were quantitatively assessed using a susceptibility index. Thus the use of less susceptible cultivars might reduce crop losses (Miller, 1980).

In storage

To avoid losses in storage due to soft rot caused by *Ps. marginalis*: physical damage should be avoided as much as possible, low storage temperatures (close to 1°C) and low humidity should be maintained (Wright, 1993). Controlled storage atmospheres (with higher carbon dioxide levels) may reduce storage rots by limiting growth (Barriga *et al.*, 1989).

Pseudomonas cichorii

Diseases

Lettuce

Varnish spot, head rot, midrib rot, stem rot

Chicory/Endive

Centre rot of chicory, Endive bacterial blight

Symptoms

Varnish spot

The term Varnish spot was first used by California lettuce growers in the mid 1970s to describe specific disease symptoms on crisphead lettuce.

The disease is characterised by dark-brown shiny necrotic spots a few mm across (i.e. varnish spots) which occur on the inner leaves, typically 2-3 layers down from the outside wrapper leaves. Lesions are not delimited by veins, but areas along veins are most often affected. The outer leaves generally do not show any symptoms, so that the disease does not become apparent until a crop is harvested and heads trimmed or cut open. This absence of external symptoms makes selective harvesting of healthy heads difficult or impossible and increases the effective losses due to the disease, leading to the abandonment of entire fields. (Grogan *et al.*, 1977; Koike & Davis, 2007b)

Head rots

Many reports of *Ps. cichorii* on lettuce, both before and since Grogan *et al.* (1977) first reported varnish spot, refer to the symptoms as more general 'rots' or 'head rots' (Stapp, 1935; Burkholder, 1954; Ohata *et al.*, 1979; Dhanvantari, 1990; Shirikawa *et al.*, 1998; Bleyaert *et al.*, 1999; Aysan *et al.*, 2003; Elmhirst, 2006), with little or no mention of spots. This may be simply a question of emphasis, or timing in relation to the observation of symptoms, or perhaps due to particular conditions giving rise to the predominance of different symptoms.

Midrib rot, stem rot (glasshouse butterhead).

Dark greenish-black slimy rot along the midrib of one or more inner wrapper leaves (Dhanvantari, 1990; Bleyaert *et al.*, 1999; Elmhirst, 2006; Cottyn *et al.*, 2007).

Chicory & Endive

Endive leaf spot, endive bacterial blight. Dry, dark grey-to-black lesions on leaves that expand to several cm in diameter (Pernezny & Raid, 2001).

Taxonomy and History

Synonyms: *Phytomonas cichorii*, *Bacterium cichorii*, *Bacterium endiviae*, *Pseudomonas endiviae*, *Phytomonas endiviae*

Pseudomonas cichorii was identified as the cause of varnish spot by Grogan *et al.* (1977). It was first reported as causing a rot on lettuce in Germany (Stapp, 1935) and later in Brazil (Freire, 1954) and the USA (Burkholder, 1954).

Even before it was reported as a pathogen of lettuce, *Ps. cichorii* was first described (as *Phytomonas cichorii*) in 1925 (Swingle, 1925) as causing a centre-rot of chicory, and has also been reported as causing disease on cabbage (Wehlburg, 1963), celery (Thayer & Wehlburg, 1965), tomato and chrysanthemum (McFadden, 1961) and a number of other crops. Bradbury (1986) lists over 40 species of vegetables and ornamentals as 'natural' hosts and provides a further list of hosts 'by inoculation'. More hosts have been added

recently, e.g.: *Ficus* (Chase, 1987), *Lobelia* (Putnam, 1999), turmeric (Maringoni *et al.*, 2003).

Distribution

Ps. cichorii has a worldwide distribution (Bradbury, 1986).

Description

Ps. cichorii is an aerobic, Gram-negative, rod-shaped bacterium, motile by polar flagellae, and produces a fluorescent pigment on certain agar media. It belongs to Pseudomonas rRNA Group I, and is differentiated from other members of the group on the basis of its 'LOPAT' characters (Lelliot *et al.*, 1966; Lelliot & Stead, 1987). Placed in LOPAT Group III, it is Levan negative, Oxidase positive, Potato rot negative, Arginine dihydrolase negative, Tobacco hypersensitivity positive (LOPAT – + – – +). Of particular note is that unlike *Ps. marginalis/fluorescens*, it does not produce pectolytic enzymes and rot potato slices.

Aetiology/Infection

Following artificial inoculation, disease symptoms are produced after 24-36 h at 23°C (Grogan *et al.*, 1977). In Japan, the prevalence of *Ps. cichorii* in lettuce in different cropping areas seems related to the climate: the disease was prevalent in the spring-cropping types in northern Japan, the summer-cropping type in the central highlands and the autumn-cropping type in the ordinary areas, but seldom occurred in the winter-cropping type in central or south-western Japan (Ohata *et al.*, 1979). On celery, the pathogenicity of *Ps. cichorii* was favoured by higher temperatures than *Ps. syringae* pv. *apii* (30 vs. 20°C) (Thayer, 1965), but on chrysanthemums is inhibited above 28°C (Jones *et al.*, 1984). It would seem that in the UK, *Ps. cichorii* is likely to be favoured by warmer conditions than those which favour *Ps. marginalis/fluorescens*.

In studies using fluorescently-labelled antibodies to track the bacteria, Hikichi *et al.* (1996a) found that *Ps. cichorii* entered lettuce leaves through stomata, then multiplied in intercellular spaces of the epidermis and colonised intercellular spaces of mesophyll. Further studies using a *lux*-marked (bioluminescent) strain demonstrated that the bacteria then moved into the vascular bundles (Hikichi *et al.*, 1998)

A peptide toxin (chichorin) is responsible for the development of the brown lesions (Shirikawa *et al.*, 1998) which also requires *de novo* protein synthesis in the host plant (Hikichi *et al.*, 1998; Shirikawa *et al.*, 1998), i.e. symptom development requires an active host-response.

The disease only appears in the field as heads approach maturity, and this probably results from increased susceptibility to infection in mature leaves/plants (Grogan *et al.*, 1977; Hikichi *et al.*, 1996b).

Epidemiology

Grogan *et al.* (1977) state that *Ps. cichorii* is soil-borne, and this is frequently repeated in a number of subsequent publications. However, they (Grogan *et al.*, 1977) found *Ps. cichorii* represented only 2 out of 196 strains isolated from two out of four fields with a previous history of disease. Hikichi *et al.* (1996b) isolated *Ps. cichorii* from soil in Japan following a severely infected crop.

Bazzi *et al.* (1984) studied the survival of marked strains in the soil in Italy. The marked mutant that they used was successfully re-isolated from lettuce debris on the soil surface, but not from the soil after it had been incorporated. Nevertheless, 115 days after incorporation of the debris, the mutant was found associated with vein lesions in lettuces planted the following year in the same field. They concluded that *Ps. cichorii*

survives in the soil, associated with infected lettuce debris, but that the population level was below detection threshold of the test method.

On the basis of these studies it seems that *Ps. cichorii* has the potential to survive in the soil in association with crop debris from a previously infected crop, but there is no evidence that *Ps. cichorii* is a soil inhabitant, or is able to survive in the soil free of plant debris. Arguably therefore, it is not truly soil-borne, in the same sense as e.g. *Agrobacterium* spp., *Pythium*, or club-root.

Seed transmission does not appear to have been studied.

Ps. cichorii can survive as epiphyte on leaf surfaces in the absence of symptoms (Jones *et al.*, 1990; Hikichi *et al.*, 1996b) and has been detected on lettuce leaves prior to head formation (Hikichi *et al.*, 1996b).

Cottyn *et al.* (2007) suggest that the pathogen may be introduced with planting material or irrigation water. According to the University of California Pest Management Guidelines (Koike & Davis, 2007b), varnish spot often occurs in places where *Ps. cichorii* contaminates water in reservoirs. When such water is used for sprinkler irrigation of head lettuce crops at the rosette stage, the bacteria are introduced into the developing head.

Control

Hikichi *et al.* (1998) indicate that *Ps. cichorii* is hard to control in the highlands of Japan, as crop rotation and soil fumigation are practically ineffective.

The University of California Pest Management Guidelines (Koike & Davis, 2007b) recommend avoiding the use of contaminated reservoir water when sprinkler irrigating head lettuce at susceptible stages and to rotate away from susceptible crops for one year.

Discussion and Conclusions

The literature on bacterial diseases of lettuce was reviewed, with information drawn from some 233 references. The majority of the research has been done in the USA and Japan, with relatively little in UK. The majority of the research has focussed on identification, characterisation and taxonomy of the pathogens, with relatively little definitive work looking at epidemiology and/or developing practical control measures.

Several of the pathogens are reported to cause similar symptoms, especially those characterised as rots. Thus, *Pseudomonas cichorii*, *Pseudomonas marginalis/fluorescens*, *Pectobacterium carotovorum*, *Xanthomonas axonopodis* pv. *vitians* are all reported to cause 'Head rots'. This overlap in the use of disease names in the literature presented some problems in searching and interpreting the literature. This was further compounded by changes in the nomenclature and accepted taxonomy of the pathogens, especially in the case of the 'two' main *Pseudomonas* pathogens, and in the earlier literature where there are sometimes discrepancies in the descriptions of their characteristics. With the advent of modern molecular DNA tools, the taxonomy and nomenclature of all bacterial pathogens has undergone some revisions in recent years. However, there is by no means a universally accepted nomenclature at this time.

One of the five pathogens, *X. axonopodis* pv. *vitians*, is a quarantine organism in the UK, although, given that it is seedborne and that there is no statutory requirement for testing of lettuce seed, it is quite likely that it could be introduced at some point (if not already). Given suitable climatic conditions (increasingly likely with the advent of global warming), this pathogen could potentially cause significant losses.

Several of the bacterial pathogens of lettuce are widely considered to be ubiquitous and soil-borne, however convincing evidence for either is often lacking. It is important to distinguish between bacteria that are soil inhabitants and maintain a consistent population from those which have been introduced with infected crop debris and survive in declining numbers. The evidence suggests that, except for the corky root pathogen, *Sphingomonas*, the other pathogens fall into the latter group: they may survive in association with infected crop debris for varying periods depending on the environmental conditions and the other microflora present.

The potential for transmission of the *Pseudomonas* pathogens on seed seems to have been ignored by nearly all researchers, perhaps because of assumptions about their ubiquitous nature. Only a single and very limited study has been done by the author (Roberts & Conway, 2001); this study demonstrated the transmission of a *Ps. fluorescens* strain belonging to LOPAT Group IVb (i.e. not *marginalis*) from lettuce seed to seedlings.

For most of the pathogens, the control options extracted from the literature are rather limited or vague, and could be generally stated/applied for almost any bacterial disease, e.g. rotations, avoiding wet conditions, copper sprays, etc. The one exception is BLS, where the seedborne nature of the disease is well established and therefore the use of clean seed is the main means of control.

For some of the diseases there are indications that some lettuce varieties may be less susceptible than others, especially in the case of the diseases caused by *Xanthomonas*, *Sphingomonas*, and *Ps. fluorescens/marginalis*.

Recommendations for further work

Some of the disease symptoms seen in recent disease outbreaks in field crisphead lettuce are consistent with varnish spot, other symptoms are not so specific and could be characterised as head rots. Thus a vital first step in any work is to identify the primary pathogen or pathogens.

Based on this review of the literature and the personal experience of the author, a 'magic bullet' solution to the recent problems in field grown lettuce crops is unlikely to be found. In common with many other bacterial plant diseases, successful disease management will depend on avoiding the introduction of primary inoculum, minimising its spread, and the use of 'less susceptible' cultivars.

The following approach is recommended for future work:

1. Determine/identify the primary pathogen(s) responsible for recent bacterial problems in (outdoor) lettuce.
2. Develop methods for detection of primary pathogen(s) in soil, water, seeds, and plant material.
3. Identify the main sources of the pathogen(s): i.e. sample and test soil, water sources, seeds and plant material associated with disease outbreaks and at different stages.
4. Monitor 'high-risk' crops: in attempt to identify particular pre-disposing or disease risk factors.
5. Compare the susceptibility of commonly grown varieties to the primary pathogen or pathogens.
6. Based on results of 1 to 5, devise and test disease management strategies.

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