Chapter 3
Pectobacterium and *Dickeya:* Environment to Disease Development

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Abstract The soft rot *Pectobacteriaceae* (SRP) infect a wide range of plants worldwide and cause economic damage to crops and ornamentals but can also colonize other plants as part of their natural life cycle. They are found in a variety of environmental niches, including water, soil and insects, where they may spread to susceptible plants and cause disease. In this chapter, we look in detail at the plants colonized

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and infected by these pathogens and at the diseases and symptoms they cause. We also focus on where in the environment these organisms are found and their ability to survive and thrive there. Finally, we present evidence that SRP may assist the colonization of human enteric pathogens on plants, potentially implicating them in aspects of human/animal as well as plant health.

3.1 Introduction

Soft Rot *Pectobacteriaceae* (SRP) live on a wide range of plants and cause disease on many of them. Some SRP have wide host ranges, while others have only one known host, suggesting a degree of specialization. Unfortunately, many ornamentals and crops, including some of our main global staple crops, are affected by such diseases. While potato is particularly affected by SRP-associated diseases in terms of their economic damage, other plants see disease more sporadically but when it occurs it can be equally as damaging. Rice, maize, banana and other major crops are all affected but, thankfully, global annual losses are limited. Ornamental plants can be lost to disease but may also play a role in the spread of SRP to crops due to the large number of these plants that move around the world. The bacteria live in, and are spread from, a variety of environmental niches including soil, water and insects, with some species of SRP being found only in a particular environment with no evidence of a plant host, e.g. there have been five new species identified from water sources in the past year (Table 3.1). It is clear, therefore, that as we turn our focus away from plants, and especially diseased plants, there may be a much greater number of species in the environment than was originally thought, potentially with new capabilities that we know little about. Where SRP do cause disease in plants, the source and method of spread, process of infection and disease symptoms are surprisingly similar, leading to anything from minor disease through to large areas of cultivation being lost. The use of contaminated planting material and climate in any particular year are the main factors that determine this incidence and severity. SRP are also very closely related to enteric animal and human pathogens, which are known to live and even cause disease in plants. It is no surprise, therefore, that they can co-exist on plants, potentially competing against each other but also with the latter providing a rich supply of food for their counterparts. In this chapter, we discuss host range, infection pathways, disease progression and symptoms. We also investigate SRP in the wider environment and discuss the potential for many more species being present—a journey that we have only just begun. We will finish with a look at how SRP interact with animal and human enteric pathogens in an area that is so far little understood.

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Table 3.1 List of known plant hosts for current *Dickeya* and *Pectobacterium* species.

Dickeya
D. aquatica
Isolated from water, *Daucus carota* (1)
D. chrysanthemi
Agave cupreata (2), *Chrysanthemum* sp., *Cichorium intybus* (3), *Euphorbia sp.* (3), *Kalanchoe*sp. (3), *Partheniums*p. (3), *Solanum melongena* (3) *Vanda* sp.
D. dadantii* subsp. *dadantii* and subsp. *dieffenbachiae
Amorphophallus konjac, *Anubias barteri*, *Brassica rapa*, *Daucus carota* (3), *Euphorbia pulcherrima* (12), *Fragaria*sp. (3), *Ipomoea batatas* (3), *Kalanchoe*sp. (3), *Malus domestica* (4), *Malus pumila* (5), *Musa* sp., *Phalaenopsis aphrodite*, *Philodendron*, *Saintpaulia ionantha(6), Solanum tuberosum* (3), *Tagetes patula*, *Vanilla planifolia*, *Zea mays* (7)
D. dianthicola
Begonia bertinii (8), *Chrysanthemum morifolium* (8), *Cichorium intybus*, *Cynara scolymus(9), Dahlia*sp. (8), *Dianthus caryophyllus*, *Hyacinthus* sp. (10), *Kalanchoe* sp., *Lycopersicon esculentum(9), Sedum*sp. (8), *Solanum tuberosum*
D. fangzhongdai
*Aglonema*sp. (3), *Allium fistulosum* (11), *Artocarpus heterophyllus* (13), *Cattleya*sp. (3), *Clivia miniata* (3), *Colocasia esculenta* (3), *Dracaneas*p. (3), *Iris*sp. (3), *Oncidium*sp. (3), *Phalaenopsis*sp. (14), *Pyrus*sp. (15), *Raphanus sativus* (16), *Vanda*sp. (3), *Yucca*sp. (3)
D. lacustris
Isolated from water; no known plant hosts (17)
D. paradisiaca
Musa sp., *Solanum tuberosum* (18)
D. poaceiphila
Megathyrsus maximus (19), *Saccharum officinarum* (19)
D. solani
Hyacinthus orientalis, *Muscari*sp. (20), *Solanum tuberosum*
D. undicola
Isolated from water; no known plant hosts (21)
D. zeae/D. oryzae
Ananas comosus (22), *Asimina triloba* (23), *Calanthe*sp. (3), *Canna edulis* (24), *Clivia miniata* (23), *Musa* sp., *Oryza sativa*, *Setaria*sp. (3), *Solanum tuberosum* (3), *Zea mays*
Pectobacterium
P. aquaticum
Isolated from water; no known plant hosts (24)
P. actinidiae
Actinidia chinensis (25), *Actinidia deliciosa*
P. aroidearum
Cucurbita pepo, *Ornithogalum dubium*, *Persea americana*, *Saccharum*, *Solanum tuberosum*, *Zantedeschia aethiopica*

(continued)

Table 3.1 (continued)

Dickeya
P. atrosepticum
Brassica rapa (26), *Helianthus annuus*, *Solanum melongena*, *Solanum tuberosum*, *Zantedeschia aethiopica*
P. betavasculorum
Beta vulgaris
P. brasiliense
Beta vulgaris, *Brassica oleracea*, *Capsicum annuum*, *Citrullus lanatus* (27), *Cucumis sativus*, *Cucurbita pepo*, *Cynara cardunculus*, *Neobuxbaumia tetetzo* (28), *Nicotiana tabacum*, *Raphanus sativus* (29), *Solanum lycopersicum*, *Solanum tuberosum*
P. cacticida
Carnegiea gigantea, *Helianthus annuus*
P. carotovorum
Abelmoschus esculentus, *Allium sativum* (30), *Artemisia absinthium*, *Brassica oleracea*, *Cichorium intybus*, *Citrellus lanatus*, *Cucumis sativus*, *Cynara cardunculus*, *Daucus carota* (1), Echonipsis chamaecereus (syn. *Chamaecereus silvestrii*), *Fritillaria imperialis*, *Hawthoria*, *Ipomoea batatas*, *Kalanchoe tubiflora*, *Lactuca sativa*, *Musa*sp. (31), *Opuntia* sp., *Orostachys japonica*, *Orostachys malacophylla*, *Papaver somniferum*, *Peperomia obtusifolia*, *Peperomia caperata*, *Plectranthus australis*, *Pilea cadierei*, *Pinellia ternata*, *Rheum rhabarbarum*, *Silybum marianum*, *Saintpaulia ionantha*, *Solanum lycopersicum*, *Solanum melongena* (32), *Solanum tuberosum*, *Spathiphyllum wallisii*, *Typhonium giganteum*
P. fontis
Isolated from water; no known plant hosts (33)
P. odoriferum
Allium ampeloprasum, *Allium cepa*, *Apium graveolens*, *Brassica oleracea*, *Brassica rapa*, *Cichorium endivia*, *Cichorium intybus*, *Daucus carota*, *Ipomoea batatas*, *Petroselinum crispum*
P. parmentieri
Solanum tuberosum
P. parvum
Solanum tuberosum (34)
P. peruviense
Solanum tuberosum (35)
P. polaris
Solanum tuberosum (36)
P. polonicum
Groundwater from a vegetable field (37)
P. punjabense
Solanum tuberosum (38)
P. versatile

(continued)

Table 3.1 (continued)

Dickeya
Allium porrom (39), *Brassica oleara* (39), *Cichorium intybus* (39), *Cynara scolymus* (39), *Chrysanthemum*sp. (39), *Cyclamen*sp. (39), *Daucus carota* (39), *Hyacinthus orientalis* (39), *Iris*sp. (39), *Lactuca sativa* (39), *Primula*sp. (39), *Solanum tuberosum* (39)
P. wasabiae
Brassica oleracea[a], *Eutrema japonicum*, *Ipomoea batatas*[a], *Solanum lycopersicum*[a], *Solanum melongena*
P. zantedeschiae
*Zantedeschiae*sp. (40)

Data from Charkowski (2018) with additional names underlined and corresponding references as follows: (1) Zaczek-Moczydlowska et al. 2019, (2) Cabrera-Huerta et al. 2019, (3) Suharjo et al. 2014), (12) Wei et al. 2018, (4) Fujikawa et al. 2019, (5) Ogoshi et al. 2019, (6) Boccara et al. 1991, (7) Askari et al. 2018, (8) Parkinson et al. 2009, (9) Samson et al. 2005, (10) van Doorn et al. 2011, (11) Tsai et al. 2019, (12) Jaffar et al. 2019, (13) Ališ et al. 2018, (14) Tian et al. 2016, (15) ncbi, microbial genomes, (16) Hugouvieux-Cotte-Pattat et al. 2019, (17) Hugouvieux-Cotte-Pattat et al. 2020, (18) Pritchard et al. 2013, (19) Khayi et al. 2015, (20) Oulghazi et al. 2019a, (21) Nor et al. 2019, (22) Yang et al. 2018, (23) Hu et al. 2018, (24) Pédron et al. 2019, (25) Yan et al. 2019, (26) Sadeghi-Seraji et al. 2018, (27) Zlatkovic et al. 2019, (28) Mejia-Sanchez et al. 2019, (29) Liu et al. 2019, (30) Xie et al. 2018, (31) Basim et al. 2019, (32) Huang et al. 2017, (33) Oulghazi et al. 2019b, (34) Pasanen et al. 2020, (35) Waleron et al. 2018, (36) Dees et al. 2017, (37) Waleron et al. 2019a, (38) Sarfraz et al. 2018, (39) Portier et al. 2019, (40) Waleron et al. 2019b.
[a]may be *P. parmentieri*

3.2 Plant Hosts of Soft Rot *Pectobacteriaceae*

SRP are broad host range pathogens able to colonize and sometimes infect a wide range of plant species, from potato to carnation, and are present in all climatic zones where plants are cultivated (Pérombelon 1988; Charkowski 2006). Although it is largely acknowledged that potatoes are the most economically important crop affected by SRP, these bacteria are also found on many other plants including other crops, ornamentals, weeds/wild plants and plant debris, across at least 35 % of angiosperm plant orders, as well as in irrigation and surface water, aerosols, insects and on contaminated tools and equipment (Charkowski 2018; Ma et al. 2007; Pérombelon 2002). When not causing disease, the bacteria live largely unnoticed on plants and in these different environments (Pérombelon and Hyman 1989; Ma et al. 2007; Toth et al. 2011). However, where disease is present it appears to affect mainly vegetables and ornamental plants, although other more economically important crops are affected, e.g. maize, rice, date palm and banana (Charkowski 2018). A detailed list of plant hosts is given in Table 3.1 (updated from Charkowski 2018), with some described in further detail below.

From Table 3.1, it can be seen that while some SRP have a wide host range, e.g. *D. dadantii*, *D. dianthicola, D. fangzhongdai*, *P. brasiliense*, *P. carotovorum*, *P. odoriferum* and *P. versatile*, others appear to have a much narrower one, e.g. *D. paradisiaca* and *D. actinidiae*, with some having only a single known host, e.g.

D. aquatica (*Daucus carota*—carrot), *P. betavasculorum* (*Beta vulgaris*), *P. zantedeschiae* (*Zantadeschia* sp.) and *P. parmentieri*, *P. parvum*, *P. peruviense*, *P. polaris* and *P. punjabense* (*Solanum tuberosum*—potato), with a final group having no known plant hosts, e.g. *D. lacustris*, *D. undicola*, *P. aquaticum*, *P. polonicum* and *P. fontis* (all water-associated). Interestingly, species with only potato as a host have all been named within the last 4 years, and those with no known host in the last year. This suggests a recent focus towards research on potato or water sources using new molecular methods of taxonomic identification (See Chap. 2). In time, new plant hosts for these water-associated species may be uncovered. For example, *D. aquatica* was identified only from water sources when originally published (Parkinson et al. 2014a) but was later found to infect carrot (Zaczek-Moczydlowska et al. 2019). Table 3.1 thus offers what is almost certainly an incomplete view of potential host plants for the different *Dickeya* and *Pectobacterium* spp. based on the limited number of plant species tested.

3.2.1 Potato and Other Solanaceae *Plants*

SRP infect a wide range of crops, especially those with soft flesh. While potato is economically the most important (see Chap. 8), other crops include chicory, carrot, eggplant (aubergine), maize, rice, sweet potato, date palm, tomato, tobacco, and brassica crops such as bok choy, Brussel sprouts, cabbage, cauliflower, Chinese cabbage, kale and turnip, along with fruits including apple, pear, strawberry, water melon, banana and Sharon fruit (Table 3.1). These infections are observed in most countries of the world (see Chap. 7).

Potato (a member of the genus *Solanum*—the most commonly cultivated species of which is *S. tuberosum*) is the most notable crop due to its production volume (368 M tonnes from 17.5 M hectares—FAOSTAT 2018) and its importance as a staple crop in many countries, combined with the extent of losses caused by SRP-related diseases. The ability of SRP to infect potato is therefore covered in detail throughout this book. Potato cultivation in China, Africa and elsewhere is expanding rapidly, especially in low income food deficient countries (a doubling of production over the last 20 years) with a global increase in production intensity on a decreasing area of land (FAOSTAT 2018). It is highly likely, therefore, that soft rot and blackleg diseases of potato will increase significantly in the future with associated economic losses. An example of the economic consequences of SRP on potato in Switzerland and extrapolation to the European Union is given in Chap. 8.

In addition to potato, SRP have been shown to cause disease on other *Solanum* spp. including tomato (*Solanum lycopersicum*) and eggplant (*Solanum melongena*) but have also been repeatedly isolated from symptomless *Solanum dulcamara* plants (a wild species with preference for wetlands) from natural habitats associated with potato production. *S. dulcamara* could therefore act as a reservoir for contamination of potato. Olsson (1985) reported the isolation of *Dickeya* spp. from symptomless *S. dulcamara* growing in a watercourse used for irrigation in Sweden (Olsson 1985).

Fikowicz-Krosko et al. (2017) reported *P. carotovorum* isolated from symptomless roots of *S. dulcamara* growing in a potato cultivation region in northern Poland. Similarly, *D. dianthicola* was found to infect *S. dulcamara* under glasshouse conditions, with only minor symptoms observed (Elphinstone 2008). However, Fikowicz-Krosko and Czajkowski (2018) recently reported the development of disease symptoms and systemic colonization of *S. dulcamara* plants (in culture tubes) inoculated with *D. solani*, similar to those observed on in vitro cultivated potato plants. In contrast, *S. dulcamara* plants grown in potting compost in a growth chamber did not develop symptoms after stem stab-inoculation with *D. solani* despite the relatively high inoculum of 10^5 cfu per inoculation point (Fikowicz-Krosko and Czajkowski 2017). This may further indicate that although SRP are able to colonize *S. dulcamara*, they may encounter problems in establishing infections.

3.2.2 Other Crops

Other crops infected by SRP include a wide range of fruit and vegetables with rice, maize and banana, together with potato, representing some of the world's most highly grown crops (FAOSTAT 2018). Bacterial stork rot and top rot are diseases of maize in tropical and subtropical countries, including Iran (*D. dadantii*), India, Mexico, Pakistan and the USA (*D. zeae*) and, like other soft rot diseases in these regions, they are particularly severe under high temperature and humidity conditions (Ahmed et al. 2000; Askari et al. 2018; Kumar et al. 2017; Lopez et al. 1986; Martinez-Cisneros et al. 2014). For example, a serious outbreak in Iran led to up to 50 % of plants in the diseased area being severely affected (Askari et al. 2018). Foot rot of rice, caused by *D. zeae*, was first reported in the 1970s in Japan and affects rice quality and yield (Goto 1979), with an increase in outbreaks more recently in Southeast Asia and Southern China, possibly due to changes in rice cultivation methods and climatic conditions (Liu et al. 2013; Pu et al. 2012). One of the most effective methods to control the disease in rice is the use of resistant varieties (Sect. 6.6; Li et al. 2018a). A recent study recognized two clades within *D. zeae* strains (Pédron and Van Gijsegem 2019), one of which has been renamed *D. oryzae* following reanalysis of rice strains (Wang et al. 2020). Banana is globally the most widely grown fruit and has a production of 116 M tonnes, rising six-fold in the last 60 years (FAO 2018). It is produced in over 150 countries worldwide with half the production in Asia. Outbreaks of soft rot disease in banana continue to cause substantial economic losses in China (*D. zeae*—Zhang et al. 2014), across South and Central America (*D. paradisiaca*—Blomme et al. 2017) and other countries including Korea, Iran, Turkey (*P. carotovorum* - Basim et al. 2019; Chio et al. 1988; Hassanzadeh 1990; Snehalatharani et al. 2010), and India (*D. paradisiaca* and *P. carotovorum*—Chattopadhyay et al. 1986; Gokul et al. 2019). For example, in 2009 a bacterial soft rot outbreak in China caused by *D. zeae* resulted in up to 82 % yield loss in the infected area, with a subsequent increase in incidence and severity to 6000 ha in 2012. Disease incidence ranged from 20–70 % and up to 90 % in some cases, with infected plants dying one week

after the appearance of symptoms. The importance of seedling quarantine has been identified as a major route to disease reduction, in a similar way to that of potato and other crops (Arun et al. 2012; Zhang et al. 2014). There is a relatively small amount of research on the above diseases in rice, maize and banana etc., especially given the high global production of these crops. This suggests that, while losses are potentially high for any given outbreak, they may have relatively minor economic impact globally compared to other pests and diseases of these crops or of SRP on potato.

3.2.3 Ornamental Plants

Soft rot disease by SRP in ornamental crops occurs mostly in herbaceous perennial geophytes (plants with underground storage organs) also known as flower bulbs. There are no reports of the disease in woody ornamentals. Ornamental geophytes are often characterized by fleshy organs such as leaves or petioles and a carbohydrate rich underground storage organ, i.e. a corm, tuber, rhizome or bulb that contains renewal buds located underground. In most cases, the typical ornamental SRP strains display a wide host range, overlapping hosts and have a wide geographical distribution (Charkowski 2018; Ma et al. 2007; Yishay et al. 2008). Other bacterial genera, such as *Bacillus*, *Burkholderia*, *Clostridia*, *Enterobacter* and *Pseudomonas* may also cause soft rot symptoms in storage organs of bulbous plants (Charkowski 2018; Dahaghin and Shams-Bakhsh 2014). Several hosts of soft rot disease are eudicot plants that hold storage organs or fleshy leaves, including *Begonia*, *Cyclamen*, *Dahlia, Kalanchoe, Pelargonium, Primula* and *Saintpaulia* (Dahaghin and Shams-Bakhsh 2014; O'Neill et al. 2012; Table 3.1). Other eudicot genera are *Chrysanthemum* and *Dianthus* (carnation) both of which are members of the top 5 most sold flowers, with various cultivars worldwide (Hanks 2018). These are frequently reported as hosts of *Dickeya* spp. and mainly *D. chrysanthemi*, *D. dadantii* and *D. dianthicola* (Charkowski 2018; Ma et al. 2007; Table 3.1). Another group of hosts include the families *Asphodelaceae*, *Agavaceae*, and *Cactaceae*, with fleshy species of Agave, Aloe vera and cacti such as *Acanthocereus, Chamacererus* and *Schlumbergera* often reported as hosts of *P. carotovorum* (Dahaghin and Shams-Bakhsh 2014; Ma et al. 2007). The most significant group of plant hosts of SRP are monocot bulb crops, which are traded as cut flowers, garden plants and potted plants. Several examples are *Clivia*, *Crinum*, *Crocus*, *Freesia*, *Fritillaria*, *Gladiolus*, *Hosta*, *Hyacinthus*, *Iris*, *Lilium*, *Ornithogalum*, *Tulipa* and *Zantedeschia.* Highly susceptible plants from this group belong to the family *Araceae* and include *Aglaonema*, *Dieffenbachia*, *Philodenderon*, *Scindapsus*, *Spathiphyllum*, *Syngonium* as well as *Zantedeschia*, all with high commercial importance as potted and garden plants, and mostly mentioned as hosts of SRP (Dahaghin and Shams-Bakhsh 2014; Ma et al. 2007; Table 3.1). Since many reports concerning ornamental hosts are from 1950–2000, several misidentified strains and species probably exist for both soft rot genera.

In Europe, *D. dianthicola* was first recorded as causing slow wilting and stunting on *Dianthus* in the Netherlands, UK and Denmark but has since appeared in other European nations (EFSA Scientific Opinion 2013). It was estimated that in 1958 26.2 % of carnation stocks in Denmark were affected by the disease (Hellmers 1958). *D. dianthicola* was thereafter listed as a quarantine organism on *Dianthus* (Council Directive 2000/29/EC) but damage has been limited in recent years due to strict glasshouse hygiene and certification of plant material (Toth et al. 2011). Janse and Ruissen (1988) suggested a degree of host specialisation for *D. dianthicola* strains involved in infection, as a strain isolated from *Dianthus* (NCPPB 453) was unable to cause symptoms in Kalanchoe. Although *Dickeya* spp. have been detected on a wide range of ornamental plants in Europe, only *D. dianthicola* and *D. solani* have also been found to infect potato, fuelling speculation that some *Dickeya* strains may have spread to potato from ornamental host plants. For example, *D. solani* strains isolated from potato in multiple countries were found to be closely related to a Dutch strain from *Hyacinthus*, while VNTR profiles within *D. dianthicola* and *D. solani* isolates from ornamentals and potato revealed common profiles between hosts (Parkinson et al. 2014b ;Toth et al. 2011; van der Wolf et al. 2014). While import of potatoes into Europe is controlled, the import of ornamentals is less closely regulated with the entry of many millions of plants for planting, e.g. in 2010 the Netherlands, Germany, Italy and France imported 160 M units of Kalanchoe, 53 M Begonia and 27 M Dahlia (EFSA Scientific Opinion). As some ornamental plants are grown in fields in rotation with potato, whether in Europe or elsewhere in the world, this could aid transmission to or from potato and potentially other crops (Parkinson et al. 2014b).

Pectobacterium spp., while causing disease on ornamental plants, show different host specialization, with *P. zantedeschiae* appearing to specialise on its host plant *Zantedeschia*, while *P. carotovorum* and other species have a wider host range on ornamental and other plants (Table 3.1). Atypical strains of *P. carotovorum* with a preference for monocot plants have been reported from several herbaceous monocot hosts including *Allium sativum* (Smith and Bartz 1990; Wright 1998; Seo et al. 2002), *Zantedeschia* sp. (Smith and Bartz 1990; Byther and Chastagner 1993; Wright 1998; Snijder and van Tuyl 2002; Wang et al. 2018), *Dieffenbachia* sp., *Scindapsus aureus* (Norman et al. 2003), *Ornithogalum* sp. (Ma et al. 2007), *Fritillaria imperialis* (Mahmoudi et al. 2007) and *Pinellia ternate* (Ying et al. 2007), where they have been shown to cause disease (Smith and Bartz 1990; Ying et al. 2007). A wide phylogenetic study suggested that these isolates (represented by an isolate from *Ornithogalum dubium* Ec106) were members of a larger "monocot clade", as they did not cluster with typical *P. carotovorum* strains (Ma et al. 2007). Isolates from the aroid houseplant *Syngonium podophyllum* and bulbs of *Iris* sp., also grouped with the isolate Ec 106 from *Ornithogalum* (Baghaee-Ravari et al. 2011). A survey carried out in Israel in commercial plots of *Zantedeschia* and *Ornithogalum* showed that about 80 % of the isolates displayed "monocot clade" characteristics. Testing a larger number of isolates from monocot hosts from several geographical locations, using internally transcribed spacer-PCR, 16S rRNA gene sequence analysis and AFLP, revealed that these isolates cluster together independently of their geographical origin (Yedidia et al. 2011). Finally, based on a large collection of representative *Pectobacterium*

strains, AFLP and MLSA phylogenies clustered most isolates from monocot hosts together in a unique cluster (cluster Pc V) (Nabhan et al. 2012). This cluster includes the strains SCRI109^T, SCRI121, SCRI3, SCRI102 and Pc1, three of which were initially identified as '*Erwinia aroideae'* by Townsend in 1904 describing soft rot bacteria from arum (*Zantedeschia* sp.) in the family *Araceae* (Nabhan et al. 2013). Accordingly, *P. aroidearum* was suggested and is now accepted as a new species, which mainly but not exclusively causes soft rot diseases on monocot hosts (Nabhan et al. 2013).

Soft rot is an economically damaging disease of orchids and was first reported on *Dendrobium* and *Phalaenopsis* sp. in South Korea (Lee et al. 1999). Soft rot disease of orchids is a major disease problem of *Phalaenopsis* in Florida (McMillan et al. 2007), with symptoms including macerated, brown and water-soaked leaves (Cating et al. 2008). It has also been found worldwide on other orchid species including Vanda, Oncidium and Tolumnia, with *Dickeya* spp. identified as the causal agent (Cating et al. 2009, 2010; Li et al. 2009). For example, Lin et al. (2015) showed that *Dickeya* spp. and not *Pectobacterium* spp. were the dominant soft rot pathogens of Onicidium orchid. Detached leaf assays have been developed for testing germplasm and progeny resistance in various orchid breeding programmes (Sudarsono et al. 2018). Recently, *Dickeya* spp. isolated from orchid, water and pears were identified as a new species following genomic analysis and named *D. fangzhongdai*. The first genomes of *Dickeya* isolates from orchid were sequenced in 2015 (Alic et al. 2015). However, later sequencing of *D. fangzhongdai* isolates revealed that the species represents typical orchid-associated strains and is phylogenetically similar to *D. solani* and *D. dadantii* but lacks the Stt Type II secretion system of *D. dadantii* (Zhang et al. 2018). The authors found that only orchid-associated strains were able to cause soft rot on orchids when reinoculated, suggesting a degree of host specificity.

3.2.4 Weeds Present Near Potato Production Areas

The survival of SRP on weeds has been recognized since the late 1960s (Burr and Schroth 1977; Kikumoto and Sakamoto 1969), and in more recent decades SRP strains have been isolated successfully from various weed and crop plants, including their consistent isolation from the rhizosphere of brassica plants (Burr and Schroth 1977; Gudmestad and Secor 1983; Pérombelon and Hyman 1989; Toth et al. 2015; Tsror et al. 2011; Zoledowska et al. 2018). Over 24 and 47 plant species in Colorado and Scotland, respectively, taken from both potato fields and fields with a history of potatoes, were found to be colonized mainly with *P. carotovorum* but also in some cases with *P. atrosepticum*. Weeds from virgin land (no history of potatoes) in Scotland but not Colorado were also found to yield *P. carotovorum* in some cases. Contamination increased as the season progressed to its highest in summer and appeared to be linked to temperature and moisture conditions (McCarter-Zorner et al. 1984, 1985).

In more recent surveys in Israel, symptomless plants of 12 species (*Cyperus rotundus*, *Orobanche aegyptiaca*, *Amaranthus spinosus*, *Polygonum equisetiforme*, *Chenopodium* sp., *Heliotropium* sp., *Centaurea iberica*, *Sorghum haepense*, *Malva nicaeensis*, *Cynodon dactylon*, *Amaranthus blitum* and *Solanum elaeagnifolium*) were collected from potato fields where *Dickeya*-infected potato plants were detected. *D. solani* was isolated only from *C. rotundus*, with 6.7 and 14.3 % of plants harboring the pathogen in 2009 and 2010, respectively (Tsror et al. 2011). In a more recent survey again in Israel, symptomless weed plants from 12 genera and 9 families (*Polygonum equisetiforme* (*Polygonaceae*), *Centaurea procurrens*, *Sonchus oleraceus* (*Asteraceae*), *Lolium rigidum*, *Phalaris brachystachys, Avena sterilis* (*Poaceae*), *Malva nicaeensis* (*Malvaceae*), *Amaranthus blitoides* (*Amaranthaceae*), *Chenopodium murale* (*Chenopodiaceae*), *Chrozophora tinctoria* (*Euphorbiaceae*), *Orobanche aegyptiaca* (*Orobanchaceae*), *Erucaria rostrate* (*Brassicaceae*)) were collected from potato fields where *Pectobacterium*- and *Dickeya*-infected plants were detected. Only *Malva nicaeensis* was found to be latently infected (with *P. brasiliense*) (Tsror et al. 2019). Weeds, although unspecified, from potato fields throughout Poland were found to harbor *P. parmentieri* that were indistinct from those on potato plants and tubers (Zoledowska et al. 2018). Similarly, Toth et al. (2015) also identified that *P. atrosepticum* was able to bind to unspecified weed species with similar efficiency to that on potato roots but that subsequent colonization was plant species dependent. They concluded that weeds, and potentially other crops, may be potential sources of contamination to potatoes in the field.

3.3 Environmental Niches, Survival and Dispersal of SRP in the Environment

Plants can become colonised/contaminated with SRP from a variety of environmental sources, e.g. in the case of potato from soil, aerosols, irrigation, rainwater and insects (Pérombelon and Salmond 1995). Recent research on SRP in environmental niches has used modern taxonomic methods to determine the species present (see below). However, in earlier studies characterizations of the isolates consisted mostly of biochemical and serological analyses, where most strains were classified as *Erwinia carotovora* subsp. *carotovora* or *Erwinia chrysanthemi*, indicating that isolates belonged simply to the present *Pectobacterium* or *Dickeya* genera. Serological analysis performed in these early works identified up to 21 serogroups, and a significant proportion of the isolates did not belong to known serogroups, pointing out the wide diversity of these isolates (Cappaert et al. 1988; Peltzer and Sivasithamparam 1988; Powelson and Apple 1984). Unfortunately, most of the strains isolated in non-host environments in these studies were not deposited in international collections. A survey of five international collections performed in 2018 indicated that amongst the 1293 *Pectobacterium* and *Dickeya* strains available, only 17 were isolated from non-host environments. Out of these 17 strains, twelve were isolated from water,

four from soils and one from plant-derived food. It is not possible therefore to assess today the taxonomic status of the strains isolated in these early studies and the extent to which species are presence away from plants remains an unanswered question. To overcome this issue, it is recommended that resampling is carried out in non-host environments to understand the full extent of SRP species present. Ideally, sampling would be extended to countries from different geographic regions and with different climates. Indeed, early studies were generally performed in a temperate region, but the relative proportion of the different species is likely to vary with climate. While water and soil are perhaps the most obvious environments for sampling, as SRP are known to be found there, it is possible that other environments, which have been much less or never studied, could also act as reservoirs of SRP, e.g. *Pseudomonas syringae* has been found in snow, alpine streams and lakes, and epilithic (attached to gravel and stone) river biofilms (Morris et al. 2013).

3.3.1 Soft Rot Pectobacteriaceae *in Water*

SRP have been identified in waterways globally, including in Australia, Finland, France, Malaisia, Poland, UK, Spain, Switzerland, and USA (Cahill et al. 2010; Hugouvieux Cotte Pattat et al. 2019; McCarter-Zorner et al. 1984; Harrison et al. 1987; Laurila et al. 2008; Laurila et al. 2010; Oulghazi et al. 2019a, 2019b; Palacio-Bielsa et al. 2010; Parkinson et al. 2014a; Pédron et al. 2019; Potrykus et al. 2016; Sueno et al. 2014; Waleron et al. 2019b). Surveys were performed both next to crop species/weeds but also in pristine alpine water or moorland, and positive samples were found even in areas remote from arable land, indicating a large circulation of these species. However, the frequency of detection tended to increase in rivers close to arable land, suggesting that irrigation water can serve as a potential source of inoculum for SRP species. Numerous reports have pointed to the contamination of surface water by SRP (Cappaert et al. 1988; Gudmestad and Secor 1983; McCarter-Zorner et al. 1984; Peltzer and Sivasithamparam 1988) and the potential contamination of plants via water reservoirs (Franc and Harrison 1987).

The presence of *Pectobacterium* spp. in surface water has been well documented in studies testing water from different sources, geographical locations and climates. *Pectobacterium* spp. have been isolated from winter snow in the mountains, a waterfall, rain, river, sea-, well- and ground-water and they are thus considered ubiquitous in nature (Pédron et al. 2019; McCarter-Zorner et al. 1984; Harrison et al. 1987; Maddox and Harrison 1988; Waleron 2019b). Sea water is considered as a reservoir from which *Pectobacterium* spp. are spread into the air as aerosols that are formed through the action of waves (Pérombelon and Kelman 1980). The bacteria are also thought to spread in the air as aerosols formed during rain splash, sprinkler irrigation and mechanical pulverization. These aerosols may play a role in spread of the bacteria to clean mini-tubers, which can be contaminated by SRP during the first field generation (Graham et al. 1979; Elphinstone and Pérombelon 1987).

Very early reports allude to the fact that infection of plants can occur via irrigation with contaminated water (Cappaert and Powelson 1987; Franc and Harrison 1987). Later studies focused on test water sources for the presence of SRP and the role that irrigation water plays in dissemination of these pathogens. For example, McCarter-Zorner et al. (1984) tested surface water in southern Scotland and Colorado and, from 572 water samples tested, 439 were positive for pectinolytic bacteria; 95 % being classified as *Pectobacterium* spp. and 9.8 % as *P. atrosepticum.* Similar results were obtained by Jorge and Harrison (1986), Maddox and Harrison (1988) and Pérombelon and Hyman (1987) who showed the predominance of *Pectobacterium* spp. (80 % compared to 99 %) and *P. atrosepticum* specifically (20 % compared to 1 %) in surface water in northern Colorado and eastern Scotland, respectively. In Oregon and Colorado, isolations from surface irrigation water and well water in 1985 and 1986 also commonly yielded *Pectobacterium* spp., followed by *Dickeya* spp. as the second most isolated SRP, although *P. atrosepticum* was rarely isolated (Cappaert et al. 1988). Furthermore, out of the 1436 strains isolated only 30 % could be characterized by serology, illustrating the great diversity of isolates obtained. In Australia and Finland, river surveys identified *Dickeya* spp. as the dominant genus at the time of the study (Cother and Gilbert 1990; Laurila et al. 2008). In the Australian survey, all positive samples were from water with a temperature above 16.2 °C (a climate where *Dickeya* spp. are more likely to be present on plants), which may explain why they were dominant in these samples compared to *Pectobacterium* spp. that have a lower optimal temperature (du Raan et al. 2016). Serological analysis of the 56 Australian isolates differentiated the *Dickeya* isolates into two serogroups representing the two Australian rivers sampled (Cother et al. 1992). The Finnish survey showed three distinct bacterial clades following analysis of 16S and 16S-23S sequences of the 24 *Dickeya* isolates, two of which were different from previously isolated *Dickeya* spp., while the third clade corresponded to *D. dianthicola.* Water isolates of *D. dianthicola* appeared to be more aggressive than those isolated from diseased potato plants (Laurila et al. 2008). These results again point to the large diversity of SRP isolates from water and their varying geographical distribution.

Populations of bacteria in water were shown to peak in mid- to late summer in Oregon and Colorado in the USA and in Scotland, coinciding with lush crop canopy growth and a conducive micro-climate for epiphytic growth and survival of bacteria (Jorge and Harrison 1986; Pérombelon and Hyman 1987; Cappaert and Powelson 1987). It is possible that with successive irrigation events during the summer months the numbers of bacteria on plants increase, leading to disease (Cappaert and Powelson 1987). In contrast, there was no seasonal variation in populations of SRP found in water sources in Florida, although strains of both *Dickeya* and *Pectobacterium* spp. were isolated from nursery retention ponds and lakes (Norman et al. 2003). The authors attributed this to a mild winter climate, drought during the sampling period, the nutrient-rich nature of the sampled water or the year-round cropping cycle in Florida (Norman et al. 2003). The levels of SRP in nursery retention ponds were higher than in natural lakes, indicating the possible role of recycled irrigation water in contamination of water sources (Norman et al. 2003). Armon et al. (1995) also warned of the risk of irrigation with reused water or water sources with high nitrate content,

as these sources may sustain the survival of SRP and in some cases allow regrowth of the bacteria. van Doorn et al. (2011) showed that *Dickeya* spp. survived poorly in rain and ditch water (surviving for only a few hours) compare to *P. atrosepticum* and *P. carotovorum*, both of which survived with little loss of viability for over 150 days. In tap water, *Dickeya* spp. also survived poorly but the *Pectobacterium* spp. also only survived for ca 2 days, presumably due to chemical treatment of the water. Recently, two strains belonging to the recently named *P. peruviense* species were isolated from river samples in France (Faye et al. 2018) indicating that "*P. peruviense*" has a wider geographic distribution than the Peruvian altiplano (Waleron et al. 2018).

Compared to *Pectobacterium* spp., *Dickeya* spp. are less commonly isolated from water. To understand which particular *Dickeya* spp. are recovered from water, detection of *Dickeya* positive samples was achieved through dedicated PCR screening of 7902 water samples from rivers, lakes, ponds and drainage ditches in Poland (Potrykus et al. 2016) and 230 samples from water courses in Scotland (Cahill et al. 2010). Overall *Dickeya* spp. detection was low (1.7 % of the Polish samples and 0.36 % of the Scottish samples), and in both countries *D. zeae* was the most abundant species recovered, followed by *D. chrysanthemi* in Polish samples. Among the Scottish samples, an undefined *Dickeya* sp. was also recovered together with a single finding of *D. solani*. The detection and positive identification of this latter species, coupled with its increased impact on potato production in other European countries and Israel (Laurila et al. 2008; Tsror et al. 2009, Sławiak et al. 2009), highlights the importance of careful and ongoing water surveys. A more recent PCR screening for *Dickeya* spp. in Hawaiian irrigation water, using REP-PCR, identified a new clade that grouped most of the strains isolated from water. This suggests the presence of natural genetically distinct populations of water-borne *Dickeya* spp. (Sueno et al. 2014) that may not be directly related to strains causing disease on crops but could be from plant hosts not yet identified.

Several new species of *Pectobacterium* and *Dickeya* have recently been described following isolation from water. *Dickeya* species include *D. aquatica, D. lacustris* and *D. undicola*: *D. aquatica* was isolated from rivers in Finland and Scotland and showed low pathogenicity in potato field trials (Parkinson et al. 2014a, b; Laurila et al. 2010). *D. lacustris*, which is closely related to *D. aquatica,* was isolated from nutrient-rich lakes in France, although the behaviour of *D. lacustris* strains on plants is still unknown (Hugouvieux Cotte–Pattat et al. 2019). *D. undicola* was isolated from freshwater samples in both Asia and Europe (Oulghazi et al. 2019a). *Pectobacterium* species isolated from water include *P. aquaticum*, *P. fontis* and *P. polonicum*: *P. aquaticum* was isolated from rivers in France and can rot potato slices but their virulence on plants has yet to be determined, while its closest relative using ANI/dDDH analyses is *P. carotovorum* (Pédron et al. 2019). *P. fontis* is a new species isolated from a waterfall in Malaysia (Oulghazi et al. 2019b) representing a novel clade that is distinct from other *Pectobacterium* spp. Virulence assays on potato tubers showed that *P. fontis* was able to induce a weaker decay on potato tubers than other *Pectobacterium* spp. such as *P. parmentieri* and *P. brasiliense*. *P. polonicum* was isolated from groundwater from a vegetable field in Poland and found to be a new species using *is* DDH and ANI analyses. Its closest relatives are *P. punjabense*, *P. parmentieri* and

P. wasabiae (Waleron et al. 2019b). Of these new species, only *D. aquatica* has so far also been found on plants; carrot (*Daucus carota*) (Zaczek-Moczydlowska et al. 2019). As stated above, whether this increase in water-specific species is due to more recent and intense analyses of water sources or whether it is due to improvements in taxonomic methods, and ultimately these species will also be found on nearby plants, remains to be seen.

The levels and species of bacteria found in water are likely to be affected by climate, geographical region and land use surrounding water sources. According to Cother et al. (1992), water can be considered part of the continuum of diverse environments that support the growth and survival of SRP. In future studies, systematic measurements during water sampling could include more information on water temperature, nutrients (including organic matter) and a description of the uses of surrounding land, to help to better understand the distribution of particular species in a given water source environment. This work, coupled with precise taxonomic characterization and determination of known SRP detected in water sources used for irrigation, is necessary to better characterize the risks associated with SRP circulation in irrigation water (Kastelein et al. 2020).

3.3.2 Soft Rot Pectobacteriaceae *in Soil*

Data on the survival of SRP in naturally infested substrates is restricted due to a limitation in the detection thresholds for soil (De Boer et al. 1979; Meneley and Stanghellini 1976). Nevertheless, SRP populations are often detected following potato planting, but then rapidly disappear over winter to very low levels. SRP have also been detected, albeit at low frequency, in fields in the absence of potato regardless of their cropping history, suggesting that SRP may be endemic in the tested soils and possibly therefore the plants growing in those soils (Pérombelon and Hyman 1989). Detection of SRP in soil is not only hampered by the detection threshold of the assays, but likely also by the heterogeneous distribution of SRP in soil, although solid data on this are lacking. In addition, direct methods such as DNA-based amplification and ELISA will detect dead bacterial cells resulting in an overestimation of the risks for infection. To improve the diagnostic sensitivity of assays, incubation of soil samples in a broth under low oxygen conditions can be done, which allows multiplication of SRP and enhances the probability of detecting and isolating the target bacteria (Peltzer and Sivasithamparam 1988; Powelson and Apple 1984). The efficiency of cultivation-based techniques, however, can be affected by the high microbial background in the soil that interferes with the growth of SRP. Enrichment negatively affects the possibilities of quantifying bacterial densities in soil.

An unresolved issue remains the detection of low densities of cells that may exist in soil in a viable but non culturable (VBNC) state (Gorshkov et al. 2009). A VBNC state was artificially induced using copper sulphate in *D. dianthicola,* with at least 90 % of cells tested entering the VBNC state and remaining so for 2 months at 28 °C (the length of the study). This suggests that this state may help to protect the bacteria

from application of copper products in seed treatments and may also assist survival through the winter months (Ge et al. 2017).

Although it is possible that SRP exist in soils in the absence of crop residues, most isolations appear to be from soils in which host crops have been grown (Burr and Schroth 1977; Powelson and Apple 1984). Bacteria detected in soil are probably associated with the rhizosphere of (perennial) weeds and crop debris (Burr and Schroth 1977; Gudmestad and Secor 1983; McCarter Zorner et al. 1985) or as a result of decaying plant material (Lapwood and Harris 1982). In Scotland, survival was best in the rhizosphere soil of *Brassicaceae*, moderate in soil of grasses and cereals, and least on soil of certain weeds and (surprisingly) potato (Pérombelon and Hyman 1989). However, in the USA in spring, SRP were detected more frequently from soils in which potato was planted in the previous year than other crops such as bean and maize, indicating an influence of crop rotation schemes on soil infestation (De Boer et al. 1979). In Australia in spring, 25 % of all soil samples taken from fields the year before potatoes were planted, were contaminated with SRP including 93 % *P. carotovorum*, 5.6 % *P. atrosepticum*, and 1.9 % *Dickeya* spp. (Peltzer and Sivasithamparam 1988).

Pectobacterium spp. appear to survive better in soils than *Dickeya* spp. In general, *P. carotovorum* is more frequently found in soil than *P. atrosepticum* and *Dickeya* spp., e.g. in studies in Scotland *P. carotovorum* predominated (91 %) (Pérombelon and Hyman 1989). Studies in the Netherlands showed that *Dickeya* isolates from potato and hyacinth could not survive for more than seven days when added to different soils at 6 °C and 50 % field moisture capacity, compared with 42 days for *Pectobacterium* isolates (Van der Wolf et al. 2009).

Survival in soil depends on numerous biotic and abiotic factors in an environment that in general will be hostile to the pathogen in the absence of plant material. In sterilized soil there is a prolonged survival of SRP indicating a negative effect of other microbes in the soil (Anilkumar and Chakravarti 1970; Armon et al. 1995; Ficke et al. 1973; Rangarajan and Chakravarti 1970). In comparative studies with *P. carotovorum,* using non-sterile and heat-sterilized sand and mixtures of soil and sand, populations declined below the detection limit in one month in all non-sterile soils (Armon et al. 1995). In heat-sterilized soils, however, populations initially increased in size and could be detected 60 days after the last sampling date. Similarly, survival studies in which microcosms with a loam soil were used showed that in non-sterile soil in 50 days, a 10,000-fold decrease ($10E^8$-$10E^4$ cells/ml) in the population density was found, while in gamma-radiated soils there was only a 100-fold decrease (Orvos et al. 1990). Lytic bacteriophages against SRP can be isolated relatively easily from soils in which infected plants are grown (Adriaenssens et al. 2012; Czajkowski et al. 2014; Lim et al. 2013). Survival of SRP may be influenced by parasitic organisms such as *Bdellovibrio* (Jurkevitch et al. 2000) and *Myxococcus* (Li et al. 2018b), which are soil bacteria that are often present in relatively high abundance. Numerous bacteria isolated from soil can compete with SRP through production of antimicrobial compounds, siderophores or interference via quorum quenching (Cirou et al. 2012; Czajkowski et al. 2012b; Jafra et al. 2009; Krzyzanowska et al. 2012). It is also possible that antagonistic fungi affect the survival of SRP in soil (Miles et al. 2012).

Various abiotic factors have been found to influence the survival of SRP in soil, including temperature, moisture level and pH (Anilkumar and Chakravarti 1970; Ficke et al. 1973; Gudmestad and Secor 1983; Pérombelon and Hyman 1989). Studies on survival of *P. atrosepticum* in a loam soil indicated that the pathogen survived for a period of two months at a temperature of 2–10 °C compared to only 0.5 month at 20 °C. However, even in a sterile soil at 2–10 °C, the pathogen could not be detected after 4 months (Ficke et al. 1973). In these experiments, amending soil with organic material extended the survival periods: with alfalfa up to 260 days and with straw to a period even longer than 260 days (Ficke et al. 1973). *P. atrosepticum* survived for six months in various soils outside in Germany during wintertime. Survival of *Dickeya* sp. that can cause stalk-rot in maize was also favoured by a low temperature in soil, with the pathogen surviving in a loamy sand for 38 days at 8 °C, for 22 days at 20 °C and for 12 days at 30 °C (Anilkumar and Chakravarti 1970). Survival was negatively influenced if the pH of the soil was adjusted from 8.3 to 4.8, i.e. from 26 to 12 days (Anilkumar and Chakravarti 1970). Slightly longer survival periods (32 days) were found at low soil moisture levels (30 %) than at those exceeding 60 % (22 days) (Anilkumar and Chakravarti 1970). Similarly, in Scotland longevity of *P. carotovorum* was greater in dry (10 % moisture) than in wet (21 % moisture) soils (Pérombelon and Hyman 1989). In other studies with a plant-free loam soil, a stalk rot causing agent described as *P. carotovorum*, survived for three months at 22 °C (Rangarajan and Chakravarti 1970). In comparison, in infected corn stalks, the pathogen could survive up to 22 months at 0–5 °C but only for 7–8 months at 20–37 °C. Addition of sodium nitrate (70 mg l^{-1}) into non-sterile soil extended the survival period of *P. carotovorum* from 35 to 60 days (Armon et al. 1995). The authors concluded that irrigation with nitrate rich water may result in prolonged survival periods for *P. carotovorum* in soil. Survival of *P. carotovorum* was dependent on the soil depth; at a depth of 50 cm the period was shorter than at 30 or 10 cm. Seemingly in contrast, in North Dakota *P. carotovorum* and *P. atrosepticum* were most frequently isolated in the 31–71 cm soil depth, suggesting that at this depth the bacteria were more protected from fluctuating moisture and temperature conditions (Gudmestad and Secor 1983). For potting media in glasshouses, a maximum survival period of 12 months for *Dickeya* spp. was reported (Haygood et al. 1982). The absence of strong fluctuating environmental conditions in greenhouses in comparison to field conditions may account for this long survival period.

Infected plant tissues, including roots, tubers and bulbs, can provide a source of bacteria to the soil, which may then be transmitted via free soil water, such as through irrigation or rainfall, to pathogen-free neighbouring plants. Water logging will also favour infection of tubers as a result of an impaired resistance against the pathogen (Smid et al. 1993). Field studies in the Netherlands were conducted in which an infected tuber was planted between pathogen-free mini-tubers. At the end of the growing season, the pathogen was found on up to the third plant in the same row and in a neighbouring plant of an adjacent row (Velvis and Van der Wolf 2009).

The risks of pathogen transmission from soil into a crop free of SRP are largely unknown. In the Netherlands, infected crop residues buried in soil in the autumn showed some transmission to *Dickeya*-free mini-tubers in the next growing season,

but other infection sources could not be excluded (Velvis and Van der Wolf 2008). For bulbous ornamental crops there are also no indications that soil-borne inoculum plays a role in the epidemiology of the pathogen (van Doorn et al. 2011). Experiments in the Netherlands, in which crops inoculated with *Dickeya* spp. (hyacinth, iris, dahlia and muscari) or *Pectobacterium* spp. (zantedeschia) were grown in a field with a sandy soil, did not result in the following year in an increase of symptomatic plants from a non-inoculated crop grown in the same rotation (Van Doorn et al. 2011).

In conclusion, it appears unlikely that SRP persist for a period longer than one year in soil, at least in the absence of plant material (Anilkumar and Chakravarti 1970; Rangarajan and Chakravarti 1970; Lim 1975; Pérombelon and Hyman 1988). However, it cannot be ruled out that, under certain circumstances (e.g. temperature, water availability, plants present), levels of bacteria undetectable by current detection methodology may increase in number to colonize and even cause disease in suitable plant hosts.

3.3.3 *Soft Rot* Pectobacteriaceae *and the Role of Insects and Other Invertebrates*

Since the 1920s, it has been hypothesized that insects contribute to transmission of SRP. In an early example, it was observed that *Delia platura* (seedcorn maggot) laid eggs near seed tuber pieces shortly after planting and it was suspected that the larvae transmitted SRP to the tubers by boring into them (Leech 1926). Similarly, *Delia radicum* (cabbage root fly) and *Delia antiqua* (onion fly) were suggested to be closely associated with SRP and involved in the transmission of the bacteria to their respective host plants (Bonde 1930; Doane 1953; Doane and Chapman 1964). Later, it was shown that *D. platura* transmitted *P. carotovorum* from decayed tubers to wounded potato plants in a cage experiment (Phillips and Kelman 1982). The *Delia* genus belongs to the family *Anthomyiidae* ('root-maggot') and includes multiple species that are notorious plant pests on several crops. *Delia* species and SRP have a widely overlapping host-spectrum, giving far-reaching implications to the notion of a mutual relationship between the two. Furthermore, it was show that *Drosophila melanogaster* could transmit SRP from infected to healthy potato plants, while artificial inoculation of *P. carotovorum* and *P. atrosepticum* into *Drosophila melanogaster* showed that the bacteria could be transmitted to injured plants in the field (Kloepper et al. 1981; Molina et al. 1974). SRP were found to survive both internally and externally on *Drosophila melanogaster* and *Drosophila buskii* with some strains surviving in *Drosophila* spp. for at least 72 h (Brewer et al. 1980, 1981).

In a Colorado field study, 10 genera from 9 families of dipterous insects ('true flies') collected in the field in the San Luis Valley of Colorado were contaminated with SRP (Kloepper et al. 1979). Recent research showed that SRP were ubiquitously present in or on insects, mainly *Diptera*, trapped in various potato fields spanning six latitudes and different climate zones throughout Norway (Rossmann et al. 2018).

The insects that harboured SRP belonged to more than 90 different insect species, among which *Delia* species were most frequently found to be carriers. In addition to *Delia platura*, *Delia coarctata* ('wheat bulb fly'), *Delia florilega* ('bean seed maggot') and *Delia radicum* were among the insects most often associated with SRP. The widespread presence of SRP in various fly species is further supported by their detection in microbiome studies of house- and blowflies, as well as cactophilic (organisms adapted to survive in arid habitats) *Drosophila* species (Martinson et al. 2017; Junqueira et al. 2017). 16S barcoding has highlighted the abundance of OTU (operational taxonomy unit) related to *Pectobacterium* in the gut of *Hyalesthes obsoletus* (Hemiptera: Cixiidae), which is an important vector of phytoplasma diseases in grapevine (Iasur-Kruh et al. 2017), and in the gut of oriental fruit fly *Bactrocera dorsalis* (Wang et al. 2011). In addition, in several triatomine bugs, which are vectors of the protozoan parasite *Trypanosoma cruzi*, the causal agent of Chagas disease, *Pectobacterium* related OTU is also dominant (Díaz et al. 2016). The gut of the terrestrial slug *Arion ater* also hosted bacteria related to *Pectobacterium* (Joynson et al. 2014).

A general function of SRP in herbivorous insect species might explain their presence in so many insect species. SRP are notorious producers of a variety of plant cell wall-degrading enzymes (PCWDE) that are secreted to the extracellular environment, which could play a role in various insect-plant interactions. For example, the bacteria are thought to be generally beneficial to larval development of various *Delia* species by inducing rots. This perhaps helps the larvae to burrow into plant seeds, stems or roots where they feed until pupation or for the movement of the maize borer larvae — (*Chilo partellus*) through wound sites in growing maize crops (Dalmacio et al. 2007; Rossmann et al. 2018). They may also be involved in digestion in insects, e.g. pectinase producing bacteria in the guts of longhorn beetles or in helping to break down toxic plant components (Ivanova et al. 2006; Park et al. 2007). Many SRP species also possess genes related to nitrogen fixation (Bell et al. 2004; Toth et al. 2006), which has been demonstrated in vitro in several, but not all, strains of *P. atrosepticum*, *P. carotovorum* and *D. dadantii* (Toth I.K. and Brurberg M.B., unpublished results). Nitrogen fixation activity could in principle benefit hosts that feed on nitrogen deficient diets. Furthermore, SRP in the gut of *D. radicum* were shown to possess the ability to degrade a toxin produced by its host plants (Welte et al. 2015, 2016).

To date, no general molecular mechanisms governing an association between SRP and insects have been identified. However, for two SRP species, *D. dadantii* and *P. carotovorum*, specific molecular interactions with their respective insect hosts have been investigated in-depth. A cluster of four genes (*cytA*, *cytB*, *cytC* and *cytD*) encoding proteins homologous to *Bacillus thuringensis* Cyt toxins was identified in the genome of *D. dadantii* 3937 (Grenier et al. 2006). In *B. thuringensis*, these toxins are produced together with the Cry toxins in parasporal crystals during sporulation and they have a cytolytic activity on insect cells. Very few bacteria outside *B. thuringensis* produce these toxins and *cyt* genes are not present in *Pectobacterium* spp. In laboratory experiments, *D. dadantii* was able to multiply and kill the pea aphid *Acyrtosiphon pisum* after 4–5 days following ingestion of an inoculum as low as 100

bacteria. At the time of death, the insect contained up to 10^7 bacteria (Costechareyre et al. 2012). A strain deleted in the four *cyt* genes had a reduced virulence on aphids but no difference on plant aggressiveness was observed. Purified proteins from these genes were also found to kill aphids and may thus be a weapon against insects. Despite the presence of *cyt* genes, *D. dadantii* 3937 is not able to kill all insects. The bee *Apis mellifera,* the Lepidoptera *Spodoptora littoralis* and the fly *Drosophila melanogaster* were not affected by *D. dadantii* ingestion. The presence of *cyt* genes in most *Dickeya* spp. suggests an ecological importance of these toxins, probably to kill some insects. Which insects are killed by *Dickeya* spp. and why is unknown. The cluster of four *cyt* genes is found in most *Dickeya* genomes, including the deep branching *D. paradisiaca*, indicating that it was present in the ancestor of *Dickeya.* However, it appears to be absent in *D. fangzhongdai* and in some *D. zeae* strains (Guy Condemine, INSA, Lyon, France, pers. comm.), although the ability of these strains to develop in or to kill aphids has not been tested. A study of the expression of *D. dadantii cyt* genes showed that they are regulated by the same regulators that control plant virulence factors. However, this regulation occurs in an opposite way, e.g. activators of plant virulence are repressors of Cyt production, suggesting that virulence against insects is integrated into the global bacterial virulence regulatory network (Costechareyre et al. 2010). To identify other genes involved in insect killing, a transcriptomic study of *D. dadantii* in *A. pisum* was performed. Although many genes in *D. dadantii* were induced whilst inside the insect, no other toxin or virulence genes were identified (Costechareyre et al. 2013).

Interactions between *Pectobacterium* spp. and insects have been less well studied. In a study to identify bacteria able to induce an immune response in *D. melanogaster*, Basset et al. (2000) identified the *P. carotovorum* 15 (Ecc15) strain, which is able to survive in the gut of the insect. A single gene, *evf*, is responsible for the colonization of the gut and overproduction of Evf allows a colonization of the body cavity, although its function is not known. The *evf* gene is not present in all *Pectobacterium* strains, and there are currently eight *P. carotovorum* strains and three *P. versatile* strains that encode proteins with identical sequences to the Ecc15 Evf, all deposited in GenBank (Basset et al. 2003).

While insect transmission of SRP to potato tubers and plants has been shown, it is unclear how frequently this occurs in agricultural settings, and which other crop plants may be affected. The recent findings of an association of various *Pectobacterium* spp. and *D. solani* with a wide variety of insect species, suggests that transmission of SRP by insects may be more common than previously assumed, which is especially relevant in the initial infection of clean seed material such as potato mini-tubers (Rossmann et al. 2018). However, it is not yet fully understood whether SRP are a mutualistic part of the microbiome of certain insect species, randomly acquired passengers or even pathogenic to insects that carry them.

In addition to insects, SRP have recently been found in other plant-associated animals, i.e. nematodes and gastropods. Grazing experiments performed with the model nematode *Caenorhabditis elegans* showed that *P. atrosepticum* is able to persist inside the nematode during digestion and can be released into the environment (Nykyri et al. 2014). Similarly, Chantanao and Jensen (1969) showed that *P.*

carotovorum can survive passage through the nematode *Pristionchus lheritieri* and be defecated (Chantanao and Jensen 1969). When *C. elegans* was fed with *P. carotovorum*, *P. atrosepticum* or *P. wasabiae*, surface sterilized and placed onto potato tuber slices, soft rot symptoms could be detected after 2 days showing that nematodes may be a vector for these bacteria. The same result was obtained with the nematode *Pristionchus* sp. FIN-1, isolated from a tuber showing soft-rot symptoms (Nykyri et al. 2014). Thus, nematodes that are present in large numbers in the soil or decaying material could be vectors for SRP over short distances (or further in surface water and on machinery). *D. dadantii* and *P. carotovorum* have also been found in the intestinal microbiome of the black slug *Arion ater* (Joynson et al. 2017). These animals, which feed on a variety of plants, alive or decaying, can travel long distances and survive winter freezing conditions. If SRP are stable members of their microbiome, slugs could also be responsible for spread of SRP (Joynson et al. 2017).

3.4 Colonisation, Infection and Symptoms of Plant Hosts

3.4.1 Colonisation and Infection

SRP are present in multiple environments including soil, water, air, insects and nematodes (see Sect. 3.3). The pathogens can be present on the surface of field and processing machinery, stores and storage boxes and graders etc. (Elphinstone and Pérombelon 1986; Fehres and Linkies 2018; Kang et al. 2019). van Doorn et al. (2008) showed survival rates of different SRP on hard surfaces (including steel, concrete and PVC) and under different relative humidity (RH), e.g. survival only occurred on concrete at 95 % humidity for any of these bacteria, for 6 h on PVC at 45 % RH but 48 h at 95 % RH, while on PVC in the presence of plant resin bacteria survived for up to 100 days. SRP may also occur in artificial media used to grow plants, e.g. a major problem for cut flowers (Jowkar et al. 2013). There are therefore multiple sources from which plants can become contaminated. SRP often colonise the surface of different plants both with and without subsequent disease development and it is likely, therefore, that this colonisation is a natural part of SRP life cycle. For example, Buonaurio et al. (2015), identified *Pectobacterium* spp. as one of many natural colonisers of the aerial parts of olive trees and discussed the possibility that one or more of these bacterial species may assist the pathogen *Pseudomonas savastanoi* in the development of olive knot disease. Mutai et al. (2016), on the other hand, isolated *Pectobacterium* spp. as part of a natural diverse bacterial population from the roots of *Brachiaria* grass but not from the leaves, where other non-*Pectobacterium* spp. populations were present. There are also several examples of SRP being present on the roots of weed species within potato fields (see Sect. 3.2.4). It is therefore no surprise that roots, tubers and bulbs of crops and ornamental plants can become contaminated in a similar way.

In potato, the main source of tuber contamination begins in lenticels and the stolon end. Under wet conditions, a layer of moisture forms around tubers leading to anaerobiosis, which causes opening of the lenticels, swelling of the cortical cells and increased cell membrane permeability, resulting in leakage and increased nutrient availability (Pérombelon 2002). Chemotaxis and motility then play a role in guiding SRP to these sites (Antunes-Lamas et al. 2009). Upon entry, the bacteria can remain in a latent state until conditions are conducive to bacterial multiplication. The exact conditions of latency are unclear but involve low numbers of bacteria prior to bacterial multiplication and may involve an equilibrium between protection and repair mechanisms in the pathogen, e.g. peptide methionine sulphoxide reductase (MsrA), and reactive oxygen levels in the plant (El-Hassouni et al. 1999; Pérombelon 2002). Anaerobiosis also reduces the effectiveness of oxygen-dependent plant defence mechanisms while allowing SRP to grow microaerophilically (Burton and Wigginton 1970). Free water, optimal temperature for bacterial growth, which differs between species, and reduced plant defences thus leads to bacterial growth.

Contamination (including a more permanent latent infection) of tubers is widespread in most commercial potato stocks and, where they are used for seed, early growth of the bacteria can prevent the plant from initiating (blanking), while later growth leads to cells moving into the growing plant stems (Pérombelon 1992). Once bacteria move from the mother tuber into the plant stem, they can colonise the cortex, multiply and are rapidly transported through the apoplastic spaces to the vascular system, where they first colonise parenchyma and then xylem tissues (Pérombelon et al. 1989). To achieve this, SRP produce a wide range of pathogenicity determinants, including PCWDE, and must also protect themselves from a variety of plant defence mechanisms (see Chap. 4).

As the bacteria spread through the vascular tissues, they can also move down the stolon into the developing progeny tubers, contaminating the stolon end of the tuber and adding to any new lenticellular contamination already present. Movement of the bacterial cells from here can in some infections by *Dickeya* spp. lead to a browning of the tuber vascular tissue (Toth et al. 2011). The fact that lenticels and the stolon end can both become contaminated by the bacteria, has led to both tissues being tested as part of diagnostics to measure the presence and level of SRP. While it is acknowledged that disease development is mainly initiated from contaminated mother tubers under disease-inducing conditions the bacteria, following contamination of the progeny tubers, can multiply within the tuber and cause local rots, including lenticellular/pit or stolon-end rot, which under extreme conditions can lead to severe damage or loss of the progeny tubers (see Sect. 3.5).

While mother tubers are the major route to invasion of potato plants and subsequent disease development, bacteria can also enter via the roots and canopy. Following inoculation of *D. solani* onto undamaged potato roots, bacteria were found inside the roots, stems and stolons 15 days after inoculation, with numbers increasing when damaged roots were used. Bacterial populations were found to be 2–3 times higher in the roots than the other structures (Czajkowski et al. 2010a). In roots, the bacteria were found associated with the parenchyma cells of the cortex and in the xylem and protoxylem of the stem. After 30 days following stem inoculation, *D. solani*

was detected in the stems but also in the stem base, roots and to a lesser extent in the stolons and the stolon end of progeny tubers. Following leaf inoculation, at 42 dpi *D. solani* was detected in leaves, stems, stolons and occasionally in tubers, whereas *P. parmentieri* was restricted to leaves, stems and stolons, and could not be detected in tubers. The infection percentage was higher for plants with wounded leaves than for plants with untouched leaves, and higher at greater inoculum densities. Nevertheless, infection of leaves could also occur at low densities of *D. solani* (10^2 cfu mL^{-1}). Microscopic analysis indicated that both pathogens were able to penetrate and colonize hydathodes, stomata and wounds of inoculated leaves (Czajkowski et al. 2010b; Czajkowski et al. 2012). Similarly, Kubheka et al. (2013) observed that wounded and unwounded potato roots can become infected by *P. brasiliense* directly from the soil. However, wilting was more associated with seed borne than with soil-borne inoculum (Ansernet et al. 2016). Chemotaxis, in addition to searching out nutrients, may also be involved in identifying sites of entry, and was found to have a more pronounced effect at colonising and entering some structures than others. For example, chemotaxis and motility mutants of *D. dadantii* were impaired in their ability to penetrate leaves of arabidopsis to a greater extent than their capacity to penetrate potato tubers, suggesting that chemotaxis and motility may be required as a more active entry mechanism for leaves than for tubers (Antunes-Lamas et al. 2008).

Once inside the xylem tissues, under conditions of low nutrient availability, *P. atrosepticum* and possibly other SRP produce extracellular polysaccharide (EPS), which surround the cells in a fibrous coat and, together with other bacterial structures (e.g. adhesins) and the bacterial-induced release of pectic polysaccharides (e.g. rhamnogalacturonan I) from the plant cell walls, leads to bacterial cell attachment and aggregation (Gorshkov et al. 2014, 2016; Rojas et al. 2002). Such biofilm structures support SRP to withstand water flow within the xylem and protect against plant defence mechanisms and is thought to be necessary for successful colonisation in xylem colonising bacteria (Leigh and Coplin 1992). In addition to biofilms, EPS-based multi-cellular structures called bacterial 'emboli' may be present, which appear not to be attached to the vessel walls (Gorshkov et al. 2014). Where bacterial cells aggregate in the xylem, in some cases the xylem becomes occluded leading to reducing water flow, wilting and eventually disease symptoms. However, where SRP are present in the xylem but the vessels are not occluded and no symptoms are apparent, transpiration is unaffected (Ansermet et al. 2016). At some point while in the xylem, probably following the production of EPS and formation of these multi-cellular structures, the bacteria begin to multiply and reach cell densities sufficiently high to trigger quorum sensing, a cell density-dependent regulatory process that triggers major changes in gene regulation (up to 26 % of the genome) and with it the production of multiple, coordinated, pathogenicity determinants (Liu et al 2008; see Chap. 4). From this point, further bacterial multiplication, movement and occlusion of the xylem takes place followed by wilting and rotting. Intriguingly, Kubheka et al. (2013) showed that biofilm structures were more likely to be observed in susceptible

potato cultivars, while in more tolerant cultivars bacterial cells remained in a free-swimming planktonic state, suggesting that mechanisms that limit biofilm formation may be the basis of tolerance in at least some cultivars.

While there is much less information on contamination (including source) and infection in plants other than potato, infections appear to follow a similar pattern. In a study in the Netherlands, *Dickeya* spp. were isolated from hyacinth and daffodil and *P. carotovorum* from *Zantedeschia*, with plants showing common symptoms of wilting, soft rot and decline (van Doorn et al. 2008). Disease incidence in several flower crops was found to be from bacteria present on the planted crop rather than transmitted from the soil (with few exceptions), in a similar way to contamination of seed potatoes. However, in *Dieffenbachia*, it was shown that a *Dickeya* sp. was able to infect via the roots initially to the xylem and then around the whole plant (Neivesbrun 1985). In *Kalanchoe, Dickeya* spp. were found in different parts of the plant including the stem base and upper parts (Bech 1994). Impaired host resistance due to water logging, optimal temperature, and wounding all increased infection and disease incidence caused by *P. carotovorum* in *Zantedeschia* (Wright et al. 2011).

Infection of maize by *Dickeya* spp. causes rots throughout the plant and occurs in the rainy season in the Philippines and elsewhere. The bacterium survives on crop residues and spreads to growing maize crops via water splash and insects (including the maize borer larvae—*Chilo partellus*) including through wound sites (Dalmacio et al. 2007; Thind and Singh 1975). In date palm trees, leaves turn yellow and vascular tissues (including those in the roots) discolour, suggesting that movement and establishment of the causal agent, *Dickeya* spp., occurs in the vessels, blocks transpiration and leads to rotting throughout the plant (Abdalla 2001). For sweet potato, bacteria can be present as latent infections (Duarte and Clark 1992), with oxygen deprivation and thresholds for both soil and air temperatures contributing to disease development (Edmunds et al. 2015).

3.4.2 Disease Symptoms

Diseases of potato tubers and plants caused by SRP induce a range of symptoms that can develop at every stage of the potato production cycle (Table 3.2). Soft rot symptoms can also be observed in ornamentals and in many vegetable crops.

3.4.2.1 Soft Rot and Lenticel Rot of Potato Tubers

Soft rot of potato tubers caused by SRP can occur in the field and in storage (Charkowski 2018). Early infection of seed tubers after planting can result in blanking (rotting or failure of the seed tuber to sprout) if the mother tuber rots or if young shoots are contaminated and killed before or just after emergence. During the growth of the potato plant, the bacteria can spread from the seed tuber to rot the stem and may also enter the progeny tubers via the stolons (Fig. 3.1A), where they can cause

Table 3.2 Terminology of potato symptoms caused by SRP (from Pérombelon and Kelman 1987)

Term	Explanation
Non-emergence	Results from decay of seed tuber or early sprout death below ground
Blackleg	Infection originating from mother tuber and moving into the stem; symptoms variable, ranging from black to dark brown basal stem rot to wilting leaves/stems with or without yellowing. Infection is either limited to the basal part of the plant or extended up to the top of the stem, eventually associated with a hollowing of the stem
Wilt	Stem and leaf wilting often caused under warm conditions but with no water deficit (stress) and with no stem rotting expression
Aerial stem rot	Tan, brown to black decay lesion of the stem not originating at the attachment point to the seed tuber
Stolon end rot	Affects mostly progeny tubers of plants expressing blackleg symptoms; brown to black necrosis
Tuber soft rot	Cream to tan colour and soft, granular consistency with brown colour often developing at margins of decayed tissue; foul odour often associated to the decayed tissue
Lenticel rot or pit rot	Sunken brown to black decayed spots at points where lenticels become infected. Can be limited to hard and dry symptoms when decay is stopped at early stages after lenticel infection

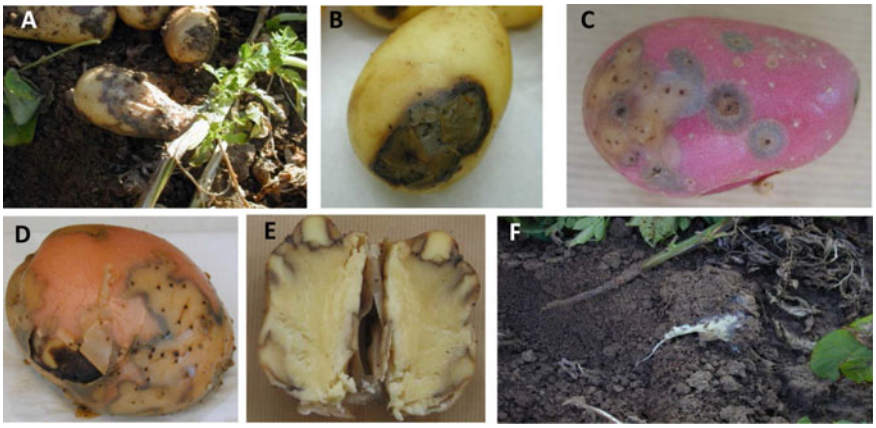

Fig. 3.1 Soft rot symptoms in potato tubers. (a) and (b) stolon end rot originating from the mother plant; (c) rotting of lenticels due to bacteria spreading into the tubers from soil; (d) and (e) advanced state of rotting of progeny tubers during field growth or in storage and (f) totally liquefied mother tuber in the field. Image credits: (a, b, d and f) Image credit Leah Tsror, Agricultural Research Organization, Gilat Center; (c and e) Valérie Hélias, French Federation of Seed Potato Growers, Rennes

stolon end rot (Fig. 3.1B). During rainy weather, the bacteria can spread from infected plants into the soil, where they further spread with soil water (see Sect. 3.3) and infect tubers through lenticels, resulting in lenticel rot (Fig. 3.1C). In the later stages of tuber symptoms, a smelly rot develops and the whole tubers may rot (Fig. 3.1D), where the original site of infection is no longer obvious (Fig. 3.1E, F).

Rotting symptoms caused by different species of SRP are usually not distinguishable. However, at high temperatures (>27 °C), soft rot caused by *D. solani* can produce a creamy, cheesy rot developing to complete decay (Toth et al. 2011). It has been observed in Finland that the rot caused by *D. solani* can also occasionally appear pinkish in the early stages of the infection (Minna Pirhonen, personal information).

Rotting of the infected progeny tubers often only becomes visible at harvest or during storage, when rots may (further) develop under warm and humid conditions. Furthermore, the bacteria can spread from rotten plants and tubers through wounds caused at harvest, grading and packing. Sometimes, a localized sunken soft rot lesion, known as lenticel hard rot or pit rot, may develop on harvested tubers that have been covered with a film of water for some time and then become dry (Pérombelon and Kelman 1987).

3.4.2.2 Potato Blackleg Symptoms

The typical black rot of the stem base is called potato blackleg disease and is caused by the spread of bacteria from decaying mother tubers into the stem (Pérombelon and Kelman 1987). Blackleg symptoms can extend from one to several or all stems of the diseased potato plant. During the first stage of infection, the top leaves of affected stems turn light green to yellow and start to roll upward (Harrison and Nielsen 1986) (Fig. 3.2A). The entire stem then wilts, declines and dies. Symptoms occur at any stage of plant development but are much more likely during the summer months and towards the end of the growing season.

Blackleg symptoms can vary widely depending on prevailing environmental conditions. Usually, only the basal part of the stem turns black but in favourable conditions (high humidity) the decay may spread to the upper part of the stem (Fig. 3.2B) killing the whole plant (Fig. 3.2C). In wet conditions, blackleg symptoms are similar for *Dickeya* and *Pectobacterium* spp. (*i.e. P. atrosepticum*, *P. brasiliense*, *P. parmentieri* and *P. punjabense*) (Valérie Hélias, Leah Tsror, Minna Pirhonen, personal communication) regardless the temperature. Infected stems with the external darkening of typical blackleg (Fig. 3.2D) may or may not show symptoms of internal pith necrosis (Fig. 3.2E). The stem above the blackened part is often hollow and black.

Under dry warm conditions, infected tissues become dry and are often restricted to the underground portion of the stem but wilting, increased leaf desiccation, stem browning and hollowing of the stem may take place (Fig. 3.2F) (Tsror et al. 2009, Tsror et al. 2013). In contrast, under cool wet conditions, blackleg symptoms can develop without clear wilting (Czajkowski et al. 2011).

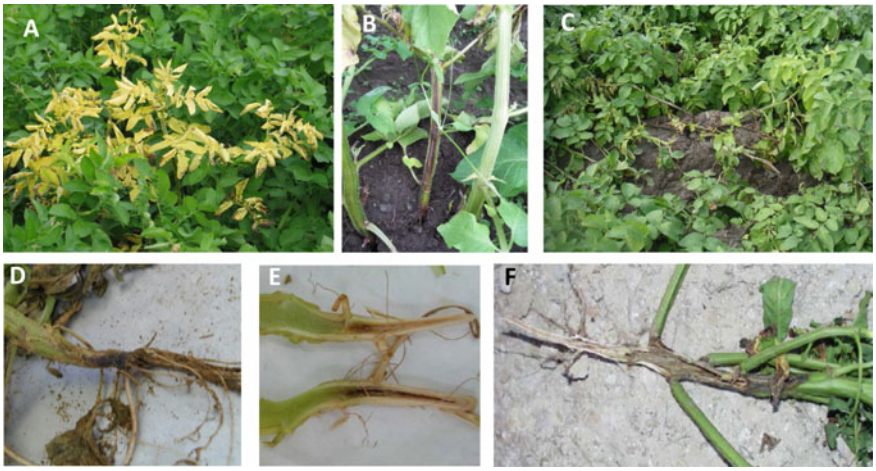

Fig. 3.2 Symptoms of potato blackleg. (a) yellowing is often the first symptom of blackleg followed by (b) rotting of the stems and (c) total collapse of the plants. (d) basal stem necrosis and (e) browning of the vascular tissue can be seen in the plants, together with (f) hollow stems, especially in warmer climates and in response to *Dickeya* spp. Image credits: (a) Asko Hannukkala, Natural Resources Institute LUKE, Jokioinen, Finland; (b and c) Minna Pirhonen, Department of Agricultural Sciences, University of Helsinki; (d and e) Leah Tsror, Agricultural Research Organization, Gilat Center; (f) Valérie Hélias, French Federation of Seed Potato Growers, Rennes

3.4.2.3 Slow Wilting of Plants

The typical symptom of *D. solani* in a hot climate (>25° C) is slow wilt, which starts at the top leaves (Fig. 3.3A), spreads to the lower ones, and is then followed by desiccation of the entire plant, often without any visible blackleg symptoms (Fig. 3.3B, Fig. 3.4) (Tsror et al. 2009). Wilting is usually accompanied with a brown discoloration of the vascular system in the stem base (Fig. 3.3C).

In severe infections, the stem or whole plant dries out. This wilting and vascular browning resembles wilt caused by the fungal pathogen *Verticillium dahliae* (causal

Fig. 3.3 Slow wilting of potato plants in warm climate. (a) *Dickeya solani* causes wilting of the potato plants that leads to leaf desiccation and (b) finally drying of the whole plants; (c) wilt is usually associated to discoloration of the stem base vascular system. Image credits: Leah Tsror, Agricultural Research Organization, Gilat Center

Fig. 3.4 Wilt and desiccation of the potato plants in the field. Image credit: Leah Tsror, Agricultural Research Organization, Gilat Center

agent of Verticillium wilt) and can occur immediately after irrigation under warm temperatures regardless the water status of the plant.

3.4.2.4 Aerial Potato Stem Rot

Aerial stem rot is a tan to brown decay lesion of the stem not originating at the attachment point of the seed tuber. It usually begins at breakage points in the stem, which then shows signs of rot at any level between the base and the top of the plant. In wet conditions, decay is a soft water-soaked rot that can expand along the stem and into the leaves and may spread to the entire plant (Fig. 3.5) (Harrison and Nielsen 1986). Stems, petioles, and leaves may become infected through wounds such as petiole scars, hail or wind damage or frequent overhead irrigation (Pérombelon and Kelman 1987). Lodged crops, with stems lying on the ground, often show aerial stem rot. This happens usually towards the end of the vegetative period when stems/crops are tall.

Fig. 3.5 Aerial stem rot of potato seen as watery rotten stems in the upper parts of the potato plant not originating at attachment point to seed tuber. Image credit: Valérie Hélias, French Federation of Seed Potato Growers, Rennes

3.4.2.5 Symptoms of Soft Rot in Ornamental Plants

Calla lily (*Zantedeschia*) (Araceae) is a genus of about eight species native to South Africa, all producing tuberous or rhizomatous storage organs that may be contaminated by *P. carotovorum* in the field or in storage (Snijder and van Tuyl 2002; Wright 1998). The first symptoms of soft rot disease in Calla lily plants are poor shoot growth and yellowing of the leaves (Luzzatto et al. 2007). Most often the leaves collapse, before the water soaked lesions appear. Under favorable warm and wet conditions the lesions enlarge rapidly, resulting in a soft decay of the whole plant. Usually the rot begins at the base of the leaf petioles (Fig. 3.6A) below or at the soil surface and may progress up the stems and down into the tubers (Snijder and van Tuyl 2002; Wright 1998). In some cases, the symptoms resemble black discoloration of healthy stems, accompanied by a rapid wilting, and yellowing of the leaves (Fig. 3.6B). Once the first disease symptoms occur under commercial greenhouse conditions, the dispersal may be rapid and losses may reach 50 % of the yield (Fig. 3.6C).

Ornithogalum is a genus of ornamental flower bulbs belonging to the family *Asparagaceae*, that contains about 250–300 species, widely distributed in Asia and Africa (Littlejohn 2006). The African varieties of the plant are produced commercially as cut flowers and pot plants in South Africa, the USA, the Netherlands and Israel. The plant's potential as a cut flower or gardening plant is severely hampered by its susceptibility to bacterial soft rot caused by *Pectobacterium* spp. (Lipsky et al. 2014). *Ornithogalum* spp. are most suitable for the Mediterranean climate as they are easily forced to flower during the winter season. The first typical soft rot symptoms in *Ornithogalum* include small water-soaked lesions that appear on the leaf bases at the heart of the rosette (Fig. 3.7A). The typical lesions are apparently dependent on tiny water reservoirs at the leaf base, where bacteria may proliferate and intiate infection. Characteristic symptoms include small watery lesions that enlarge

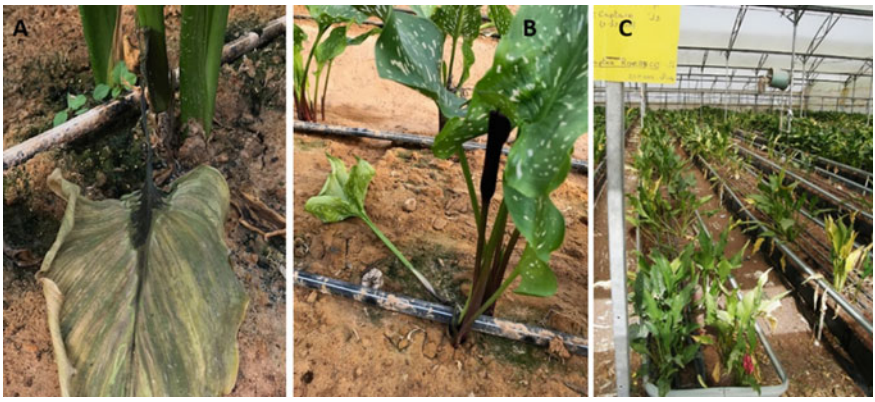

Fig. 3.6 Hybrid *Zantedeschia* plants displaying soft rot symptoms caused by *Pectobacterium aroidearum* infection, under greenhouse conditions at southern Israel. (a) blackening of the leaf petiole; (b) *Zantedeschia* hybrids planted in sandy soil, first soft rot symptoms occur when leaves are turning yellow and collapse; (c) *Zantedeschia* plants grown with drip irrigation on flower beds with soilless mixture of coil, peat moss and volcanic ash. Soft rot disease spreads throughout the flower beds with the irrigation lines. Image credits: Iris Yedidia, Agricultural Research Organization, Volcani Center

Fig. 3.7 Soft rot symptoms in *Ornithogalum dubium* plants, grown under greenhouse conditions during the winter season in Israel. (a) development of watery lesions at the heart of the leaves rosette and spread the neighboring plant; (b) severe soft rot decay and collapse of a mature flowering *O. dubium* plant; (c) *Pectobacterium aroidearum* spread at the greenhouse producing large rotten parches. Image credits: Iris Yedidia, Agricultural Research Organization, Volcani Center

rapidly to the entire plant and spread to the lower leaves and neighboring plants. Eventually, the stem and leaves are completely rotted (Fig. 3.7B) and the plant collapses, producing circles of decaying plant in the greenhouse (Fig. 3.7C).

On *Phalaenopsis* orchid, infection begins as water-soaked spots on leaves pale to dark brown in colour. Some leaves have a yellow halo. As temperature and humidity increase, the spots enlarge to extend over the entire leaf blade exhibiting a light tan shade with darker brown boarder. Leaf tissues collapse and the infection spreads to the stem and pedicle, with the leaves eventually becoming dry (Zhou et al. 2012).

3.4.2.6 Soft Rot Symptoms in Other Plants

Pectobacterium and *Dickeya* spp. produce large quantities of cell wall degrading enzymes, which enable them to macerate and rot parenchymatous tissues of a wide range of plants (Fig. 3.8). The number of different crops associated with frequent and severe attacks, either before or after harvest, is significantly lower than the actual number of host species that become infected. The soft rot bacteria can infect plant material on their own or following attack by other pests and pathogens (Pérombelon and Salmond 1995). Soft rot can occur on a growing plant or on the harvested crop, in either storage or transit. Crops that are vegetatively reproduced (such as potato or carnation) can be systematically infected from the beginning of the production cycle. In most crops that are not reproduced in this way, soft rot lesions usually first occur on the aerial parts of the plant. Harvested crops, such as fleshy and leafy vegetables, exhibit similar symptoms (Pérombelon and Kelman 1980).

3.5 Interactions Between SRP and Enteric Human Pathogens

Enteric bacterial pathogens responsible for food borne diseases, such as non-typhoidal *Salmonella* spp. or pathogenic *Escherichia coli,* are traditionally associated with products of animal origin. However, outbreaks linked to the consumption of fresh fruits and vegetables presents a major public concern, with the number of cases of non-typhoidal *Salmonella* illness linked to fresh produce, spices and nuts surpassing those linked to foods of animal origin (Brandl et al. 2013). These human pathogens are not usually considered to cause disease on plants, but they can survive on leaves, penetrate plant tissues and maintain their population in the plant mesophyll. Furthermore, it is believed that *Salmonella* can sense the genotype or physiological state of its plant host and respond with distinct patterns of gene expression suggesting that plant colonization by *Salmonella* can be part of its life cycle (Brandl et al. 2013). This is hardly surprising since the genomes of the enteric human pathogens, particularly those associated with plants, share much in common with SRP (Toth et al. 2006).

The presence of phytopathogens, and particularly SRP, on fresh produce is a significant risk factor associated with increased *Salmonella* carriage on fruits and vegetables. This was first observed in supermarket fresh produce surveys, which demonstrated that 60 % of fresh produce showing symptoms of soft rot also harboured

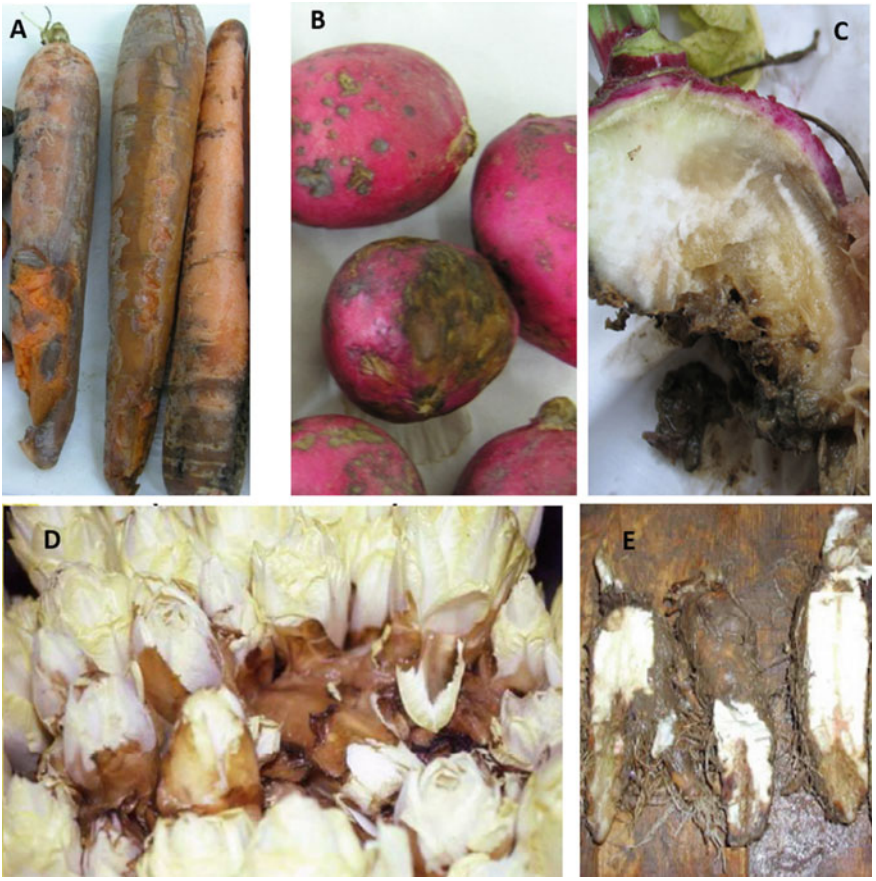

Fig. 3.8 Soft rot symptoms caused by *Pectobacterium or Dickeya* in vegetables such as (a) carrot, (b) radish including (c) radish seed crop, and (d) witloof leaves or (e) roots. Image credits: (a and b) Leah Tsror, Agricultural Research Organization, Gilat Center; (c–e) Valérie Hélias, French Federation of Seed Potato Growers, Rennes

presumptive *Salmonella* (Wells and Butterfield 1997). It was later documented by laboratory studies that maceration of plant tissues by *D. dadantii* or *P. carotovorum* promoted growth of *Salmonella enterica* and *E. coli* O157:H7, which reached population densities 10^1–10^3 times greater on soft rot symptoms than on healthy plants (Brandl et al. 2013). This increase in human pathogen growth in the presence of soft rot symptoms was not observed after co-inoculation with SRP mutants impaired in the type II secretion system (Out), which prevents the secretion of SRP PCWDE out of the bacterial cell. This suggests that it may be plant tissue maceration rather than the presence of SRP that promotes enteric human pathogen growth (Yamazaki et al. 2011; George et al. 2018). This was further supported by studies on the *S. enterica* AHL receptor SdiA, which responds to the production of quorum sensing

AHL signals by *P. carotovorum* in vitro but not in vivo. Analysis of SdiA mutants further demonstrated that detection of AHL produced by the soft rot bacterium *P. carotovorum* does not contribute to the fitness of *S. enterica* within tomato fruit (Noel et al. 2010). In a similar way, despite the fact that the *Salmonella luxS* gene was expressed during its invasion of a soft rot lesion, AI-2-based quorum sensing signalling in this pathogen did not appear to have an important role during its interactions with the plant pathogen *P. carotovorum* on tomato fruit (Cox et al. 2013). Thus, both sets of data appear to exclude the role of QS communication in *Salmonella* when present *in planta* together with SRP.

As maceration of plant tissues by SRP liberates a range of nutrients, metabolic interactions between *Salmonella* and SRP were investigated. Even though *P. carotovorum* lacks the enzymatic processes to utilise starch it is known to liberate amylose and amylopectin during the degradation of plant cells, while *Salmonella* spp. can digest starch. *Salmonella* starch utilization genes, such as *amyA,* are up-regulated in tomatoes macerated by *P. carotovorum*, although the corresponding *Salmonella* mutants exhibit the same fitness as the wild type parent *in planta,* indicating that starch utilization is not required for fitness within soft rot lesions (George et al. 2018).

Unlike phytopathogens, neither *S. enterica* nor *E. coli* can degrade pectin, although they can take up and metabolize pectin oligomers and monomers through a metabolic pathway identical to that of SRP (see Fig. 4.1). The genes involved in this pathway are up-regulated during growth on soft rotted plants. However, single or multiple mutations in genes of this pathway did not decrease the competitive fitness of the strains *in planta*, indicating that these genes are not required for *Salmonella* enhanced growth in macerated plant tissues (George et al. 2016). Transcriptomic profiling in lettuce and cilantro (Gaudeau et al. 2013) and transposon insertion sequencing, coupled with the phenotypic characterization of the mutants in healthy versus soft rotted tomatoes (George et al. 2018), both indicate that *Salmonella* spp. experience a metabolic shift in response to the changes in the environment brought on by *D. dadantii* or *Pectobacterium* spp. during plant tissue maceration. For example, *Salmonella* cells colonizing lettuce and cilantro leaf soft rot lesions caused by *D. dadantii* utilize a broad range of nutrients made available through the pectinolytic activity of the plant pathogen. These include fucose and rhamnose, two components of the plant cell wall that *Salmonella* can use as substrates to produce propanediol that, along with ethanolamine, can serve as carbon sources under anaerobic conditions (Gaudeau et al. 2013). This may explain the phenotype of *Salmonella* mutants deleted in the *kdgR* gene, which encodes a negative regulator of the pectin degradation pathway (see Sect. 4.2.7). A significant increase in the fitness of the *kdgR* mutant was observed in soft-rotted but not healthy tomatoes when compared to the fitness of the wild type parent (George et al. 2016). Even though the pectin degradation pathway is not involved in *Salmonella* enhanced fitness in soft rot tomatoes, metabolic profiling revealed that a *kdgR* mutant was able to better utilize over 40 substrates, including rhamnose (George et al. 2016).

Goudeau et al. (2013) demonstrated considerable overlap in genes up-regulated in cilantro and lettuce soft rot and in the animal intestine. Three-quarters of these up-regulated genes are involved in metabolic processes, including propanediol production and metabolism, and propanediol utilization is required for *Salmonella* replication in macrophages and colonization of the chicken intestine (Goudeau et al. 2013). This indicates commonalities between conditions encountered by *Salmonella* in soft rot lesions and the host intestine and may give a clue to the adaptation of *Salmonella* spp. to macerated leaf tissue (Goudeau et al. 2013). Since SRP do not possess the propanediol catabolic pathway, Goudeau et al. (2013) proposed that, by macerating plant tissues, SRP provide to *Salmonella* spp. the necessary substrates for propanediol biosynthesis and catabolism, while using the oligogalacturonides released by lysis of the plant cell wall and thus create a nutritional environment with partitioned resources and an apparent lack of competition between both bacterial species. The situation is different in a micro-aerophilic environment, such as that encountered in modified atmosphere packaging (MAP) used to extend shelf life of produce by reducing the rate of plant respiration, ethylene production and growth of microorganisms responsible for spoilage. Under these conditions, *S. enterica* growth was still enhanced by the presence of *P. carotovorum* while *S. enterica,* but not *E. coli* O157:H7, reduced *P. carotovorum* growth rates, final population densities and soft rot progression (Kwan et al. 2013). This is partly due to pH manipulation of the rooted tissues by *Salmonella* spp. Indeed, under micro-aerophilic conditions, *S. enterica* acidifies the phyllosphere due to production of organic acids during fermentation. This acidification interferes with the ability of *P. carotovorum* to alkalinize plant tissues to reach the pH required for optimal activity of the pectate lyases responsible for plant tissue maceration (Kwan et al. 2013).

3.6 Conclusions

SRP cause diseases on a wide range of plants globally. Some have wide host ranges while others appear to infect a single plant species. In other cases, particularly newly named species, SRP have been found in the wider environment not associated with plants e.g. water systems. Future research may tell us whether these niches are their natural habitat or whether plant hosts (that develop disease or not) are out there yet to be discovered. While we know surprisingly little about SRP in the wider environment and their life away from the diseased host, we do know that for some plants, particularly crops and ornamentals, disease can be devastating. While this is particularly true for potato and other ‘soft fleshed’ vegetables, where disease losses can be huge, we must be thankful that other main staple crops such as maize and rice, which may also succumb to SRP diseases, do so to a much lesser extent. Even where SRP are present on a plant that does not normally succumb to disease, their proximity to crops and ornamentals, e.g. weeds in a field, offers the potential for spread and subsequent disease development.

These pathogens appear to live in the environment as part of their natural existence and can be found in water, soil and in the atmosphere. However, these niches also provide a means to spread these bacteria leading to colonisation of plants, e.g. through irrigation, growth in soil and in aerosols, the latter two particularly under wet conditions. There is also evidence that insects and other invertebrates help to spread SRP although, surprisingly, the extent to which this occurs is unclear.

For many plants SRP do no more than colonise, and whether this has a neutral, negative or even positive effect is not known. However, in certain environmental conditions, mostly a suitable temperature and a wet environment with reduced oxygen availability, infection takes place leading, in some cases, to disease symptoms and losses. Whatever the plant being infected, the process and ultimate symptoms are strikingly similar across different plant types, which might also suggest common approaches to disease control.

Finally, disease and subsequent economic losses may not be the only thing arising from the presence of SRP on plants. There is growing evidence that they may also co-exist with enteric human and animal pathogens, e.g. *E. coli* and *Salmonella* spp., to help promote the growth of, and share nutrients with, these closely related pathogens thus bringing a human and animal health aspect to their presence on plants.

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