Soft rot Pectobacteriaceae: A Brief Overview

Plant Diseases Caused by Dickeya and Pectobacterium Species

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Chapter 1
Soft Rot *Pectobacteriaceae*: A Brief Overview

Frédérique Van Gijsegem, Ian K. Toth, and Jan M. van der Wolf

Abstract Bacterial soft rot diseases devastate a wide range of crops, vegetables and ornamental plants worldwide. Amongst the most damaging agents of these diseases are members of the *Pectobacterium* and *Dickeya* genera belonging to the family *Pectobacteriaceae* in the order Enterobacterales. As an introduction to the topics of this book, this chapter presents a brief overview on taxonomy history, presence in multiple environments, disease characteristics, population dynamics, management and economic impact of these bacteria.

Bacterial soft rot diseases devastate a wide range of crops, vegetables and ornamental plants worldwide and are caused by species from genera including *Pseudomonas*, *Bacillus*, *Burkholderia*, *Pantoea*, *Enterobacter*, *Klebsiella*, *Leuconostoc* and *Clostridium* (Charkowski 2018). In addition, and amongst the most damaging of these, are members of the *Pectobacterium* and *Dickeya* genera belonging to the family *Pectobacteriaceae* in the order *Enterobacterales* (Adeolu et al. 2016).

The present book focuses exclusively on the Soft Rot *Pectobacteriaceae* (SRP), *Pectobacterium* and *Dickeya,* and to our knowledge this is the first book to do so. It covers a wide range of topics in relation to these organisms in a series of chapters introduced below. To avoid repeating ourselves where information between chapters inevitably overlaps, we have chosen to focus information in one chapter while briefly mentioning it in others and cross-referencing to the main text. The reader will see time and again reference to potato in this and other chapters. This is also inevitable as there is so much more research carried out on this crop than any other. However, we know that many of the environments, infection pathways and modes of disease are

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similar in most plants and so we hope that you will be able to make direct comparisons to your own plants of interest.

1.1 A Brief History of Taxonomy

Soft rot bacteria have been known for more than a century. Indeed, the first report on the association of a non-fungal microorganism with soft rot of diverse plants, and the transmissibility of this disease via rotted plant material, dates to 1868 (Paulin et al. 2001). From then on, these bacteria have been renamed several times often making it difficult to relate findings from one named species/subspecies to those of another. The first isolation on carrot and other vegetables of what was then called *Bacillu*s *carotovorus* was reported in 1900 (Jones 1900). The name *Bacillus atrosepticus* was then created to designate bacterial pathogens causing potato blackleg disease (van Hall 1902). Jones showed the importance of a pectinolytic enzyme produced by these bacteria that dissolved the middle lamella and broke apart cells during rapid bacterial progression through storage organs of plants including tubers, bulbs or rhizomes (Jones 1909).

In 1920, the Committee of the Society of American Bacteriologists on characterization and classification of bacterial types united all Gram-negative, fermentative, non-sporulating, peritrichous flagellated plant pathogenic bacteria into one ‘tribe’ named erwiniae in honour of the American phytopathologist Erwin F. Smith. In this tribe, which still includes other species such as *E. amylovora* and *E. stewartii,* pectinolytic bacteria were named *Erwinia carotovora* and were classified into two subspecies: *E. carotovora* subsp. *atroseptica* for potato blackleg causing pathogens and *E. carotovora* subsp. *carotovora* (Winslow et al. 1920). Pathogens isolated from several hosts were also further classified into the *E. carotovora* species based on the exhaustive study of Dye (1969), who concluded that all such pathogens represent a single species based on their common biochemical characteristics. Three other pathogens were also more recently described as subspecies of *E. carotovora*: subsp. *betavasculorum*, responsible for vascular necrosis of sugar beet (Thomson et al. 1981), subsp. *wasabiae*, responsible for internal discoloration of rhizomes of wasabi (Goto and Matsumoto 1987), and subsp. *odorifera*, responsible for slimy rot of witloof chicory (Gallois et al. 1992).

A second species of soft rot-causing pathogens was created in 1953; *Erwinia chrysanthemi* so named because of its first isolation on chrysanthemum (Burkholder et al. 1953). The species was found to be diverse in phenotypic properties including host range. However, such a broad classification in species did not always meet the needs of phytobacteriologists, who preferred to have bacterial names that clearly indicated differences in pathogenicity and plant hosts. For this reason, the epithet “pathovar” was proposed to deal with the differences in pathogenicity between groups within the same species. *E. chrysanthemi* was thus subdivided in six pathovars (pv. *chrysanthem*i, pv. *dianthicola*, pv. *dieffenbachiae*, pv. *parthenii*, pv. *zeae* and pv. *paradisiaca*) (Dye et al. 1980; Young et al. 1996). The practice of using pathogenicity to determine the pathovar, however, proved difficult to implement due to overlapping host range and the lack of reproducibility of the bioassays. Alternatives were proposed to characterize all strains of the soft rot *Erwinia* complex including the classification of strains into serovars by serological tests (Samson 1973; De Boer et al. 1979) or into biovars using batteries of differential biochemical tests (Dye 1969). The classifications in pathovars, serovars and/or biovars were unfortunately often not in concordance.

The advent of DNA sequencing techniques allowed the relationships between *Erwinia* species and subspecies to be studied based on genetic evolutionary trees. The first studies were based on 16S rDNA sequence. Using such methods, Hauben et al. (1998) united the members of the soft rot erwiniae, including *Erwinia carotovora*, *Erwinia cacticida*, *Erwinia chrysanthemi* and *Erwinia cypripedi* into the genus *Pectobacterium*, adopting an earlier proposition by Waldee (1945) who proposed the inclusion of all pectinolytic enterobacteria into a single genus. Samson et al. (2005) then renamed *E. chrysanthemi* as a new genus, *Dickeya,* after the famous American phytobacteriologist Robert S. Dickey and defined six *Dickeya* species that largely fitted with the previous classification in pathovars. The accumulation of genomic sequences now available in databases, thanks to increasingly cost-effective, high-throughput DNA sequencing technologies, allowed whole genome comparisons that resulted in a major re-evaluation of pectinolytic bacterial taxonomy. Adeolu et al. (2016) reclassified the family *Enterobacteriaceae* as an order (*Enterobacterales*) that comprises the *Enterobacteriaceae* but also other families. One such family is *Pectobacteriaceae,* which contains the genera *Pectobacterium* and *Dickeya* together with the plant pathogen genera *Lonsdalea* and *Brenneria. Pectobacterium* and *Dickeya* spp., formerly termed 'Soft Rot erwiniae', and then 'Soft Rot *Enterobacteriaceae* in an attempt to use the same acronym (SRE), have more recently been termed 'Soft Rot *Pectobacteriaceae* (SRP)' as used throughout this book. Genomic analyses have more recently re-defined multiple SRP species leading to the current description of nineteen *Pectobacterium* and twelve *Dickeya* species as described in Chap. 2.

Taxonomy of the SRP has been and remains a complex field and so we have attempted to simplify it in the book by using, where possible, the most recent name for the genus or species. For example, a previous study that refers to *Erwinia chrysanthemi*, in the absence of further pathovar information has been referred to as '*Dickeya* spp.' but, where a pathovar is noted, e.g. *Erwinia chrysanthemi* pathovar *dianthicola*, we have referred to it by its current name '*Dickeya dianthicola*'.

1.2 Host Range and Environmental Sources

Collectively, SRP have a very broad host range. Indeed, Ma et al. (2007) recorded SRP hosts in 35 % of angiosperm plant orders, including both dicot and monocot plants (Ma et al. 2007) and this catalogue is still expanding to include woody plants (Charkowski 2018; Tian et al. 2016). While several *Pectobacterium* spp. have been reported on a specific host, e.g. *P. atrosepticum*, *P. parmentieri* and *P. polaris* on potato and *P. betavascularum* on sugar beet, others have been isolated from a large variety of plants, often belonging to both dicots and monocots. Conversely, some plants may act as hosts for several SRP species. For example, potato is infected by half the SRP species currently described (5 *Dickeya* and 9 *Pectobacterium* spp.). This reflects, in part, the extensive research characterising potato blackleg causing agents over recent decades. The diversity of SRP plant hosts is described in Chap. 3 together with modes of infection and disease development. This chapter also explores the numerous environments outside plants that SRP inhabit and their role as possible sources of plant contamination.

1.3 The Nature of Disease

Because SRP can be found in association with asymptomatic plants and rely mainly on the production of plant cell wall degrading enzymes (PCWDE) for their pathogenicity, they have often been viewed as "brute force" opportunistic pathogens. However, characterisation of the virulence factors and the highly sophisticated regulatory networks that control their production, in addition to the intense cross-talk governing the interactions of these pathogens with their plant hosts, show that SRP are much more than producers of PCWDE but instead behave as true stealth force pathogens (De Boer 2003; Toth and Birch 2005).

SRP may survive in a latent state within the plant without producing symptoms. There is also now good evidence that SRP can live on plants [particularly roots] away from a susceptible host, suggestive of a more natural lifestyle in the wider environment as outlined in Chap. 3. Whether on such plants or in the apoplast of a susceptible host, they can multiply and persist using the nutrients present and have developed a large array of metabolic pathways to adapt to such environments. These metabolic pathways are tightly controlled by regulatory networks intertwined with those governing the production of PCWDE, and in some cases clearly act as virulence factors. The reason why these bacteria can grow on some plants in the absence of disease, while causing devastating diseases on others, remains unclear. However, when in a susceptible host, this biotrophic lifestyle may persist for months when the environmental conditions are not favourable to disease initiation (De Boer 2002), further suggesting the hemi-biotroph nature of these pathogens (Kraepiel and Barny 2016).

For decades, analyses of SRP-host plant interactions have led to the characterisation of a range of factors involved in SRP virulence, including the key virulence factors, PCWDE, and their secretion systems but also other protein secretion systems, the production of toxins and plant hormones, and motility, as well as plant responses to SRP infections. This has been extensively reviewed (Davisson et al. 2013; Reverchon et al. 2016; Toth et al. 2006; Charkowski et al. 2012). More recently, gene expression analyses, both in vitro, in conditions mimicking the plant environment, and directly *in planta*, have allowed the identification of complex regulatory networks that permit the sequential production of virulence factors in the different phases of infection (Liu et al. 2008; Venkatesh et al. 2006; Jiang et al. 2016; Bellieny-Rabelo et al. 2019; Chapelle et al. 2015; Gorshkov et al. 2018; Pédron et al. 2018; Raoul des Essarts et al. 2019). The most recent advances in molecular interactions between SRP and plants are summarized in Chap. 4 with a special emphasis on the importance of metabolic activities in plant-bacteria interactions and a comparison of the strategies used by both *Pectobacterium* and *Dickeya* spp. for controlling the coordinated and "at the right time" expression of virulence factors during infection. Indeed, the control levers regulating virulence gene expression in both genera are quite similar, e.g. quorum sensing, metabolic status and environmental conditions but the genetic components governing the regulatory networks vary in both genera. While this cannot be all encompassing, Chap. 4 summarises the main areas and, like other chapters, helps to guide the reader to further detailed information.

Despite the high conservation of regulatory networks, the expression profiles of even closely related species during infection may vary for several genes, including those involved in virulence and regulation as exemplified in the comparison of the two closely related *D. solani* and *D. dianthicola* expression profiles in infected potato tubers (Raoul des Essarts et al. 2019). It is even more striking within the species *D. solani,* where several strains are clonal and differ at the DNA level in only a few SNP/InDels and genes, and yet exhibit widely contrasting aggressiveness and large variation in expression of virulence genes, including those encoding the PCWDE (Khayi et al. 2015; Golanowska et al. 2018). Genomic analyses have also revealed genes encoding virulence factors and metabolism associated with horizontally transferred genomic regions and prophages, indicating genome plasticity. Chapter 2 also explores the levers of evolution in SRP genomes and how this may pave the way to rapid evolution of SRP for easy adaptation to different environments and/or new hosts.

1.4 Managing Diseases

Diagnostics play an important part in disease management as they identify the presence and level of a pathogen even in the absence of symptoms. Indeed they are essential to identify and track disease outbreaks caused by SRP and play an important role in monitoring the presence of certifiable pathogens, e.g. as used in Scotland where there is legislation to prevent the import of *Dickeya* spp. (Toth et al. 2011). Detection and diagnostics are vital areas if we are to understand how these pathogens move between plants, through trade routes, contaminated crops and much more, and this area is covered in Chap. 5. Diagnostics have changed considerably and for the better in recent years thanks to advances in genomics and the characterisation of numerous new SRP species, linking closely information in Chap. 5 with that on taxonomy in Chap. 2.

Ultimately, research on the SRP has been undertaken for the purpose of improving existing or identifying new methods of disease control. Control of these pathogens has never been straightforward due mainly to the lack of chemical control options but also, and at least currently, the lack of disease resistance (Czajkowski et al. 2011). With these two main control options unavailable, the industry has instead relied on a toolbox of different, less effective, but nevertheless useful options. Hygiene of machinery, equipment, glasshouses, and stores etc. also has a high priority. Simple disinfectants are highly effective against these pathogens but the logistics of undertaking hygiene measures in vast storage units or large constantly used machinery is very much more difficult and can often get neglected (Czajkowski et al. 2013). While not every region or crop production system undertakes control in the same way, control often begins with the use of microplants grown in the laboratory and free from the pathogen. In the case of potato, these are then grown as minitubers under covered conditions before going to the field. Certifying through inspection, removal of diseased plants (roguing) and, where necessary, rejecting or down-grading crops based on the presence of the pathogen or disease symptoms is also an essential part of any well-managed system. Chapter 6 looks at disease management and the different options available. This is perhaps the pinnacle of the book as all previous chapters are there exclusively with control in mind. This is a very difficult pathogen to control but with recent advances we are hoping that new possibilities may be just around the corner.

1.5 Population Dynamics

It is noteworthy that the dynamics of SRP populations responsible for potato diseases, and also perhaps less studied diseases, have been changing worldwide over the last decades. In Europe, for example, until the 1970s *P. atrosepticum* was the major SRP responsible for disease on potato. At this time, sporadic infections by *D. dianthicola* were recorded, which later increased across much of Europe. At the beginning of the twenty-first century, a new species emerged, *D. solani*, again spreading across potato-producing countries in Europe and, by around 2010, this species had become the most important blackleg agent in several of these countries. Over the past decade, other species of the so called "*P. carotovorum* complex", including *P. brasiliense* and *P. parmentieri,* have emerged and become predominant. Interestingly, several of these emerging SRP have recently been found in historic bacterial culture collections (classified under the generic term *Erwinia carotovora*), suggesting that they may have been previously 'unnoticed' rather than 'new-comers'. Nevertheless, the emergence of totally new SRP variants by genetic changes cannot be ruled out. Genomic analyses have revealed genes encoding virulence factors and metabolism associated with horizontally transferred genomic regions and prophages, indicating genome plasticity. As several SRP can occupy the same niche in infected plant, a rapid evolution of SRP can be expected to adapt to new environments and/or new hosts (Chap. 3). Chapter 7 describes the global reach of SRP, and the different genera and species responsible for diseases, by taking key examples from around the world of plants affected by SRP and the pathogens responsible. It has not been possible to include all countries affected by these pathogens and we apologise in advance for those regions that have not been included.

1.6 Economic Impact

As recorded in Chap. 7, SRP cause severe losses in important economical crops in many countries around the world and, consequently, have been ranked in the top ten plant pathogenic bacteria in 2010 (Mansfield et al. 2012). They cause diseases in three of the four most important crops worldwide: rice, maize and potato (but not wheat). Over the last decades, the potato seed industry has faced several outbreaks corresponding to the emergence of SRP, including *D. solani* and *P. brasiliense* in Europe and *D. dianthicola* in the USA (Toth et al. 2011; Nunes Leite et al. 2014; Charkowski 2018). These outbreaks have led to the rejection or downgrading of substantial amounts of seed potato crops, e.g. leading to average annual losses of 12 million euros in the Netherlands (Prins and Breukers 2008). No recent reports are available on the global economic impacts of SRP on potato or on diseases of rice or maize, although Thind and Pavak (1985) reported bacterial stalk rot caused by *D. zeae* as one of the four major maize stalk diseases in India with an incidence of up to 80–85 %.

Soft rot is one of the most destructive diseases of vegetables during production and post-harvest with, for example, severe losses observed in the production of chicory in Europe since the 1990s. Under conditions favourable for the pathogens, crop losses of chicory roots due to soft rot infection by *P. carotovorum* can exceed 50 % and can rise to up to 90 % for *Dickeya* spp. (Le Hingrat et al. 2012). There are no accurate values for losses caused by SRP in fleshy fruits and vegetables post-harvest. However, estimates vary between 15 and 30 % of the harvested crop (Agrios 2006). A survey of the post-harvest fruit rot diseases of tomato in Nigeria revealed that soft rot can cause 25 % loss at harvest and 34 % loss of the remaining product in transit, storage and market stalls (Fajola 1978).

SRP also cause destruction of many flowers and ornamental crops both in the field and in glasshouses, including a recent finding of soft rot on orchid caused by *Dickeya fangzhongdai*—an ornamental that has an export market valued of 500 million euro in the Netherlands alone (Alic et al. 2017; Hinsley et al. 2018). In the 1950s bacterial stunt disease caused by *D. dianthicola* affected 26.5 % of carnation stocks in Denmark (Hellmers 1958). The disease was so destructive that the European and Mediterranean Plant Protection Organization (EPPO) classified *D. dianthicola* as a quarantine organism in carnation production. However, due to good phytosanitary measures, the absence of the bacterium and only negligible amounts of damage to carnation production in recent years, this regulation has recently been removed (EFSA 2013). Chapter 8 gives a specific example of the economic consequences of SRP diseases by taking an in depth look at the situation for potato in Switzerland. There is an expectation that the findings can be extended to losses that might occur in other countries and on other crops.

Finally, Chap. 9 gives a brief outlook moving ahead. It begins by reiterating the difficulties of finding solutions to SRP disease control but finishes with some tangible possibilities for the future. Options for control in the future may include improved diagnostics, novel resistances (with the use of biotechnology helping to achieve this) and biocontrol (Chap. 9; Czajkowski et al. 2011). The term integrated pest management (IPM) was first used in the 1970s mainly in response to the desire for reduced pesticide use and alternatives to disease control. In recent years, the term IPM is now widely used to reflect a desire to find new integrated solutions to replace or reduce the use of chemicals. It is interesting to reflect, therefore, that control of SRP has never been anything other than an IPM system and may be one of the original examples of its use.

We hope you enjoy!

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