

## PLANT AND HUMAN PATHOGENIC BACTERIA EXCHANGING THEIR PRIMARY HOST ENVIRONMENTS

### A review

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### ABSTRACT

Adaptation of plant and human pathogenic bacteria to niches of existence differing from their original ones is a sophisticated mechanism for survival. Research indicates that certain plant bacterial pathogens are capable of causing disease in humans, and some human bacterial pathogens can inhabit the plant environment and cause disease in plants. The infection of humans by plant bacteria may occur at direct physical contact with diseased plants and/or via the respiratory tract in mainly immunocompromised or otherwise stressed individuals. Indirect transmitters of plant and human microbes can be wind, rain, dust, insects, and animals. Human pathogenic bacteria may contaminate the soil and irrigation water, colonize the rhizosphere, more rarely also the phyllosphere, and can survive as epiphytes. Thus, the plant environment may become a reservoir of human pathogens. A source of foodborne human pathogenic bacteria can be unprocessed or unwashed fruits and vegetables. Especially during the last decade, the processes underlying the cross-kingdom performance of pathogenic bacteria are intensively researched. However, in reality, the risk for human health at infections by plant bacteria and by human bacterial pathogens surviving in the plant environment is still underestimated. The goal of the current review is to increase the interest in these issues in agricultural and general environments. Some basic strategies for infection and symptoms of diseases caused by the microorganisms under consideration are described. The potency of certain plant bacterial pathogens to surpass barriers towards humans and the interaction of human bacterial pathogens with the plant environment are addressed and the existing information is critically discussed.

**Key words:** bacterial pathogens, crossing kingdom borders, human diseases, plant diseases, primary and secondary hosts

### INTRODUCTION

It is estimated that among thousands of cultivable bacterial species at least 150 of them cause plant diseases (Kannan et al. 2015), and more are constantly discovered. A relevant question in a broader environmental and evolutionary framework is whether the plant pathogenic bacteria (PPB) may colonize and cause diseases in humans and vice versa, whether some human pathogenic bacteria (HPB) may colonize plant environment and cause diseases in plants. In the agricultural practice and in other circumstances of contact between humans and plants, such performance deserves special attention and, especially in recent years,

is a subject of intensive research. The ability of bacterial plant and human pathogens to surpass barriers between the kingdoms as a possibility for survival, by adapting to new hosts, has been studied in experimental models and under natural conditions (van Baarlen et al. 2007; Tyler & Triplett 2008; Holden et al. 2009; Kirzinger et al. 2011; Lim et al. 2014; Bulgari et al. 2019; Kim et al. 2020). It is hypothesized that the extent to which pathogenic microorganisms may “jump” toward novel hosts depends on their potential to accommodate to environments different from those in their primary hosts, the level of their molecular evolution, and their ability to recombine (Bonneaud et al. 2019).

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The data indicate that certain PPB may infect humans mainly at direct contact with the plant via skin injuries and/or through the respiratory tract. They can be transmitted by wind, rain, dust, insects, and animals (Kirzinger et al. 2011; Nadarasah & Stavrinides 2011; Kim et al. 2020). Some PPB may cause diseases and sometimes even death, especially for individuals with compromised immunity, reduced resistance to stresses, or exposure to contaminated clinical equipment. On the other hand, human pathogens have been detected in the rhizosphere and phyllosphere (Berg et al. 2005; Tyler & Triplett 2008; Kirzinger et al. 2011). Transmitted to the soil via feces, manure, waste, and water, some human pathogens may colonize the roots, move from there into the vascular system, spread, and inhabit various organs of the above-ground part of the plant (Hirneisen et al. 2012). The contaminated plant environment may serve as a niche for human pathogens (especially gastroenteric bacteria), thus enabling their survival and becoming a potential risk to humans (Holden et al. 2009). The consumption of unwashed, unprocessed fresh or stored fruits, and vegetables contaminated with HPB may impose an additional risk to human health. In this review, some more important findings showing the ability of several PPB to cause human diseases and examples documenting survival on and colonization of plants by HPB are discussed. Some basic strategies for infection and pathogenesis of plant and human diseases, caused by the bacteria under consideration, are also addressed.

## PLANT PATHOGENIC BACTERIA

Plant pathogenic bacteria develop in host plants as parasites (biotrophs and/or necrotrophs), but most of them can survive without infection as epiphytes or endophytes and sometimes as saprotrophs on dead tissues and in plant debris or in soil (Janse 2005; Kado 2010, Sobiczewski et al. 2017). The range of host plants for an individual bacterial species may vary from very wide, including several hundred plant species, e.g., plant tumor-forming *Agrobacterium tumefaciens* (Janse 2005), to very narrow, e.g., *Xanthomonas fragariae* that affects only strawberry (Roberts et al. 1996). Some species include pathovars, i.e., variants that differ in host range, and biovars that

differ in phenotypic characteristics. Symptoms of plant bacterial diseases are mainly spots, blights, cankers, wilts, soft (wet) rots, and galls (overgrowths and/or proliferation of organs) (Kado 2010). Based on the symptoms they cause, PPB can be divided into necrogens, macrogens, and oncogens (Billing 1987).

Plant infection proceeds in several stages, including attachment of the bacterium to appropriate sites on the plant surface and entering through natural openings such as stomata, hydathodes, nectaries, trichomes, lenticels, and via wounds, caused by, e.g., pest feeding, hail, or by other factors. The pathogens engage various strategies to infect the plant. Soft rot-causing bacteria, such as *Pectobacterium* spp. and *Dickeya* spp. produce a wide variety of plant cell wall-degrading enzymes such as pectinases, cellulases, proteases, and xylanases (Charkowski et al. 2012; Golanowska & Łojkowska 2016). Certain plant pathogenic *Pseudomonas* spp. produce toxins such as coronatine or syringomycin, that induce chlorosis or necrosis, respectively (Gross & Cody 1985; Bender 1999). Exopolysaccharides are important virulence factors of PPB. They can cause clogging of the vascular tissues and are responsible, among others, for plant wilting (Janse 2005; Kado 2010). Other factors involved in the pathogenicity of bacteria include lipopolysaccharides (LPSs). These molecules are incorporated into the outer membrane of the bacterial cell wall and prevent the pathogen from the action of compounds involved in host defense (Kutschera & Ranf 2019). On the other hand, to benefit the infected plants, LPSs stimulate signaling pathways, leading to the synthesis of pathogenesis-related proteins, including glucanases, chitinases, proteinase inhibitors, defensins, and peroxidases, that play a role in plant defense mechanisms (Agrios 2005). Lipopolysaccharides belong to pathogen-associated molecular patterns – virulence factors that are small molecules released by the bacterium into intercellular spaces and apoplast. They are recognized by specific receptors in the host cell and activate the plant-innate immune response (Yakura 2020; Kumar et al. 2021). Regarding plant defense against pathogenic microbes, it is also important to consider the hypersensitive response (HR), a type of programmed cell death event that is local cell death at and in the vicinity of the place of bacterial attack and is aimed at limiting the spread

of infection throughout plant tissues. This process is characterized by typical morphological features and involves a complex network of signal transduction cascades leading to oxidative stress, activation of cell-death-associated enzymes, and expression of cell-death-related genes (Mur et al. 2008). An example from our studies is *Erwinia amylovora*-induced HR in tobacco and apple leaves (Iakimova et al. 2013; Sobiczewski et al. 2017).

Among the weapons of bacterial plant pathogens is their ability to produce siderophores that are chelated compounds binding trivalent iron ions and playing an important role in the pathogenesis of diseases (Kado 2010). Some bacteria inhabiting the same biotope may exchange genetic material during the conjugation process, i.e., transfer a part of the chromosomal or plasmid DNA (horizontal gene transfer, HGT) from a donor cell to a recipient cell (Soucy et al. 2015; Arnold et al. 2022). Documented cases of HGT have shown acquisition of pathogenic capacity by nonpathogenic bacteria belonging to the genus *Agrobacterium* (Platt et al. 2014) or development of resistance to antibiotics of bacteria belonging to the genera *Pseudomonas*, *Erwinia*, and *Xanthomonas* (Sundin & Wang 2018).

#### BACTERIAL PLANT PATHOGENS SHARING PLANT AND HUMAN HOSTS

Clinical research over at least the past 40 years has shown that some PPB may occasionally infect humans, animals, and other organisms outside the plant kingdom (Kim et al. 2020). In this section, their capacity to infect both plants and humans, and the symptoms of the diseases they cause, are commented.

*Agrobacterium tumefaciens*, the cause of crown gall, a neoplastic tumor disease of many plant species, and its nontumorigenic, saprotrophic relative *A. radiobacter* (syn. *Rhizobium radiobacter*), were found as occasional human pathogens causing bacteremia (blood poisoning) or septicemia (serious bloodstream infection that can lead to sepsis), mainly in patients with compromised immune systems (Paphitou & Rolston 2003; Mantadakis et al. 2010; Casanova et al. 2019). Plant infection by *A. tumefaciens* involves inserting into the plant genome a fragment of the so-called tumor-inducing (Ti) bacterial plasmid, containing genes encoding the production of an unbalanced

amount of phytohormones (jasmonic acid, ethylene, abscisic acid, auxins, and cytokinins). Hormonal imbalance of cells leads to the formation of tumors, mainly on the roots or the root collar of the plant (Veselov et al. 2003). Under experimental conditions, it has been shown that *A. tumefaciens* can infect human cells through HGT, considered by some researchers to be the main factor in bacterial evolution (Lacroix et al. 2006; Soucy et al. 2015). It should be noted that regarding the taxonomy, agrobacteria (both plant pathogenic and nonpathogenic) have undergone numerous changes and reclassifications over almost 100 years (Flores-Félix et al. 2020). Currently, genus *Agrobacterium* contains 14 species, including the old species *A. radiobacter* and *A. tumefaciens*. Most of these species are able to produce tumors in different plants, nevertheless that this genus also encompasses nonplant pathogenic species, including one able to nodulate legumes and one pathogenic to human (*A. pusense* formerly *Rhizobium pusense*) (Flores-Félix et al. 2020).

When analyzing the literature in terms of agrobacteria as human pathogens, it is noted that clinical specialists rarely discriminate sufficiently between plant tumorigenic *A. tumefaciens* (having Ti plasmid) and nontumorigenic *A. radiobacter* (lacking this plasmid). However, it seems that this is practically often the case with nontumorigenic strains. Hulse et al. (1993) analyzed 25 cases with agrobacteria infections or contaminations. Most of them were central venous catheter-associated infections, but some referred to peritonitis or continuous ambulatory peritoneal dialysis. The authors concluded that those bacteria should be recognized as opportunistic (occasional) pathogens in the immunocompromised hosts, particularly in those with plastic catheters. Later, Southern (1996) reported for the first time isolation of *A. tumefaciens* (*radiobacter*) from the blood of a pregnant woman, who had no indwelling catheter or other foreign devices as well as from the blood of her stillborn, premature fetus. Lai et al. (2004) isolated *Rhizobium* (*Agrobacterium*) *radiobacter* from 13 patients. Almost all of them had underlying hematological malignancy or solid organ cancer, but six had febrile neutropenia. The majority of infections were catheter-related bacteremia. Recently, *A. radiobacter* was isolated from the blood of children with limited immunity, especially those with venous catheters suffering from acute lymphoblastic

leukemia (Mantadakis et al. 2010). In turn, Fenner et al. (2019) described a case of *R. radiobacter* infection of cornea in humans wearing contact lenses. The authors pointed out that this is the case of monomicrobial *R. radiobacter* keratitis, thus adding to the sparse literature information on this uncommon but potentially sight-threatening infection. Over 30 years ago a disease called septicemia caused by *Agrobacterium* sp. isolate, lacking Ti plasmid, had been detected in an elderly patient undergoing artificial ventilation and antibiotic therapy, who had four times more serum antibodies than healthy donors (Freney et al. 1985).

Noteworthy is the research on the bacterium *Rhizobium (Agrobacterium) pusense*. Panday et al. (2011) first described a novel bacterial strain isolated from the rhizosphere of chickpeas. It was designated with the symbol NRCPB10<sup>T</sup>. This strain appeared to be closely related to some *Agrobacterium* spp. On the basis of data from the polyphasic taxonomic study, the mentioned strain was considered to represent a novel species of the genus *Rhizobium*, for which the name *Rhizobium pusense* sp. nov. was proposed. Interestingly, the strain does not harbor the *nodA* and *nifH* genes and does not induce nitrogen-fixing nodules in chickpea or tumors in tobacco plants (Panday et al. 2011). Phylogenetic analysis of four reference strains *R. pusense*<sup>T</sup> (including NRCPB10<sup>T</sup>), and 24 isolates from humans or from clinical environments of the genomovar G2 (genovar A7) showed that they belonged to the same clade and corresponded to the same species (Aujoulat et al. 2015). Kuchibiro et al. (2018) reported the first case of sepsis caused by *R. pusense* in Japan in a 67-year-old woman with a history of hyperlipidemia, hypertension, diabetes, hypothyroidism, and osteoporosis. She had undergone cerebrovascular treatment because she was diagnosed with a subarachnoid hemorrhage. Recently, Casanova et al. (2019) described a total of eight bacteremia cases due to *Agrobacterium* genomovar G3, *A. radiobacter*, and *A. pusense*. The aim of the study was to detect possible sources of infection in clinical conditions using conventional methods and molecular biology (MALDI-TOF-MS-based). In conclusion, the authors stated that the recurrent clusters of *Agrobacterium* spp. bacteremia are more likely to have been acquired during computed tomography (CT),

angiography. By injecting a contrast medium into two different CT rooms by whole genome sequencing analysis, the isolate G could be assigned to the species *A. pusense* (= *Agrobacterium* genomovar G2) (Casanova et al. 2019). None of the isolates were found to carry pTi or pRi plasmids. In this context, of interest is the research of Basavand et al. (2021) who isolated the bacteria from galls on the crown and stem of Lawson cypress (*Chamaecyparis lawsoniana*). Based on phenotypic characteristics and DNA analyses (partial sequencing of DNA gyrase subunit B gene), they were identified as *A. pusense*. The pathogenicity of bacteria was confirmed by inoculation of Jimson weed (*Datura stramonium*) and carrot (*Daucus carota*) discs. However, no reference strain of *A. pusense* was included in these tests, but only *A. tumefaciens* strain Y15. Detection of genes involved in pathogenicity was made by performing PCR with the *virD2A/virD2C* and *VCF/VCR* primer pairs, which resulted in amplification of the expected 224 and 730 bp fragments, respectively, in all studied isolates. According to the authors, the amplification of *virC* and *virD* gene fragments implied that the *Agrobacterium* strains associated with Lawson cypress galls harbor the Ti plasmid. To summarize, the given examples indicate that *Agrobacterium* spp. are opportunistic human pathogens, able, under special conditions, to multiply and cause mainly bacteremia or septicemia.

Strains of some species of the genus *Burkholderia*, classified as plant pathogens, apart from plants, have been reported to infect animals and humans. They are grouped in the taxon *B. cepacia* complex (Bcc), including over 20 species that are characterized by great metabolic diversity, enabling them to adapt to various environments (Sousa et al. 2011; Depoorter et al. 2016). The phytopathogens cause mainly rot, including onion soft rot, manifested by the rotting of bulbs and other plant parts in storage rooms, during transport and trade (Kado 2010). In the 1980s, it was found that Bcc bacteria are important opportunistic pathogens that can cause various lung infections in cystic fibrosis (CF) patients, which may occur in an asymptomatic carrier, chronic infection, or so-called “cepacia syndrome” (a rapid decline in lung function that can include invasive disease and even premature death) (Mahenthalingam et al. 2005). Govan et al. (2007) noted that the prevalence of Bcc species varies

geographically, being *Burkholderia cenocepacia*, the most predominant species in CF centers in North America, whereas *B. multivorans* is the most common species in European CF centers. Recently, Wallner et al. (2019) reported that *B. cenocepacia* is a human opportunistic pathogen causing devastating symptoms in patients suffering from immunodeficiency and CF. Moreover, this bacterium was found also in other environmental sources ranging from aerosols to plant endosphere. Detailed study of different strains, representative of the diversity of ecological niches of *B. cenocepacia*, based on phylogenetic analyses and whole-genome general nucleotide identity, suggest that strains classified as *B. cenocepacia*, belong to at least two different species. Core-genome analyses show that the clade with environmental isolates lacks multiple key virulence factors, which are conserved in the sister clade to which most clinical isolates belong, including the highly virulent ET12 lineage. Similarly, several plant-associated genes display an opposite distribution between the two clades. As supported by the phylogenetic analysis, it is suggested that *B. cenocepacia* underwent a host “jump” from plants and their environment to animals (Wallner et al. 2019). The researchers emphasize the still poorly understood genetic differentiation between the pathogens of the genus *Burkholderia* that cause plant disease and those that cause human disease (Bulgari et al. 2019). Due to the pathogenic potential of these bacteria, a study based on multilocus sequence analysis (MLSA) and whole-genome analysis was undertaken to distinguish pathogenic from nonpathogenic strains. On the basis of obtained results, the separation of bacteria of the genus *Burkholderia* into at least two large clusters has been considered: one cluster comprising plant or animal and human pathogens, and another cluster including nonpathogenic species accompanying only plants (Suárez-Moreno et al. 2012; Bulgari et al. 2019).

Members of the genus *Pantoea*, in particular the species *P. agglomerans*, commonly found associated with plants as epi- and endophytes, have been reported to be opportunistic pathogens of animals and humans (Edens et al. 2006; Brady et al. 2011; Dutkiewicz et al. 2016). On the basis of etiological studies, *P. agglomerans* was found to be the cause of plant disease of stem and leaf dieback observed in onion seed plantations in South Africa and onion bulbs in the USA (Edens et al.

2006; Brady et al. 2011). It caused dieback and wilt of sorghum and maize plants in Mexico (Morales-Valenzuela et al. 2007). Necrosis, water-soaked spots, and/or rot of various organs of the above-ground part of plants, including cotton, grasses, and seaside peas, have been detected also in several other countries (Dutkiewicz et al. 2016). Some pathovars and strains of *P. agglomerans* caused galls on plants such as gypsophila (*Gypsophila* spp.), wisteria (e.g., *Wisteria floribunda*), and cranberries (*Vaccinium* spp.) (Manulis & Barash 2003; Best et al. 2004; Yamazaki & Sugiura 2008). This bacterium has the ability to form (at a temperature close to 0 °C) ice nuclei in plants, leading to damage or even death of the entire plant due to freezing. Under natural conditions, its synergism with frost was found in corn, rice, and tea crops (Lindow et al. 1978; Kim et al. 1989; Huang et al. 2010). Certain strains of *P. agglomerans* occur in nature as symbionts of insects and arthropods that can also be their vectors (Dutkiewicz et al. 2016). Recently, tobacco thrips (*Thrips tabaci*), which causes damage of onion crops, have been shown to be a vector of *P. agglomerans*. The protection of plants against the mentioned pest resulted in a reduction in the intensity of bacterial leaf dieback and onion rot (Grode et al. 2019).

In humans, the infection with *P. agglomerans* occurs mainly through injuries caused, for example, at contact with plants having thorns or spikes (Cruz et al. 2007). In hospital conditions, infections are usually acquired by immunocompromised people (Dutkiewicz et al. 2016). The symptoms are inflammation or synovium of the joints, inflammation inside the eyeball, of the periosteum, of endocardium (the lining of the heart cavity), and of bones and bone marrow (Cruz et al. 2007). Another important reason for clinical infection by *P. agglomerans* may be contact of hospitalized people with contaminated medical equipment, such as intravenous catheters or various types of fluids (Lotte et al. 2019). Some authors believe that although human infections with this bacterium are rare, they can cause serious illness and even mortality, especially in young patients with comorbidities (Büyükcım et al. 2018).

*Pantoea ananatis* hosts usually are cultivated crops and wild plants where it may occur as epiphyte or endophyte (Coutinho & Venter 2009; Weller-Stuart et al. 2017). Disease symptoms vary depending on the plant host and can be leaf blotches and spots, dieback, and rot of stalk, fruit, and bulb. This pathogen has been found

in pineapple, rice, *Eucalyptus*, cotton, maize, and onion in various regions of the world and in diverse environments (reviewed in Coutinho & Venter 2009; Weller-Stuart et al. 2017). Recently, *P. ananatis* was reported for the first time as a cause of leaf blight of strawberry in Canada (Bajpai et al. 2020). *P. ananatis* caused bacteremic infection in one patient hospitalized for dyspnea and bilateral ankle edema. During their hospital stay, the person expressed anal hemorrhage and developed a high fever after the colonoscopy. Isolations from blood yielded pure culture bacteria, which, after applying phenotypic tests and sequencing of the 16S rRNA gene, were identified as *P. ananatis* (De Baere et al. 2004).

Comparative studies of strains isolated from plants and clinical conditions, aimed at searching for genomic markers differentiating them, showed that most of the clinical strains are incorrectly classified as *P. agglomerans*. The obtained results were based on the multi-locus phylogenetic analysis and fluorescent amplified fragment length polymorphism (Rezzonico et al. 2009). The authors believe that it is related to previous changes in the taxonomy of the *Enterobacter agglomerans/Erwinia herbicola* complex and its grouping in one species of *P. agglomerans*. According to Cooney et al. (2014), within the *Pantoea* genus considerable taxonomic diversity with some isolates of the *Erwinia herbicola-Enterobacter agglomerans*, which are ungrouped, remains to be justified. These researchers pointed out that much work remains to be done for clarifying the phylogenetic classification of this genus.

#### BACTERIAL HUMAN PATHOGENS OCCASIONALLY CAUSING PLANT DISEASES

In the group of bacteria causing human diseases, *Pseudomonas aeruginosa* is probably the most widespread (Garrity et al. 2005). In addition to clinical conditions, this pathogen has been isolated from diverse environments, such as water and plants (Labordia et al. 2021). As an opportunistic human pathogen, *P. aeruginosa* causes diseases in immunocompromised patients, including chronic lung infections in patients with CF (Rahme et al. 1997). These infections are characterized by an intense neutrophilic response resulting in significant damage to host tissues and often exhibit resistance to antibiotics leading to mortality (Gellatly & Hancock 2013). Various virulence factors of this bacterium, such as exotoxin A, elastase, and phospholipase C, have been identified.

A subject of detailed studies was the clinical UCBPP-PA14 strain, showing the same strategy to infect both *Arabidopsis thaliana* leaves and mouse skin. It was found that mutations of genes (*toxA*, *plcS*, *gacA*) related to the pathogenicity of this strain weakened it in both tested organisms, which suggests the possibility of a common or similar mechanism of infection (Rahme et al. 1997). Studies carried out in the 1970s, involving numerous *P. aeruginosa* isolates from various environments, including plants and clinical conditions, showed their ability to cause rotting in lettuce (*Lactuca sativa* ‘Great Lakes’), celery (*Apium graveolens* ‘Dulce’), potato (*Solanum tuberosum* ‘Whitrose’), tomato (*Lycopersicon esculentum*), cucumber (*Cucumis sativus*), rutabaga (*Brassica napobrassica*), and carrot (*Daucus carota*) (Schroth et al. 2018). Although significant differences were observed in the ability to cause rotting, no substantial differences were found between isolates from clinical conditions, agricultural fields, water, and soil (Schroth et al. 2018). It should be emphasized, however, that two clinical isolates (PA13 and PA14) showed the highest virulence in causing rot of all plants tested. Research by Walker et al. (2004) established that *P. aeruginosa* can form biofilms under various conditions including in humans, and this feature enables it to survive, for example, in sick people even after persistent antibiotic treatment.

Soil components can constitute ecological niches for bacteria by providing them with nutrients released from organic matter (Kirzinger et al. 2011). Early research by Green et al. (1974) showed *P. aeruginosa* to be present in 24% of soil samples, but only in 0.13% of the vegetable samples in California. The analysis of obtained isolates, based on their ability to produce pyocins (bacteriocins – protein toxins), indicated that many of them were similar to the clinical strains. Clinical strains can survive in the soil, and they have, under favorable temperature and humidity conditions, the potential for plant colonization (Tyler & Triplett 2008; Holden et al. 2009; Kirzinger et al. 2011; Lim et al. 2014; Schroth et al. 2018). In soils of France and Burkina Faso (West Africa), however, regardless of their physicochemical composition and climate, *P. aeruginosa* was very rarely detected (Derejian et al. 2014), and dry soils were suggested not to be favorable for its survival (Schroth et al. 2018).

It was found that *P. aeruginosa* caused rot of calla lily in the state of Himachal Pradesh, India (Shanmugam et al. 2016). Symptoms were observed on the roots, rhizomes, and shoots. In Australia, *P. aeruginosa* has been established as a cause of brown rot of onion, and it was suggested that the infection may have occurred during harvesting (Cother et al. 1976). *P. aeruginosa* isolates causing onion rot were similar to the reference strains of *P. aeruginosa* (LMG 1242<sup>T</sup> from Belgium and IR07358 from the Philippines) in terms of phenotypic characteristics, including pathogenicity on onion and fatty acid methyl ester content (Hao & Xie 2006). Reports from Egypt also confirmed the pathogenicity of *P. aeruginosa* towards onions (Abd-Alla et al. 2011). In addition to the basic phenotypic features and sequence analysis of the 16S rRNA gene, the authors examined the virulence factors of a representative strain, indicating its ability to produce a complex of polysaccharides that degrade the onion cell wall and cytoplasmic membrane and induce the high activity of proteases, lipase, pectinase, and alkaline phosphates. Scanning electron microscopy showed the ability of this bacterium to form biofilms on the plant cell walls (Abd-Alla et al. 2011). Noteworthy are detailed etiological studies including phenotypic and pathogenicity tests and sequence analysis of the gene encoding for 16S rRNA of *P. aeruginosa* as the cause of soft rot of fruits of tinda (*Praecitrullus fistulosus*), a tropical plant belonging to family *Cucurbitaceae* (Mondal et al. 2012). The disease takes the epidemic form, especially during rainy and very hot periods. The symptoms appear as numerous, from light to dark brown, deep, round, soft rot lesions on the fleshy tissues, and sometimes are accompanied by bacterial leakage (Mondal et al. 2012).

The opportunistic human and animal pathogen, causing pneumonia and urinary tract disease is *Klebsiella pneumoniae* (Martínez-Romero et al. 2018; Rodríguez-Medina et al. 2019, Gorrie et al. 2022). Some strains of this bacterium cause plant diseases and some are defined as harmless or even beneficial plant endophytes (Rosenblueth et al. 2004; Huang et al. 2016; Duran-Bedolla et al. 2021; Yang et al. 2021). Noteworthy is the top rot disease of maize caused by *K. pneumoniae*, which has been observed in various maize growing regions in China (Huang et al. 2016). Symptoms on maize were chlorosis and thinning of leaves, leaf curl, incisions on the edges, apical rot, and stem rot, accompanied by an unpleasant odor.

Studies on the pathogenicity of *K. pneumoniae* isolate KpC4, originating from maize and the clinical strain Kp138, meeting Koch's postulates, confirmed their pathogenic potential towards maize and mice (Huang et al. 2016). One of the pathogen survival strategies is the ecological adaptation. It has been established that *K. pneumoniae* can survive very well for at least 6 months in corn leaves under natural conditions and in dried corn plant residues (Huang et al. 2020). Maize may therefore occasionally be a reservoir of *K. pneumoniae*, and the presented results should be treated as a warning against a potentially dangerous, opportunistic bacterial pathogen, showing the ability to infect plants, animals, and humans. Regarding the harmfulness of *K. pneumoniae* for maize crops, it is necessary to conduct more research on the pathogenesis and epidemiology of the disease and to develop a strategy for plant protection by carrying out pathogenicity and phenotypic tests, and MLSA of several core genes. In China, *K. pneumoniae* has been also shown to cause onion rot. Bacteria were isolated from affected bulbs, which were initially asymptomatic, but odoriferous when cut off. Intact bulbs eventually became soft, watery, and decayed after 6 weeks at room temperature. The diagnosis was confirmed by Biolog assay and MLSA including sequences of the *atpD*, *gyrB*, *infB*, and *rpoB* genes and 16S rRNA sequence analyses (Liu et al. 2015). Recently, Dr. M. Kałużna from the National Institute of Horticulture Research in Skierniewice, Poland, using molecular techniques and a pathogenicity test, proved that species of genus *Klebsiella*, including *K. variicola* and *K. oxytoca*, cause glassy onion rot (Kałużna M., unpublished work). Worth noting is the *K. variicola* species, isolated for the first time from various organs of banana plants in Mexico (Rosenblueth et al. 2004). The finding that it is a separate species was based on comparative analysis of the sequences of *rpoB*, *gyrA*, *mdh*, *phoE*, *infB*, and *nifH* genes as well as the results of DNA-DNA hybridization with the obtained isolates and with more than 130 isolates originating from clinical conditions (classified as *Klebsiella* spp.). Although the research did not include the pathogenicity of *K. variicola* isolates derived from plants, it demonstrated their ability to fix nitrogen. To this species belongs also clinic isolates (Rosenblueth et al. 2004). In this context, it is worth citing the study resulting from the complete genome sequencing of *K. variicola* strain DX120E (nitrogen fixing endophyte) isolated from sugar cane in China,

indicating a high degree of a whole genome and plasmid similarities between this strain and the phytopathogenic one as well as with the clinic *Klebsiella* isolates. The authors assumed that the use of DX120E as a bio-fertilizer might be very risky (Lin et al. 2015). Also in China, *K. variicola* has been shown to be pathogenic on bananas, causing the typical symptoms of yellow-brown watery spots on the petioles and necrosis of vascular bundles in the pseudostems (Fan et al. 2016).

#### OCCURRENCE OF HUMAN PATHOGENIC BACTERIA IN PLANT ENVIRONMENT

It has long been established that certain human and animal pathogenic bacteria can accidentally contaminate soil, organic fertilizers including uncomposted or improperly composted manure, irrigation water, and plant tissues, even without being pathogenic to plants. There, they can survive, adapt, and even reproduce successfully, which means that plants and their environment can serve as reservoirs for these pathogens, thus putting humans at risk of infection (Green et al. 1974; Berg et al. 2005; Holden et al. 2009; Lim et al. 2014).

A common practice in organic farming is the fertilization with manure, which, if contaminated with human or animal pathogenic bacteria, is hazardous for the development of foodborne bacteria in postharvest products. Among the most endangered are ready-to-eat leafy vegetables but also other horticultural products (Berger et al. 2010). One of the examples is the study of Szczech et al. (2018) conducted with lettuce, radish, carrot, and beetroot contaminated with *E. coli* following the application of organic and traditional fertilization systems in selected Polish farms (samples collected in 2010–2014). The risk appeared higher in organically grown vegetables following the use of manure, other animal wastes, and plant residues. For reducing the hazard it has been recommended that manure be composted and the fresh potentially contaminated plant and animal wastes subjected to heat treatment.

In order to reduce manure contamination, the United States introduced a requirement to apply a 120-day interval between its preparation and application to the soil (Alegbeleye et al. 2018). The irrigation water especially if coming from sites nearby pastures or from sources in proximity to anthropogenic wastes is considered to be one of the very dangerous

sources of plant contamination with HPB. Intestinal pathogens, including *Salmonella enterica*, *Listeria monocytogenes*, *Escherichia coli*, *Shigella* spp., *Campylobacter* spp., *Yersinia* spp., and *Staphylococcus aureus* have been isolated from fresh fruits and vegetables (Lim et al. 2014; Bintsis 2018). These products can become contaminated by poorly disinfected water used for postharvest processing (Balali et al. 2020) or at insufficient hygiene during harvesting, storage, packaging, transportation, and trading (Alegbeleye et al. 2018). Hence, they can end up in supermarkets, open markets, and storage compartments (Balali et al. 2020). Attached to the plant surface, HPB can enter internal parts of the plant tissue through natural openings such as stomata and damaged tissue (Erickson 2012; Lim et al. 2014; Alegbeleye et al. 2018).

It is worth bearing in mind that, e.g., the bacterium *L. monocytogenes*, the cause of gastroenteritis, a dangerous disease in humans with suppressed immunity, has been also detected in samples taken from door handles, floors, or walls of storage compartments (Toro et al. 2022). It was found that *S. enterica*, causing salmonellosis, can form biofilms even on stainless steel metal surfaces, making it resistant to disinfection (Galié et al. 2018). Apart from the aforementioned incidents contributing to contamination of plant products with human bacteria, these pathogens may be transferred at direct contact of an infected person with intact or harvested plant products, mainly fruits and/or vegetables (Galié et al. 2018).

Some intestinal pathogens can survive in the soil for up to one year. They may directly colonize the rhizosphere, roots, and from there the above-ground organs of the plant (Holden et al. 2009; Lim et al. 2014). It has been shown that *S. enterica* serovar Typhimurium survived in soil samples for a period of 203 to 231 days, and was detected in radish plants for 84 days after the seeds were sown and in carrot plants for 203 days (Islam et al. 2004). These bacteria survive better in soil with compost from poultry manure than in soil containing alkaline-pH-stabilized dairy cattle manure compost (Islam et al. 2004). *Salmonella* can be widely spread in the soil even in the absence of fertilization as a result of water currents, underground springs, and rain runoff carrying contaminated material (Jacobsen & Bech 2012). Regarding the survival of *Escherichia coli*, it is determined by factors such as the mechanical



composition of the soil, presence of plant debris and other microorganisms, humidity, and temperature (Holden et al. 2009). It was proved that sand soil is optimal for the survival of this bacterium as compared to loamy or loamy sand soil. At lower temperatures (25 °C) and high soil moisture (100%), it could survive for more than 80 days (Cools et al. 2001).

Using a model system with *Arabidopsis thaliana*, it was shown that under sterile conditions and at 100% humidity, *S. enterica* serovar Newport and *E. coli* O157:H7 increased populations on roots to 10<sup>9</sup> CFU per gram of root tissue. On leaf tissue, growth of both pathogens was 30–50-fold less than growth on roots, probably due to a reduction of available nutrients on the foliage surface (Cooley et al. 2003). Furthermore, root inoculation led to contamination of the entire plant, indicating that both pathogens are capable of moving on or within the plant in the absence of competition. Their survival on soil-grown plants declined as the plants matured, but both pathogens were detectable for at least 21 days. Survival of the pathogens was reduced in nonautoclaved soil, suggesting a competition between indigenous microorganisms in the soil (Cooley et al. 2003).

It is considered that in general, similar strategies are employed by bacteria to colonize any plant or animal host (Holden et al. 2009). The processes of initial adherence, invasion, and establishment may differ in terms of the specific interactions, but many parallels and similarities exist. The extensive availability of sequenced bacterial genomes permits *in silico* genomic comparisons between bacteria that are frequently or exclusively associated with plants and those that are associated with human or animal hosts. Recognition of pathogens by both animal and plant cells triggers a cascade of reactions that results in activation of the host defense response. Zarkani & Schikora (2021) pointed out that *Salmonella* uses multiple strategies to manipulate the host defense system, and highlighted the adaptation, avoidance, and suppression. It is suggested that the adaptation to plant host involves upregulation of stress-related genes, and genes encoding for the synthesis of effector proteins from bacterial type III secretion system (T3SS, virulence mechanism enabling to inject bacterial effector proteins directly into host cell) (Coburn et al. 2007).

A study has demonstrated that some strains of bacteria belonging to the genus *Shigella*, that cause

shigellosis (severe intestinal infection), can survive and multiply in damaged plant cells, roots, and leaves of *A. thaliana* (Jo et al. 2019). These bacteria proliferate in plants by adoption of type III effectors for shigellosis. Using microscopy-based analysis the authors found that for colonizing human and plant cells these bacteria employ the same immunosuppressive mechanism involving T3SS. Microscopic studies revealed that they were present inside leaves and damaged plant cells. These findings demonstrate that the human pathogen *Shigella* can proliferate in plants by adopting the immunosuppressive machinery of its original human host.

*E. coli* O157:H7 and *S. enterica* serovar Typhimurium were detected on the surface of disinfected leaves of lettuce grown in aqueous media or in soil contaminated with these bacteria (Franz et al. 2007). In addition, *S. enterica* serovar Typhimurium, added to the irrigation water for parsley, spread from the roots to the leaves and shoots (Lapidot & Yaron 2009). It was observed that the mutant of this bacterium, devoid of genes encoding for the synthesis of cellulose and curli (extracellular fibers), migrated to the leaves to a much lesser extent than the wild strains of this pathogen (Lapidot & Yaron 2009). Taking into account the risks of contamination of tomato fruit, Guo et al. (2001) documented that in tomato plants inoculated with five *S. enterica* serotypes before and after fruits set, the bacteria can survive during flowering and early stages of fruit formation. In conclusion, the authors stated that tomato stems and flowers are possible sites at which *Salmonella* may attach and remain viable during fruit development, thus serving as routes or reservoirs for contaminating ripened fruit. It is worth noting, however, that in the mentioned experiments for plant inoculation a high concentration of bacteria (10<sup>9</sup> CFU·mL<sup>-1</sup>) was used, which basically does not reflect the situation in natural conditions. Transcriptomic analysis of *S. enterica* Typhimurium genome has revealed some of the genetic mechanisms involved in its epiphytic growth and colonization of intact tomato shoot and root surfaces (Han et al. 2020).

Brandl and Amundson (2008) proved for the first time that *E. coli* O157:H7 can multiply on the leaves of romaine lettuce plants. The increases in population size in the phyllosphere of young lettuce plants ranged from 16 to 100 times under conditions of warm temperature and the presence of free water on the leaves, but varied significantly with leaf age.

A study by Jacob & Melotto (2020) showed that leaf colonization by *S. enterica* serovar Typhimurium 14028s and *E. coli* O157:H7 was affected by the genetic diversity of lettuce (*Lactuca sativa* L. and *L. serriola* L.). In particular, after surface- and syringe inoculation among 11 lettuce genotypes there was significant variation in bacterial attachment, internalization, and apoplastic persistence. A significant correlation was observed between the rate of penetration of bacterial leaves and the opening of the stomata (Jacob & Melotto 2020). In comparison to the model species *Nicotiana benthamiana*, differences in internalization and growth of *E. coli* O157:H7 into the apoplast of spinach and lettuce has been established (Wright et al. 2017). The obtained results indicate the applicability of plant breeding in order to reduce the contamination of plants with human microbial pathogens.

The bacteria *E. coli* O157:H7, *S. enterica* serovar Typhimurium, and *L. monocytogenes* introduced on the seed of carrot, cress, lettuce, radish, spinach, and tomato became rapidly established shortly after germination. The former of the mentioned pathogens penetrated the inner tissues of cress, lettuce, radish, and spinach seedlings but was not detected in the tissues of mature plants. It is suggested that *S. enterica* internalization in lettuce leaves is influenced by the growth conditions (Kroupitski et al. 2019). In contrast, *L. monocytogenes* did not spread within seedlings but did persist on the surface of plants throughout the cultivation period. Although the results suggest that the risk of internalized human pathogens in salad vegetables at harvest is low, the introduction of such pathogens early in plant development may enhance their persistence in the rhizosphere (Jablason et al. 2005).

Interestingly, the thermophilic bacterium *Campylobacter jejuni* (a causal agent of acute gastroenteritis) was unable to grow on lettuce and spinach leaves and on spinach and radish roots of plants incubated at 33 °C, a temperature that is conducive to its growth *in vitro*. However, it has been isolated from radish roots and spinach rhizosphere for respectively 23 and 28 days after its introduction into the soil and when the plants were kept at 10 °C. This pathogen persisted in the rhizosphere of spinach for prolonged periods of time at 16 °C, which indicates its ability to adapt to the plant environment and may result in contamination of plant products (Brandl et al. 2004).

Pathogenic human bacteria may not only be associated with plants and their environment but also accommodate other organisms. For example, Ye et al. (2018) detected *Achromobacter xylosoxidans* as a cause of severe rot disease in the stripe of edible mushroom *Coprinus comatus*. This bacterium has been confirmed as an important opportunistic human pathogenic bacterium isolated from respiratory samples from patients with CF. As already mentioned, carriers and hosts of human pathogenic bacteria can be insects (Kirzinger et al. 2011; Kim et al. 2020). They can transmit pathogens from humans to the general and plant environment (Steinhaus 1949; Kirzinger et al. 2011). Exemplary, a vector of *Salmonella*, *Staphylococcus*, *Enterococcus faecalis*, and *Streptococcus aureus* can be the pharaoh ant (*Monomorium pharaonis*) (Beatson 1972). According to the observations in one hospital in India (Fotedar et al. 1992), the housefly (*Musca domestica*) may be a potential vector of *P. aeruginosa*, as well as of *E. faecalis* and viridans streptococci like *S. aureus*. Transfer of human pathogens (e.g., *C. jejuni* and *E. coli*) towards the plant environment can be accomplished by chicken and occasionally wild birds as well (Humphrey et al. 2014; Shobrak & Abo-Amer 2014; Cody et al. 2015; Teplitski & de Moraes 2018).

#### OUTBREAKS OF HUMAN INFECTIONS CAUSED BY THE CONSUMPTION OF CONTAMINATED FRUITS AND VEGETABLES

Reports indicate the occurrence of human diseases due to the consumption of fresh unprocessed plant products, especially fruits and vegetables, hosting foodborne bacterial human pathogens (Lynch et al. 2009; Berger et al. 2010; Lim et al. 2014; Alegbeleye et al. 2018; Bintsis 2018; Chatziprodromidou et al. 2018; Balali et al. 2020). Still, the total number of cases caused by plant food is limited as compared to those originating from uncooked fresh meat (EFSA 2017).

Hofmann et al. (2014) reported that in the USA, *S. enterica* and *L. monocytogenes* are frequent reasons for infection of humans who had consumed unwashed, usually raw contaminated plant products. Using a model system of spinach and corn salad inoculated with these bacteria, the authors found that simple washing could reduce the contamination or even eliminate it. It has been shown that *S. enterica* expresses a high ability to colonize the epidermis and internal tissues of various plants and is the cause of frequent infectious diseases, most often in the form of acute food poisoning (Schikora et al. 2012; Alegbeleye et al. 2018;

Jechalke et al. 2019). By reviewing the documented foodborne disease outbreaks that occurred in the USA from 1999 to 2010, Bennett et al. (2015) have identified multistate outbreaks of *Salmonella* attributed to the consumption of raw tomatoes served in restaurants. The investigation of reports from that period indicated the possibility of tomatoes being contaminated at production sites, during storage, or packaging. A mathematical model for the effect of temperature and humidity on the potential of *S. enterica* to infect fresh cucumber and for predicting the risk of an outbreak has been recently developed, based on experiments with cucumber inoculated with a cocktail of *S. enterica* strains Montevideo G4639 (a cause of tomato outbreak), Saintpaul 02-517-1 (cantaloupe outbreak), and Newport H1275 and Stanley H0558 (sprout outbreaks) (Jung & Schaffner 2021).

An example of an outbreak of listeriosis in the USA is the consumption of cantaloupe (rockmelon; *Cantaloupe melo*) contaminated with *L. monocytogenes* (CDC 2011). Recently, an outbreak of foodborne *L. monocytogenes* is described in South Africa (Smith et al. 2018). More cases of human illness due to consumption of fresh horticultural products, such as broccoli, cabbage, carrots, cauliflower, cucumbers, tomatoes lettuce, radish, and potatoes, contaminated in the supply chain with *Listeria* spp. are available in the very recent review of Townsend et al. (2021). The foodborne pathogen *C. jejuni* (Altekruse et al. 1999) is another microbe able to colonize postharvest products. An example is a human gastroenteritis resulting from the outbreak of *C. jejuni* in Alaska. The disease registered at the outbreak of this bacterium has been detected in more than 60% of studied patients who have consumed raw peas (Gardner et al. 2011).

Certain exotoxin-producing strains of *E. coli* may as well be able to cause food poisoning in humans. The course of the disease varies and sometimes can be acute, but in the majority of cases is not very serious. The verotoxic *E. coli* serotype (VTEC) or O104:H4 is particularly dangerous because can cause hemolytic-uremic syndrome and damage to the central nervous system (Kaper et al. 2004). Due to outbreaks of *E. coli* O157:H7, a number of human illnesses associated with the consumption of spinach and lettuce have been found in the USA and Canada (Calvin 2007; Wang et al. 2006; Balali et al. 2020). In several USA states, in the period

of August–September 2006, illnesses due to outbreaks of *Escherichia coli* O157:H7 associated with the consumption of packed spinach have been documented (Wendel et al. 2009). Earlier, in the summer of 1995, in Montana state, *E. coli* associated with the consumption of contaminated lettuce leaves had led to the outbreak of infections of people mainly at age around 40 (Ackers et al. 1998). A representative of the risks for human health imposed by *E. coli* O104:H4 are also the cases in Europe in the year 2011 when nearly 4000 persons have been infected, 900 of which expressed hemolytic-uremic syndrome, and 54 died (Karch et al. 2012). In Germany, the sudden appearance of foodborne *E. coli* in 2011 has resulted in more than 2220 cases. Although not firmly established, sources of the bacterium have been suspected in salad sprouts grown from contaminated seeds (Buchholz et al. 2011). In the year 2005, the consumption of lettuce contaminated with verotoxic *E. coli* has been the reason for the outbreak of this bacterium in Sweden (Söderström et al. 2008). Studies in France have suggested that the virulence of *E. coli* O104:H4 in humans might be attributed to a mutation in ancestor strains (Grad et al. 2012). The possibility of its transmission from plant products to humans by still-unknown carriers has also been considered (Buchholz et al. 2012). Various other cases registered in earlier years, for illnesses caused due to consumption of *E. coli* contaminated fruits and vegetables are reviewed in Bintsis (2018). The preparation of European countries for struggling against foodborne diseases has been a subject of discussions in the workshop of the World Health Organization (2013) and the global threat of foodborne human infections outlined by Kuchenmüller et al. (2013) followed by the recent update by Pires et al. (2021).

Overall, the outbreaks of foodborne pathogenic bacteria in fruits and vegetables soundly point to the necessity of proper pre- and postharvest measures for preventing the contamination of these plant products and for avoiding the risk of human infections at their consumption.

## CONCLUSIONS

The research summarized in this review indicates that some pathogenic plant and human bacteria can survive and sometimes cause infections in conditions

differing from those in their primary host environment. Some phytopathogenic bacteria may cause diseases with a detrimental effect on human health. On the other hand, human pathogenic bacteria can inhabit the plant environment that can therefore serve as a reservoir of human bacteria. The consumption of fresh or stored raw plant food contaminated with human bacterial pathogens has been shown to be the cause of some (sometimes severe) outbreaks of diseases. The routes for possible transmission of pathogenic bacteria between plant and human host environments are illustrated in Figure 1. It is suggested that sharing the hosts is evolutionary established and can be a mechanism of environmental adaptation for the survival of bacterial strains. There are, however, many poorly understood issues related to the pathogenicity and the mechanisms of infections caused by human and plant bacteria in their opposite hosts that remain to be clarified. An issue requiring more extensive research is also the correct identification

of studied bacteria. Research using functional genetics and genomics approaches in combination with advanced “omics” technologies (genomics, proteomics, metabolomics) can help to better elucidate the interactions between pathogenic bacteria, plants, and humans. The examples presented in this review are not exhaustive for all cases described in the literature, but we believe that the information may help for raising the concern for human safety when farmers, researchers, and nonprofessionals are in contact with an environment potentially contaminated with pathogenic human or plant bacteria. A foreseeable perspective is the incorporation of efficient pest management, including biocontrol agents and improvement of the hygiene in agricultural practices, at harvesting, processing, in storage environments, and during distribution, for minimizing the risk of contamination of fresh produce and for controlling the spread and behavior of plant and human bacterial pathogens in their cross-kingdom hosts.

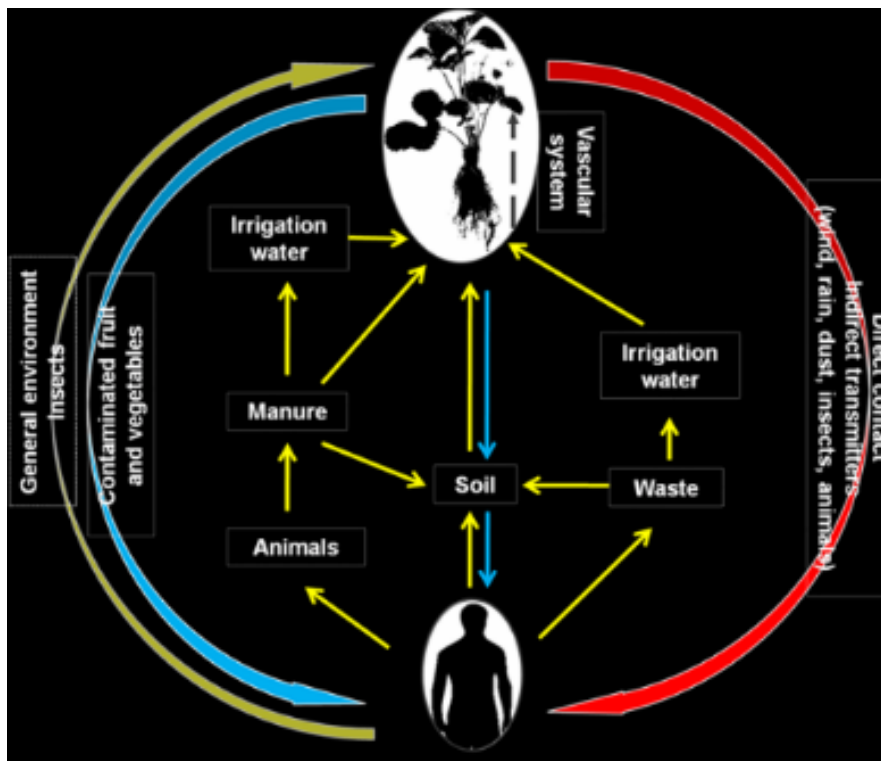


Figure 1. Schematic presentation of transmission of plant and human bacterial pathogens towards their opposite environments. Plant bacterial pathogens can infect humans at direct contact or be transferred indirectly by wind, dust, rain, insect vectors, and animals. Human bacterial pathogens can contaminate the general environment or be transmitted by insects and animals, and through manure, wastes, soil, and irrigation water, they can colonize the rhizosphere whereby via the roots and vascular system inhabit the aerial part of the plant. Transmission of human pathogenic bacteria from plant environment towards humans can occur through contaminated soil and at the consumption of contaminated fruits and vegetables. Red arrow – route of plant bacterial pathogens towards humans; yellow arrows – transfer of human bacterial pathogens towards plant environment; blue arrows – direction of human bacteria from plant environment towards humans; black dotted arrow – movement of human bacteria from rhizosphere towards aerial part of the plant

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