PATHOGENIC AND BENEFICIAL PLANT-ASSOCIATED BACTERIA

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Keywords: Phytobacteriology, pathogenicity, beneficial bacteria, plant resistance, disease control, plant immunity, systemic resistance, genome sequence, bacterial wilt, crown gall, fire blight, citrus canker, citrus greening, bacterial soft rot, Pierce’s disease, bacterial leaf blight, black rot, Bacterial fruit blotch, PGPR, biological nitrogen fixation.

Contents

Summary

Bacteria that live in association with plants greatly influence growth and yield of all agricultural crops used to sustain the increasing world population nutritional needs. Over 130 years ago a bacterium- *Erwinia amylovora*- was described for the first time as the causal agent of a plant disease, the fire blight disease of pears and apples. We now know that all major agricultural crops are affected at least by one pathogenic bacterium, and in many cases the bacterium causes a major disease in that crop. Emerging and prevalent diseases such as citrus greening, citrus canker, bacterial fruit blotch, and Pierce's Disease do not have a practical cure and methods of disease management and control are being investigated. Beneficial bacteria that live in association with plant roots or inside plants are investigated for their role in promoting plant growth directly and controlling plant pathogens. Some of these bacteria such as *Rhizobium*, *Bacillus* and *Azospirillum* strains are used commercially to improve crop yield. The mechanisms of pathogenicity, biological control and plant growth promotion have been studied intensively, and with the help of molecular biology, and more recently with genomics and post-genomics approaches, we can now understand many parts of the puzzle composing the interactions between plant and associated bacteria. The accumulated knowledge is being exploited to design new methods to improve agriculture in the 21st century.

1. Introduction

Microbes associated with plants have a strong influence on plant growth, development and yield. Natural microflora present in soil, water, air, insects, nematodes and mammals can become associated with plants and trigger beneficial or deleterious responses in them. Pathogenic bacteria can enter the plant through natural openings or wounds and colonize the host, causing diseases that can destroy entire fields of crops and cause great economic losses. Knowledge of the survival, dissemination and infection mechanisms of bacteria are crucial to developing management strategies for protection against these widespread pathogens. With advances in molecular biology over the last few decades, we have enriched our knowledge about specific and non-specific interactions between plants and microbes, which is contributing to programs to develop disease resistance in crops. Great efforts are also being made into understanding the associations between beneficial bacteria and plants in order to develop commercial products that can be exploited to improve crop growth and yield. Many products are already helping farmers around the world to protect and enhance yields of their crops.

In this chapter, we will revise current knowledge on key aspects of the interactions between plants and bacteria, both pathogenic and beneficial. Several economically important plant diseases will be reviewed and the mechanisms of pathogenicity of bacteria will be analyzed in detail, with a focus on the molecular processes associated with host responses. In our review of beneficial microflora, special attention will be paid to the current state of knowledge about mechanisms of action and the commercialization of products that use bacteria to promote plant growth. We hope this chapter will increase the interest in plant-associated bacteria and present an overview of the important role they play in agricultural production.

2. Phytopathogenic Bacteria: Worldwide Importance and Economic Impact

In terms of number of species, bacteria are the major causal agents of animal and human diseases. In contrast, while it is estimated that more than 10,000 species of fungi and fungus-like organisms cause disease in plants, the estimated number for plant pathogenic bacteria is about 100 species (Agrios, 2005). Nevertheless, most important agricultural crops suffer from at least one bacterial disease, and, for some crops, a bacterial disease is the main cause of yield losses.

As an example of a bacterial disease of huge economic importance, black rot disease of crucifer plants, caused by *Xanthomonas campestris* pathovar (pv.) *campestris*, is considered the most serious disease of cultivated brassica and radishes worldwide. Another bacterial species belonging to the *Xanthomonas* genus, *X. citri,* leads to the eradication of millions of citrus trees in Florida, São Paulo and other parts of the world. *Xanthomonas oryzae* pv. *oryzae* causes bacterial leaf blight (BLB) of rice. This is one of the most important diseases of rice in many parts of the world and is very destructive in Japan, India and other parts of Asia. As more than 50% of the world population relies on rice for basic nutrition, it is clear that damage to rice production caused by BLB poses significant economic and social risks. *Erwinia amylovora* causes the fire blight disease in a wide range of plants from the *Rosaceae* family. This is a very destructive disease, which entirely prevents cultivation of apples and pears in some parts of the world. Similarly, the European grape, *Vitis vinifera*, cannot be cultivated in certain regions of the United States due to the bacterium *Xylella fastidiosa*, the causal agent of Pierce's Disease of grapevines.

Another bacterial disease of tremendous importance is crown gall disease, caused by *Agrobacterium tumefaciens*. This bacterium affects woody and herbaceous plants belonging to more than 100 genera. *Agrobacterium tumefaciens* induces the production of galls (tumors) on the stem and/or roots of the plant. Infected plants often grow poorly and produce reduced yields. However, the importance of this disease is not limited to its phytopathological damage. During the infection process, *A. tumefaciens* introduces a fragment of its own DNA into the host plant cell. The transferred DNA fragment contains genes that are further expressed in the plant host, an essential step for gall formation and pathogenesis. Much research has been done to understand the mechanism of DNA transfer by *A. tumefaciens* and, based on the knowledge acquired from this; scientists have developed methods for genetic modification of plants using this bacterium. Indeed, *A. tumefaciens* serves today as the main tool for generation of transgenic plants for biotechnological and agricultural purposes, as well as for basic research investigations. More details about these and other bacterial diseases of high agricultural importance are provided in Section 7 of this chapter.

3. Phytopathology and Phytobacteriology: Historical Background

In the middle of the 19th century, a tragedy occurred in Ireland as a result of a disease that severely affected potato cultivation in the country. Huge reductions in potato yields due to the late blight disease first occurred in 1845 but continued during the following years. At this time, the Irish population depended almost exclusively on the potato crop for its food source. The consequences for the Irish were terrible: in few years, about 1 million people died from hunger and disease and about 1.5 million emigrated mainly to the US and Canada. A few years later, in 1861, a German scientist, Heinrich Anthon deBary, demonstrated that a fungus (today reclassified as an oomycete, a fungus-like organism), *Phytophthora infestans*, is the causal agent of the late blight disease. This was the first time a microorganism was demonstrated to be the causal agent of a plant disease, an idea that, until this discovery, was largely unaccepted by the scientific community. Moreover, deBary's findings preceded the germ theory of disease, which was proposed in 1863 by Louis Pasteur in substitution of the theory of spontaneous generation (Schumann, 1998).

deBary's studies of the late blight disease as well as other plant diseases caused by fungi and fungus-like organisms led to the foundation of Phytopathology, the scientific discipline of the study of plant diseases, in the early 1860s. However, it was only in the late 1870s and early 1880s that some scientists started to provide evidence about the association of bacteria with diseases of plants. In 1878, the American scientist Thomas J. Burrill showed that *Micrococcus amylovorus* (today known as *Erwinia amylovora*) was strongly associated with the fire blight disease of pear and apple trees. Three years later, in Holland, Jan Wakker provided strong evidence of the involvement of *Bacterium hyacinthi* (today *Xanthomonas hyacinthi*) as the causal agent of yellow disease of hyacinth. In 1885, in the U.S., Joseph C. Arthur confirmed Burrill's results with the fire blight. However, the idea that bacteria are able to cause disease in plants was still not accepted by many phytopathologists. This occurred despite the fact that in 1876 Robert Koch had already demonstrated that the bacterium *Bacillus anthracis* is responsible for anthrax disease. In fact, most phytopathologists in Europe at that time believed that bacteria cannot cause significant damage to plants, mainly because they are not likely to tolerate the acidic conditions of the plant’s intercellular spaces. The scientist, who put an end to this debate, by 1899, was the American Erwin F. Smith, who demonstrated that *Erwinia amylovora* is indeed the causal agent of fire blight disease. Smith also optimized techniques for the study of bacterial plant diseases and investigated important plant pathogenic bacteria from diverse genera including *Erwinia*, *Xanthomonas*, *Pseudomonas* and *Agrobacterium*. In view of his significant contributions, Smith is considered the "father" of modern Phytobacteriology (Volcani, 1985; Griffith, 2003; Janse, 2005).

Advances in the areas of General Microbiology and Medical Bacteriology have contributed to the rapid development of the emerging Phytobacteriology field since the beginning of the 20th century. Today, Phytobacteriology is a modern and dynamic discipline, interrelated with a great variety of basic and applied research areas, including molecular biology, genetics, biochemistry, immunology, ecology, taxonomy, epidemiology, disease control and plant breeding. The emergence of the genomic era at the end of the 20th century represents a huge contribution to research in Phytobacteriology. This issue is briefly discussed in Section 14 of this chapter.

4. Classification of Plant Pathogenic Bacteria

Classification is extremely important, especially when it comes to developing treatments to prevent or cure a disease based on the characteristics of the microbial pathogen. In the first half of the 20th century, researchers classified plant pathogenic bacteria mainly based on the plant host from which it was isolated and caused disease. There was a lack of scientific rigor in defining key characteristics separating or relating one bacterium to another. Therefore, researchers describing a new plant disease will give a new name for the causal bacteria, in what became known as the “new host-new species cliché” of the “subjective era” of classification (Starr, 1959). During the second half of the 20th century, researchers started using a systematic approach to classify phytobacteria, in what is known as the “objective era” of classification. During this time, the discipline insularity that dominated the previous “subjective era” was discarded, and researchers classified phytobacteria by comparing their characteristics with those of other microbes found in hosts from other kingdoms or the environment.

The approach to bacterial classification has been changing over time and has been an object of controversy. This probably reflects the lack of consensus when it comes to the definition of a bacterial species. The biological species concept (Mayr, 1942), where species are delineated by interbreeding populations isolated from other groups, cannot be applied to asexually-reproducing prokaryotes. The ability of bacteria to undergo homologous recombination (exchange of DNA among bacteria) may be considered an equivalent to “sexual” isolation. But this approach is encountering opposition from researchers that want to keep using phenotypic characteristics (or gene product activity) to delineate species. As we will see below, the availability of huge amounts of DNA sequences is having an impact on classification schemes.

Most bacterial plant pathogens described to date are Gram-negative bacteria classified in different subclasses of the Proteobacteria. Traditional bacterial classification is based on biochemical characteristics, and several commercial kits such as Biolog^{TM} and Oxi/Ferm tubes are fast and easy methods of identification. In recent years, more researchers are relying on DNA for bacterial classification. DNA-DNA hybridization (DDH) is used as the standard for delimitation of bacterial species (Stackebrandt et al., 2002). This technique was developed in the 1960s, and by the 1970s it was the standard method used to classify plant pathogens. The technique is very time-consuming because it relies on multiple pair-wise comparisons of highly purified DNA from diverse bacterial species. The thermal denaturation midpoint (Tm) of DNA hybrids is measured while temperature is increased and complementary DNA strands are separated from each other. It is generally accepted that the same bacterial species have >70% DDH and ΔTm <5°C (Wayne et al., 1987). Nowadays DDH is the only DNA-based method accepted taxonomically to delineate bacterial species.

For plant pathogenic bacteria, a specific epithet of classification is the pathovar (pv.) designation, which is defined as "an infrasubspecific term referring to a group of phytopathogenic bacteria differentiated principally on the basis of their host range" (Dye et al., 1980). The pathovar classification is very useful to define host specificity of a particular bacterium. When a bacterium affects a particular cultivar or line among a host species, it is classified as a specific "race", with the exception of *Ralstonia solanacearum* where races are defined by species of host affected. To avoid ambiguity, the nomenclature of phytobacteria follows the rules of the *International Code of Nomenclature of Bacteria* and the *International Standards for Naming Pathovars of Phytopathogenic Bacteria* (Bull et al., 2008; Young, 2008). A website (http://www.isppweb.org/about_tppb.asp) curated by the International Society of Plant Pathology keeps an updated list of plant pathogenic bacteria (Bull et al., 2010).

Lower DNA sequencing costs and simplified analysis software are driving the popularity of DNA sequence-based approaches for bacterial classification. The use of small subunit ribosomal RNA (16S rDNA) gene sequences has become the standard for phylogenetic relationship studies, and the number of sequences available is growing exponentially. The Ribosomal Database Project (http://rdp.cme.msu.edu/index.jsp) had more than 700,000 16S rDNA bacterial sequences deposited by April 2011. Despite the great amount of data, 16S rDNA sequences are still not taxonomically accepted for species determination. This is due in part to lack of a threshold value that could be set to delineate bacteria belonging to the same species. The increase in bacterial full genome sequences available may help the use of Average Nucleotide Identity (ANI) (Konstantinidis and Tiedje, 2005) in the future. The authors suggested that comparison of all shared genes between 2 full genomes can be used to determine species, and a value of 94-95% of ANI corresponds to the cut-off of 70% DDH.

The use of Multi Locus Sequence Typing (MLST) or Multi Locus Sequence Analysis (MLSA) is becoming very important for species delineation of plant pathogenic bacteria (Almeida et al., 2010). For MLST, isolates with identical alleles for a specified set of genes are given the same profile designation or "sequence type" for comparative purposes. This approach is used for epidemiological studies of strains within a known species. MLSA, instead of 'typing", uses the concatenated set of gene sequences for analyses, which is useful to determine the species of a strain of uncertain identity and to define phylogenetic relationships. These techniques, based on partial sequence of at least 6 housekeeping genes, were first described in 1998 (Maiden et al., 1998). MLST increases the DNA sequence data analyzed compared to 16S rDNA and reduces the risk of interference from horizontal gene transfer by looking at several genes dispersed in the genome. Homologous recombination can be detected by MLST analysis, which could help in bacterial species classification if this is considered an indication of "interbreeding". Molecular-based classifications changed the way we classify organisms and their impact will increase in the future as they become more popular.

5. Bacterial Infection Cycles: Inoculation and Spread

Survival in the environment is an important stage of the pathogen life cycle. Some plant pathogenic bacteria are adapted to survive in the soil, where they can live as saprophytes or associated with plant debris. Pathogens such as *Agrobacterium tumefaciens* and *Ralstonia solanacearum* are successful soil inhabitants, where they maintain high enough populations to be able to infect the next susceptible host that grows in the soil. However, some pathogens are very ineffective at living in the soil and can only survive inside plant tissues or associated with insects. This is the case of pathogens such as *Erwinia amylovora* and *Xylella fastidiosa*, which depend on insects for plant-to-plant transmission. Bacteria can also survive in the natural bacterial ooze they produce, in seeds or in association with insect vectors. The dissemination of bacteria can occur in association with the water cycle, where rain splashes can be an effective method of moving bacteria from one plant to the other or to different parts of the same plant. Insects, other animals and humans can disperse bacteria among plants. Lack of disinfection of pruning tools by field workers is a common mean of bacterial dissemination (Agrios, 2005).

Once the bacterium encounters a plant, it can enter only through natural openings, wounds or from introduction by insect vectors. Natural openings include stomata, used for gas exchange by the plant, and hydathodes, used for water secretion. Bacteria usually aggregate in high populations surrounding these structures as well as trichomes and depressions and cracks in leaf veins, waiting for an opportunity to enter the host. Biofilm formation in these regions is often important to protect bacteria from environmental stress and antimicrobial compounds, as well as to obtain nutrients (see Section 8.7). High inoculum densities are helpful for the invasion of the plant host by the pathogen, a process favored by the environment. Factors such as rainfall, humidity and cracks in the plant surface facilitate bacterial entry. Some other factors are produced by the pathogen itself to gain access inside the host. For instance, some bacteria produce ice nucleation protein that increases freeze damage to plants at higher environmental temperatures, and toxins that regulate closure and opening of stomata (e.g. coronatine produced by *P. syringae*; see Section 8.2). Once the bacterium enters the plant, it colonizes the apoplast, which is the space among plant cells or the vascular system, including the xylem or phloem. Inside the plant, bacteria find protection from outside environmental stresses such as UV radiation and water deficit. Nevertheless, the apoplast environment is not a perfect place to thrive, especially due to limited nutrient availability and presence of antimicrobial compounds produced by the plant, as well as imposing osmotic and pH stresses on the pathogen. However, bacteria have evolved methods to successfully colonize this environment. Traditionally the methods can be classified as: i) "brute force": this is the case of bacteria producing cell wall-degrading enzymes such as *Pectobacterium atrosepticum* that degrade host plant tissues for use as a nutrient source, behaving as a necrotroph; and ii) 'stealth': use of traits such as type III secretion systems-secreted effectors (see Section 8.1) and toxins (see Section 8.2) as mechanisms to promote disease. In this case, the pathogen modifies the physiology of the plant cell and suppresses plant defense mechanisms to their benefit. Bacteria usually multiply to high populations before causing plant death and are considered hemibiotrophs (Rico et al., 2009).

Once inside the plant, a successful pathogen will colonize and establish highly concentrated bacterial populations. This will interfere with normal physiological and morphological development of the plant, causing diverse symptoms including chlorotic or necrotic spots and vein discoloration, defoliation, scab, cankers, galls, vascular wilts and rots. Examples of symptoms of important bacterial plant diseases are described in the next section.

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Biographical Sketches

Leonardo De La Fuente received his B.Sc. in Biochemistry (1996), and M.Sc. in Microbiology (2000, advisor Alicia Arias) from the University of the Republic in Montevideo, Uruguay. He obtained his PhD. in Plant Pathology (2005) from Washington State University (USA) with advisors Profs. David Weller and Linda Thomashow. From 2005 to 2008 he worked as a postdoctoral research associate at Cornell University in the laboratory of Profs. Harvey Hoch and Tom Burr.

Since 2008 he is an assistant professor at the Department of Entomology and Plant Pathology at Auburn University (Auburn, Alabama, USA). Among other courses, he teaches Molecular Plant Pathology for graduate students. In the Faculty of Chemistry (University of the Republic, Montevideo, Uruguay) he teaches together with Saul Burdman and Maria Julia Pianzzola the graduate course Molecular Interactions Plant-Pathogens. During his career, De La Fuente worked in beneficial and pathogenic plant-associated bacteria, including *Pseudomona*s spp., rhizobia, *Xylella fastidiosa* and '*Candidatus* Liberibacter spp.'. His research interests are focused on the interactions between plants and associated microorganisms. His research group is looking at different factors influencing the infection process, host colonization, and biofilm formation of plant pathogenic bacteria. Other areas of interest include molecular characterization of populations of bacterial plant pathogens. He is a co-author of more than 30 publications in referred journals, book chapters and proceedings of international scientific conferences.

Saul Burdman received his B.Sc. degree in Horticulture, M.Sc. in Agricultural Botany and Ph.D. in Agricultural Microbiology at the Hebrew University of Jerusalem in 1993, 1996 and 2001, respectively. From 2001 to 2003 he did postdoctoral research in the lab of Prof. Pamela Ronald at University of California, Davis. He is a researcher at the Department of Plant Pathology and Microbiology of the Robert H. Smith Faculty of Agriculture, Food and Environment of the Hebrew University of Jerusalem, Rehovot, Israel. He is also a member of the faculty Otto Warburg Minerva Center for Agricultural Biotechnology.

His present research interests are in the area of plant-associated bacteria. His research group aims at enlarging our knowledge of both detrimental and beneficial interactions between plants and bacteria. Currently, his major research subjects are: the *Acidovorax citrulli*-cucurbit interaction (bacterial fruit

blotch disease), the *Xanthomonas campestris* pv. *vesicatoria*-tomato interaction (bacterial spot disease), and the plant growth promoting rhizobacterium *Azospirillum brasilense*.
He is a teacher in Plant Pathology and Phytobacteriology, and is co-author of about 50 publications in referred journals, book chapters and proceedings of international scientific conferences. In 2009 Dr. Burdman received the Prof. Moshe Shilo prize of the Israel Society for Microbiology for its contribution to the understanding of basic aspects of plant pathogenesis.