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Pantoea: A Versatile bacterial Candidate of Agricultural Importance

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Abstract

Genus Pantoea is a diverse group of the family Enterobacteriaceae which inhabit various ecological niches. Various species of Pantoea are found associated with a diverse host range that include plants, animals, insects and humans. Besides this Pantoea spp. has been widely distributed in nature including water, soil, dairy products, meat and fish. It is commonly associated with plants as epiphyte or pathogen. Pantoea was first recognized as a genus about 25 years ago, but since then, approximately 20 species with a wide range of characteristics have been discovered. Identification of plant-pathogenic Pantoea species is difficult, due to the high degree of phenotypic similarity between species of this genus and related Enterobacteriaceae. Pantoea species are typically characterized based on colony morphology, physiological and biochemical tests, and in some cases, fatty acid analysis or quinone composition. These have a wide range of plant hosts where they live as nonpathogenic endophytes as well as epiphytes that colonize the leaves, stems and roots. In this perspective, some Pantoea strains can be beneficial to the plant host by providing growth promoting substances such as the plant-growth hormone indole-acetic acid (IAA), phosphate solubilization or nitrogen fixation. Number of Pantoea species are also involved in bioremediation of various pesticides and organic chemical compounds. This indicates the potential to degrade some recalcitrant and xenobiotic compounds. Some Pantoea strains also provide effective protection to plants against various bacterial and fungal diseases and post-harvest fruit rots. On the other hand, some of the species are recognized as a human pathogen and has led to controversy as limited documented cases of P. agglomerans bacteremia and infections have been reported. Most of the cases reported among immunocompromised patients or the pediatric population. Thus, Pantoea is a multifaceted bacterium that plays a significant role in agriculture as a plant growth promoter by producing hormone like IAA, inorganic pollutant degradation by producing potent enzymes and also protects some plants against pathogens by producing antibacterial and antifungal compounds. In some cases, these also cause diseases in human beings. Therefore, this genus is very important for studies. In this review, the industrial, agricultural as well as ecological significance of the genus Pantoea is emphasized.

Keywords: *Pantoea , Versatile , bacterial*

1. Introduction

The genus Pantoea is a diverse group of yellow pigmented, gram-negative rod-shaped bacteria that belong to the Enterobacteriaceae family. Various strains of Pantoea have been isolated from various ecological niches and hosts (Muraschi et al.,1965; Ewing and Fife 1972; Brady et al., 2008; Volksch et al., 2009; Nadarasah and Stavrinides, 2014). Some Pantoea isolates produce some biocontrol products that can help to control various plant pathogens. Some strains of Pantoea play potential roles in agriculture and some are important for bioremediation and biodegradation of toxic compounds without producing harmful by-products (Pileggi et al., 2012). Pantoea isolates are ideal for not only investigating niche-specific adaptation and opportunism, but also for the development of commercially relevant medical, agricultural, and environmental products due to their ubiquity, versatility, and genetic tractability. The genus Pantoea have the ability to synthesize antagonist substances that confer significant advantages in competition with other microbes which are present in specific ecological habitats (Raaijmakers and Mazzola, 2012). Pantoea ananatis was reported as an epiphyte of rice (Watanabe et al., 1996) which may control the growth of other fungi and bacteria that may cause plant diseases. Pantoea agglomerans also show the antagonistic effect on plant pathogens like bacteria and fungi. By this way it plays an important role as a biocontrol agent which may help to reduce uses of pesticides as well as toxic chemical deposition in the environment (Morales et al., 2008). Pantoea ananatis has been reported by Simeya et al., 2003 as a biocontrol agent which can control rice blast disease caused by Pyricularia oryzae. Pantoea agglomerans has inhibitory activity towards broad range fungal plant pathogens which is responsible for serious rice disease and also produced Indole Acetic Acid (IAA) which promote rice growth in artificial environments (Kim and Lee, 2019). Phylogeny, Diversity of Species, And Classification of Pantoea.

Pantoea is a genus of Enterobacteriaceae whose name comes from the Greek word "Pantoios" which means "various kinds or sources.". This indicates the diversity of the bacteria that can be isolated from various geographical and ecological niches (Kini et al., 2018). Gavini et al., 1989 has first introduced genus Pantoea, where some of the Pantoea members were classified as Bacillus agglomerans (Beijerinck 1888) and Enterobacter agglomerans (Beijerinck 1888; Tindall, 2014). Other names associated with group members of Pantoea were also created including Bacterium herbicola, Pseudomonas herbicola, Erwinia herbicola and Erwinia milletiae. Kageyama et al., 1992 classified genus Pantoea based on DNA hybridization into three new species P. punctata, P.citrea and P.terrea. Now the Pantoea genus consists of 20 recognized species that are similar phenotypically and are comprised of 13 hybridization groups (Brady et al., 2008, 2009a, b; Popp et al., 2010; Walterson and Stavrinides 2015).

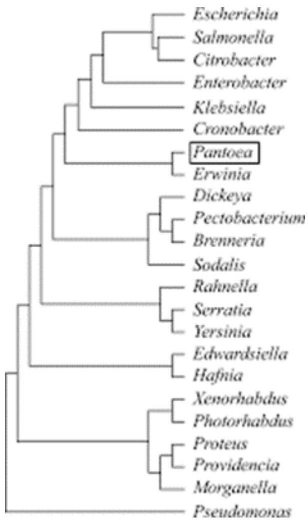

Fig 1: Cladogram obtained from the pathosystems Resource Integration Center (adapted from Watter *et al.*, 2014)

With the delineation of the genus, the identification of new *Pantoea* species has expanded substantially over the last several years. *Pantoea* is closely related to *Tatumella* and *Erwinia* (Brady *et al.* 2010a,b), that form a monophyletic group nested within the other enterobacterial genera, *Escherichia, Salmonella, Citrobacter, Enterobacter, Klebsiella* and *Cronobacter*. The basal lineage to this monophyletic group contains a second group that contains many enterobacterial plant pathogenic groups, including *Dickeya, Pectobacterium* and *Brenneria* along with the endosymbiont *Sodalis* (Stavrinides 2009). *Pantoea* is currently composed of 20 recognized species that are phenotypically similar, and which were proposed to comprise a total of 13 hybridization groups (Brady *et al.*, 2008, 2009a,b, 2011, 2012; Popp *et al.* 2010). *Pantoea* type strains that define each respective species group have been isolated from a number of sources, although mostly from plants. A rooted phylogenetic tree of *Pantoea* type strains constructed using gyrB, rpoB and 16S rRNA shows the relationships between the established species groups (Fig. 3). Species like *P. deleyi, P. anthophila, P. allii, P. cypripedii, P. wallisi, P. rodasii and P. rwandensis* have been isolated from only plant sources, *P. conspicua, P. brenneri, P. septica and P. eucrina* from only clinical sources and *P. gavinae* from only outdoor environmental sources. Isolates of *P. calida, P. dispersa and P. gavinae* were identified from the natural environment or processed products . Previously, several other species had been proposed, including *P. citrea, P. punctata and P. terrea* (Kageyama *et al*., 1992); however, these were later reclassified into the genus *Tatumella* using multilocus sequence analysis (MLSA) methods (Brady *et al.* 2010a,b). The MLSA approach based on six genes (leuS, fusA, gyrB, rpoB, and rlpB) was found to provide a more robust and reliable DNA relatedness and species delineation in *Pantoea*. Also, comparative analysis of the single gene topologies to that derived from concatenated data identified leuS as a reliable phylogenetic marker for the genus *Pantoea* (Tambong *et al.*, 2014).

The use of 16S rRNA is an essential tool for the classification and systematics of members of the genus *Pantoea*. However, 16S rRNA gene sequences show low resolution at the intrageneric level (Mulet *et al.,* 2010; Gonzalez *et al.,* 2013). Whole-genome sequencing provides complete and draft chromosome data that can be used to better understand the evolutionary and taxonomic relationships in bacteria in general (Coenye *et al.*, 2005; Mulet *et al.,* 2010; Thompson *et al*., 2013) and members of the genus *Pantoea*, in particular. The use of genome-based phylogeny is improving bacterial taxonomy leading to a substantial revision on the tree of life (Parks *et al*., 2018). Taxogenomics of bacteria could be defined as a cohesive comparative genomics approach that combines MLSA, average nucleotide identity (ANI), codon usage bias, core, and pan-genome analysis as well as super tree analysis and other genomic signatures (Thompson *et al.,* 2013). With advances in whole genome sequencing (wgs) and bioinformatics tool developments, these genome-based methods are fast replacing the wDDH techniques in classification of prokaryotes.

Is *Pantoea* spp. Beneficial, Harmful or commensal?

P.agglomerans exhibited their ability in the extracellular biosynthesis of AgNPs using cell free supernatant and $AgNO_3$ (10Mm) as a precursor. After shaking incubation for 24 hrs at 37°C at 150rpm, *P.agglomerans* have the ability in changing the color of reaction mixture from yellow to reddish brown which denotes as indicator for biosynthesis the AgNPs (Aldujaili *et al.*, 2017). *Pantoea ananatis* Sd-1 have the ability to degrade the pesticide carbaryl as carbohydrate esterase. *Pantoea ananatis* Sd-1 having high degree of lingocellulolytic activity as well as xylanse production (Yao *et al.,* 2020). Acioly *et al.,* 2017 isolated *Pantoea agglomerans* from industrial laundry effluents that *showed* tannase, polyphenoloxidase and cellulose activity and showed tolerance to high salt concentration. Madhukar *et al*., (1996) detected the enzymatic activity of amylase and cellulase from *Pantoea agglomerans* isolated from pea leaves. By this way *Pantoea agglomerans* showed the enzymatic biotechnological potential for various enzymes.

Some of the more phenotypically distinct isolates of *Pantoea* are being explored for their potential as biosensors. One *P. agglomerans* isolate was found to produce a blue pigment in a temperature-dependent manner (Fujikawa and Akimoto 2011). Pigment production was determined to be cell density dependent, with cell densities of 10^6–10^8 being required for maximal pigment production; however, biosynthesis was also temperature dependent, with bacteria acquiring the blue coloration at temperatures ≥10ºC, and retaining their characteristic yellow coloration at temperatures ≤10ºC (Fujikawa and Akimoto 2011).

Biotechnological Exploration of *Pantoea*

Role of *Pantoea* in Agriculture

Production antimicrobial compounds

P. agglomerans has been shown to have unique metabolic capabilities, including antibiotic biosynthesis (*Smith et al.* 2013). These antibiotics could be used for combating plant, animal and human pathogens or for food preservation. They include: • lipopeptide antibiotics – herbicolin A and B, which are active against sterol-containing fungi (*Greiner et al.* 1991); • pantocins A and B inhibiting growth of various Enterobacteriaceae strains, including *E. amylovora*; • the dapdiamide antibiotic – herbicolin I, produced by *P. agglomerans* and closely related species *Pantoea vagans*, active against *Erwinia amylovora*, a pathogen of apple and pear trees (Kamber *et al.*, 2012); • the peptide antibiotic called microcin produced by *P. agglomerans* strain Eh252, targeting also *E. amylovora* ; • the acidic antibiotics called agglomerins A, B, C and D which are moderately active against a wide variety of anaerobic bacteria (including *Clostridium difficile, C. perfringens, Propionibacterium acnes*) and weakly active against aerobic Gram-positive bacteria (including *Streptococcus pyogenes, S. pneumoniae*) (Shoji *et al.*, 1989); • the pseudopeptide antibiotic andrimid which is active against both Gram-negative and Gram-positive bacteria, including methicillin-resistant *Staphylococcus aureus* (MRSA), vancomycin-resistant *Enterococcus* (VRE) and *Klebsiella pneumoniae* and displays also limited antiproliferative activity against human tumor cell lines • the broadspectrum peptide antibiotic 2-amino-3-(oxirane-2,3- dicarboxamido)-propanoyl-valine (APV) produced by *P. agglomerans* strain Pa48b which was proved to suppress the growth of *E. amylovora*, the soybean pathogen: *Pseudomonas syringae* pv. (pathovar) *glycinea*, the agent of crown gall disease in many plants: *Agrobacterium tumefaciens* and the human pathogen *Candida albicans* (Sammer *et al.*, 2012); • multiple antibiotics produced by a clinical isolate *P. agglomerans* Tx10, that target *E. amylovora* and clinically relevant pathogens, *including Staphylococcus aureus, Streptococcus epidermidis*, and *Escherichia coli* • D-alanylgriseoluteic acid (AGA), a potent phenazine antibiotic produced by *P. agglomerans* strain Eh1087 which reveals a broad spectrum of antimicrobial activity and is particularly active against Gram-positive pathogens, such as *Streptococcus pneumoniae*; • the recently isolated in Korea phenazine antibiotic from *P. agglomerans* apple strain R190, active against various spoilage bacteria, including *Pectobacterium carotovorum subsp. carotovorum, Clavibacter michiganensis*, and *Burkholderia andropogonis*, as well as against foodborne pathogens such as *Escherichia coli* O157:H7 and Salmonella enterica, and other human pathogens such as *Klebsiella pneumoniae* and *Yersinia enterocolitica* (Giddens *et al.*, 2007).

Three *P. agglomerans* strains isolated from the rhizosphere of grape bushes in Uzbekistan showed a strong anti-fungal activity due to production of chitinolytic enzymes (Chernin *et al*., 1995). The stimulation of plant resistance was also considered as a mechanism that protects against fungal pathogens. Verhagen *et al.*, 2011 demonstrated that *P. agglomerans* was capable of inducing oxidative burst and phytoalexin production in grapevine, leading to differential local and systemic resistance to a fungal pathogen *Botrytis cinerea* causing grey mould disease. Similarly, Zhang *et al.*, 1998 evidenced that an application of *Pantoea agglomerans* to cucumbers significantly reduced, by inducing systemic acquired resistance, the severity of anthracnose, a disease caused by a pathogenic fungus Colletotrichum orbiculare. Vanneste *et al.*, 2002 showed that *Pantoea agglomerans* enhanced the resistance in kiwi fruit and tobacco, thus protecting these plants from a disease called white mould, caused by an ascomycete, *Sclerotinia sclerotiorum*. Very good results were obtained by the use of *P. agglomerans* for the protection of stored fruits against fungal pathogens. It has been shown that the *Pantoea agglomerans* CPA-1 and CPA-2 strains provided excellent control against fungi of the species *Botrytis cinerea*, *Penicillium expansum* that *Rhizopus stolonifer*, causing post-harvest diseases of pome fruits (pear and apple), and inhibited the accumulation of patulin, a mycotoxin produced by *P. expansum* that affects human health (Nunes *et al.*, 2002). The CPA-2 strain also significantly reduced the incidence of *Penicillium digitatum* (green mould) and *Penicillium italicum* (blue mould) on stored citrus fruits (Texido *et al*., 2001). *P. agglomerans* strain EPS125 also efficiently protected stone fruits against brown rot caused by *Monilinia laxa* and soft rot caused by *Rhizopus stolonifer* (Bonaterra *et al*., 2003), while *P. agglomerans* strains isolated from pome fruits in Turkey efficiently inhibited the growth of *Aspergillus flavus* on stored lemons. Zhang *et al.*, 2014 recently reported that the *P. agglomerans* XM2 strain isolated from prunes in China was effective in post-harvest control of black spot disease caused by the fungus *Alternaria alternata* on pears.

An effective weapon against pathogens and pests of cultivable plants Combating bacterial pathogens. *Pantoea agglomerans* has been identified as an antagonist of many plant pathogens belonging to bacteria and fungi, which is associated with the production of antibiotics or other mechanisms. This enables its use as a biocontrol, and being a healthy and environmentally-friendly procedure, permits the decrease in pesticide doses, or even avoid the use of chemicals (Morales *et al.*, 2008). Best known is its use with commercially available strains E325, P10c, C9–1 (the latter recently classified as *Pantoea vagans*) for control of the bacterial plant pathogen *Erwinia amylovora* that causes fire blight, a devastating disease of apples and pears. The effectiveness of *P. agglomerans* in treatment of this disease is primarily due to the above-mentioned production of antibiotics, some of which could target amino acid biosynthesis in the pathogen and secondly to the competition in which *P. agglomerans* is more successful than the pathogen in colonizing flower stigmas of apple and pear trees. *Pantoea agglomerans* are also effective in the protection of vegetables. Strains of this bacterium isolated from potato tubers in Canada were found to inhibit the growth of *Peptobacterium atrosepticum*, the causative agent of potato blackleg (Sturz *et al*., 1996). Hsieh *et al.*, 2005 proved that seed treatment with *P. agglomerans* may be an effective and practical method for the control of bean wilt caused by *Curtobacterium flaccumfaciens pv. flaccumfaciens*. Sadik *et al*., 2006 reported that the *P. agglomerans* 2066–7 strain was the most effective biocontrol agent against onion bacterial diseases caused by *Pseudomonas marginalis, Pantoea ananatis, Pseudomonas viridiflava* and *Xanthomonas retroflexus* in Morocco. *P. agglomerans* is also efficient for reduction of bacterial diseases of monocotyledon crops, such as a serious blight caused by *Xanthomonas oryzae pv. oryzae* in rice. Braun-Kiewnick *et al.*, 2000 demonstrated that strains of *P. agglomerans* suppressed the development of basal kernel blight of barley caused by *Pseudomonas syringae pv. syringae*, when applied to heads prior to pathogen. On the other hand, Pasichnyk *et al.*, 2005 showed that

P. agglomerans compete effectively with *Pseudomonas syringae pv. atrofaciens*, the agent of basal bacteriosis of wheat, by quicker propagation and inhibition of the pathogen's growth. Besides antibiosis and competition, the other mechanisms of the antagonistic properties of *P. agglomerans* are less well known and are often related to the induction of plant resistance. Han *et al.*, 2000 showed that *P. agglomerans* was effective in inducing systemic resistance in radish to bacterial leaf spot caused by *Xanthomonas campestris pv. armoraciae*. Ortmann and Moerschbacher, 2006 demonstrated that exopolysaccharides of this bacterium induce the disease resistance of monocotyledon plant species, such as wheat and rice, by priming their cells for potentiation of the defense response elicited by contact with the pathogen (or a corresponding substance) which could manifest by the generation of H_2O_2 defined as an 'oxidative burst'. Combating fungal pathogens. *Pantoea agglomerans* has also shown an inhibitory activity against a number of important fungal plant pathogens, including: • *Fusarium culmorum*, a soil-borne fungal pathogen that causes seedling and head blight, and foot and root rot of wheat, and *Puccinia recondita* f. sp. tritici causing brown rust of wheat; • phytopathogenic and mycotoxin-producing strains *Fusarium avenaceum*, *F. oxysporum*, and *F. gibbosum* • *Fusarium graminearum* reported as a cause of Fusarium head blight or scab, responsible for major yield and grain quality losses in wheat, maize, barley, and oats – known also as a myxotoxin producer (Romanenko *et al*., 2000); • *Magnaporthe grisea* (anamorph: Pyricularia grisea), a rice blast fungus causing a serious disease of rice, and *Cladosporium cucumerinum*, a fungal pathogen causing scab of cucurbits, a disease of cucumber, cantaloupe, honeydew, summer and winter squash, pumpkin, and gourds (Adetuyi *et al.*, 1990).

Growth promotion of cultivable plants

Growth promotion by *P. agglomerans* strains associated with the rhizosphere. *Pantoea agglomerans* strains occurring in the rhizosphere (root-soil interface) of cultivable plants may promote the growth of these plants by various mechanisms. Malboobi *et al.*, 2009 demonstrated in both the greenhouse and in field trials that *P. agglomerans* was very efficient in the promotion of potato growth, mostly if applied in combination with the other phosphate-solubilizing strains belonging to the species *Microbacterium laevaniformans* and *Pseudomonas putida*. Son *et al.*, 2006 demonstrated that *P. agglomerans* strains isolated from soil exerted a beneficial effect for crops by solubilization of otherwise insoluble inorganic phosphates.

Amellal *et al.*, 1998 observed that the *P. agglomerans* NAS206 strain isolated from the rhizosphere of wheat in Morocco secreted an exopolysaccharide which had a positive effect on rhizosphere soil aggregation and plant growth. Two strains exhibiting potent useful properties have been isolated from rhizosphere in India: the *P. agglomerans* NBRISRM strain that enhanced the macronutrient uptake by maize and chickpea and promoted the growth of these plants (Mishra *et al*., 2011) and the *Pantoea* sp. NII-186 strain, which showed multiple plant growth-promoting attributes, such as phosphate solubilization activity, as well as indole acetic acid (IAA), siderophore, and HCN production. Additionally, the latter strain showed significant growth inhibitory activity against phytopathogenic fungi, and extremely wide tolerance to different environmental conditions, such as temperature, salt concentration and pH range, which makes it an ideal candidate for a bioinoculant replacing chemical fertilizers (Dastager *et. al*., 2009). Similar properties to the NII-186 strain revealed the plant-growth-promoting *P. agglomerans* diazotrophic (N2 -fixing) lma2 strain, isolated from the wheat rhizosphere of an arid region in Algeria, recommended it as a potentially good fertilizer in arid and saline zone Salini *et al*., 2012. Earlier, the *P. agglomerans* diazotrophic strains detected in the rhizosphere of wheat and barley in Germany had been indicated as potential bio-fertilizers. *Pantoea agglomerans* and closely related *Pantoea* species produce phytase, an enzyme degrading phytate (Suleimanova *et al*., 2015). Phytate, the salt form of a saturated cyclic acid called phytic acid, occurs commonly in plants and soil, making up to 90% of the natural phosphorus in the world. However, only ruminant animals decompose phytate, whereas other animals and plants do not. Thus, phytase enzymes produced by *P. agglomerans* and other bacterial species occurring in rhizosphere and other soil layers are crucial for making this rich phosphorus source available to plants and the majority of animals. They isolated from a sample of forest soil collected in the Republic of Tatarstan, Russia, a *Pantoea* sp. 3.5.1. strain exhibiting a very high activity of phytase encoded by the agpP gene. The strain is closely related to *P. agglomerans* but probably represents a new species. The authors sequenced the full genome of this strain and proposed its potential use as an environmentally friendly biofertilizer, as a feed supplement for livestock production, or as a raw material for the industrial production of microbial phytase, which by now is mostly produced from the *Aspergillus* strains.

Khalimi *et al.*, 2012 demonstrated that treatment of rice seeds with the bacterial suspension of *P. agglomerans* strains isolated from the rhizosphere of a groundnut, significantly increased the plant growth and yield of rice in Bali, Indonesia. Lakshmanan *et al.*, 2015 proved that *Pantoea* sp. strain

EA106, a natural rice rhizospheric isolate, abates arsenic uptake in rice by a high siderophore (iron binding) activity, resulting in increasing Fe plaque formation on rice roots. This promotes rice growth and prevents accumulation of toxic arsenic in the plant tissues.

Growth promotion by the endophytic *P. agglomerans* strains. The endophytic *P. agglomerans* strains developing inside plant tissues may promote plant growth mainly by the atmospheric nitrogen (N_2) fixation ability, production of phytohormones, and disease control (Feng *et al*., 2006). Scholz-Seidel and Ruppel, 1992 demonstrated that the *P. agglomerans* strain isolated from phyllosphere (air-surface interface of plant leaves) of wheat in Germany showed the presence of nitrogenase (N_2-fixing enzyme) and phytohormone activities that promote plant growth and increase the root length and yield of winter wheat. Inoculation experiments with diazotrophic *P. agglomerans* strains on wheat and barley in temperate regions have demonstrated the possibility of increasing yield up to 500 kg/ha (Ruppel *et al*., 1992). Verma *et al*., 2001 demonstrated that *P. agglomerans* strains isolated from deepwater rice in India appear to be very competent plant growth-promoting endophytes, which are equipped with the ability to fix atmospheric nitrogen, produce indole acetic acid (IAA) and mineralize insoluble phosphates. They produce pectinases and cellulases enabling penetration and spread inside rice and providing biologically fixed nitrogen to the distant parts of the plant. Similarly, Feng *et al*., 2006 evidenced that the *P. agglomerans* YS19 diazotrophic strain identified in China as rice endophyte, produced phytohormones, enhanced transportation of the photosynthetic assimilation products and promoted host plant growth showing a potential for increasing rice production in field application. Miao *et al*., 2008 demonstrated a strong adsorption of the *P. agglomerans* YS19 cells by rice root hairs indicating a close interrelation between *P. agglomerans* and host plant. Further studies on the properties of the YS19 strain showed the presence of a quorum sensing (QS) system. In this case, QS was proved to regulate, by means of acyl-homoserine lactone (AHL) diffusible signal molecule (identified as N-3-oxooctanoyl L-homoserine lactone (OOHL)), such life functions of bacteria as forming of cell aggregates, called symplasmata, and interrelations between bacterium and host, including the colonization of plant tissues and promotion of rice growth (Jiang *et al*., 2015). The potential beneficial effects of *P. agglomerans* on rice growth has been confirmed recently by Banik *et al*., 2016 who identified the presence of *Pantoea* spp. strains among 11 diazotrophic bacterial isolates from rice plants in India, which possessed the nif H (nitrogen fixation) gene and promoted the growth of rice seedlings. All these findings are very significant because rice is the staple food of 50% of the world's population and 80% the population of Asia. A similar *Pantoea* sp. 9C diazotrophic strain with an extremely high nitrogenase activity was identified in Cuba as an endophyte of sugarcane. Similar to an Indian NII-186 strain, the sugarcane strain revealed an exceptionally wide tolerance to environmental conditions and has been proposed as a candidate for an environment friendly biofertilizer (Loiret *et al*., 2014). Gond *et al*., 2015 recently demonstrated that *P. agglomerans* isolated from teosinte (an ancestor of corn) induces salt tolerance in tropical corn, which creates the chance to increase its cultivation area and yield on saline soils. Quecine *et al*., 2012 showed that the *P. agglomerans* endophytic 33.1 strain, originally isolated from *Eucalyptus grandis*, was able to cross-colonize and promote the growth of sugarcane. It also induced the synthesis of chitinase and endoglucanase enzymes, which are associated with plant protection against pathogens. These results suggest that this strain could be used as an inoculant to improve sugarcane productivity. Andreote *et al*., 2008, have proposed using the endophytic, plasmid-harboring *P. agglomerans* strains abundantly colonizing seedlings of citrus plants and eucalyptuses, as vehicles for the introduction of exogenous genes promoting growth of these cultivars. A growth-promoting effect of inoculation with *P. agglomerans* on wheat was confirmed by Remus *et al*., 2000, who evidenced that inoculating seeds and shoots with this bacterium increased the yield of wheat grain up to 23.5%, and by Egamberdiyeva and Höflich, 2003 who noted the growth promotion of winter wheat.

Efficient Bioremediation

Strong biodegradation activity. Recent reports indicate that the bacteria of the *Pantoea* genus reveal a great potential for bioremediation, e.g. a waste management technique that involves the use of organisms to remove or neutralize chemical pollutants from the natural environment. It has been documented that the *Pantoea* strains show biodegradation activity on various substrates with aromatic rings, such as phenol (Dastager *et al*., 2009), alkylbenzosulfonate and sodium dodecyl sulphate surfactants, 2,4,6-trinitrotoluene, tannic acid and the herbicide mesotrione (Xiong *et al*., 2014). Jacobucci *et al*., 2009, found that a biosurfactant produced by *P. agglomerans* was efficient in the bioremediation of the oily effluent released by the margarine and soap industry, as shown by the reduction of the COD (Chemical Oxygen Demand) index by 70%.

Biodegradation of rice straw. The most interesting approach to this issue has been presented by Xiong *et al*., 2014, who found that the rice endophytic strain *Pantoea* sp. Sd-1, closely related to *P.*

agglomerans, showed an exceptional ability to degrade rice straw and lignin. This creates an encouraging perspective for utilizing rice straw that could be used in industry for the production of bioethanol and paper, or as a renewable energy source. At present, however, the durability of lignin is the major obstacle to the utilization of rice straw and the reason for large-scale deposition of this abundant agricultural by-product which poses a considerable threat to the natural environment. The application of *Pantoea* for biodegradation of rice straw and other materials containing lignocellulose biomass may efficiently solve this important problem.

Degradation of Hydrocarbons

Pantoea has also been identified as a member of microbial communities used for the biological degradation of polycyclic aromatic hydrocarbons, produced from the incomplete combustion of organic materials and fossil fuels in various industrial activities, and regarded as environmental pollutants of particular concern (Zhang *et al*., 2012). Vasileva-Tonkova and Gesheva, 2007 found that the *Pantoea* sp. A-13 strain isolated from soil in Antarctica produced a potent glycolipid biosurfactant which could be used for the degradation of petroleum hydrocarbons and environmental bioremediation. The research performed by a group of scientists from Pakistan and Austria has documented the outstanding potential of *Pantoea agglomerans* strains for the degradation of petroleum hydrocarbons in spilled soil (Tara *et al*., 2014). The high performance of the *P. agglomerans* BTRH79 strain in hydrocarbon removal was related to the presence of alkane hydroxylase CYP153 gene with a substrate range between C4 –C16. Further studies by the Pakistani-Austrian group (Arslan *et al*., 2014) confirmed this performance, either for the BTRH79 strain alone or in combination with the other *P. agglomerans*, *Pseudomonas* sp., and *Burkholderia* sp. inoculant strains. Based on these studies, the group proposed an efficient phytoremediation system for the reduction of hydrocarbon contamination in which the inoculation of soil with pollutant-degrading bacteria was combined with the planting of proper vegetation, and amendment of soil with nutrients, such as compost or fertilizers containing nitrogen, phosphorus and potassium. In this system of a plant-bacterium partnership, inoculated bacteria promote plant growth by both detoxification of the environment and the ACC deaminase activity, receiving in turn habitat and nutrients. *P. agglomerans* is also an important member of the microbiota found in most biological degreasing systems used for degradation and removal of oil, grease, or lubricants from the metal parts of machines or installations, as an environment-friendly alternative to hazardous chemical solvents (Boucher *et al*., 2011). Reduction of toxic metals and metalloids. The facultative anaerobic *Pantoea agglomerans* strains show a potential to detoxify the environment through the oxidation of acetate or H_2 to dissimilatory reduction of metals, such as Fe(III), Mn(IV) and the highly toxic Cr(VI) [160, 161]. These results correspond with a study performed by Ozdemir *et al.*, 2004 who demonstrated that the *Pantoea* sp. TEM18 copper tolerant strain, isolated from activated sludge of a petrochemical industry wastewater treatment plant, showed a high adsorption capacity for heavy metal ions Cr(VI), Cd(II) and Cu(II), creating a promising perspective for the effective treatment of wastewater polluted with toxic metals. *P. agglomerans* was also among 7 strains which were proved by Zaets *et al*. 2010, to be effective in the protection of soybean plants against accumulation of toxic cadmium present in soil. Similarly, Pishchik *et al*. 2009, demonstrated that inoculation of *P. agglomerans* into soil highly contaminated with toxic cadmium and lead resulted in a decrease of their content by 2–3 times and 4–5 times, respectively, and furthermore, caused a significant increase of the oats yield which exceeded even the yield noted in soils not contaminated with heavy metals. According to Tian *et al*., 2015, the *Pantoea* sp. IMH strain carrying the arsC gene and highly resistant to heavy metals, was effective in the aerobic reduction of arsenic(V) present in the solid waste released by a copper-smelting plant. Yousaf *et al*., 2010, proved a very high efficiency of hydrocarbon degradation by the *P. agglomerans* BTRH79 and ITSI10 plant isolates in combination with plants: Italian ryegrass (*Lolium multiflorum* var. Taurus) and bird's-foot trefoil (*Lotus corniculatus* var. Leo).

Prevention of Penetration of Toxic Contaminants Into Soil.

Besides significant chemical effects, *Pantoea agglomerans* may prevent penetration of harmful industrial contaminants into deeper parts of soil on a physicochemical basis. Kurlanda Witek *et al*. 2015, have experimentally demonstrated that even a thin layer of a biofilm formed by *P. agglomerans* can hinder the migration of zinc oxide nanoparticles downwards porous media. The authors postulated that such biofilms could be used as a potential remediation strategy against the migration of nanoparticle contaminants in heterogeneous aquifers.

Uses and potential uses of *Pantoea* strains for biocontrol and bioremediation.

Biocontrol			Bioremediation	
Species	Plant or crop	Pathogen/pest controlled	Source	Application
P. agglomerans	Apple	*Botrytis cinerea*1	Aquifer	Arsenic resistance and/or degradation
	Pear	*Botrytis cinerea*1	Salt pond sediment	Reduction of iron, manganese, chromium
		*Penicillium expansum*1	Iron-rich soil	Solubilization of insoluble inorganic compounds
		*Erwinia amylovora*2	Crude oil contaminated soil	Biosurfactant production
	Lentil	*Botrytis cinerea*3	Subterranean forest sediment	Reduction of iron
	Banana	*Botryodiplodia theobromae*4	Soybean rhizosphere	Solubilization of insoluble inorganic phosphates
		*Colleotrichum musae*4		
	Citrus fruit	*Penicillium digitatum*		
		Penicillium italicum		
	Lemon	*Aspergillus flavus*		
	Potato	*Pectobacterium carotovorum* ssp. *atroseptica*		
	Radish	*Xanthomonas campestris*		
	Cucumber	*Sclerotinia sclerotiorum*		
		Colletotrichum orbiculare		
	Sugar beet	*Pythium* sp.		
	Safflower	*Pythium* sp.		
	Canola	*Pythium* sp.		
	Dry pea	*Pythium* sp.		
	Olive knot	*Pseudomonas savastanoi* pv. *savastanoi*		
	Centella asiatica	*Pseudomonas aeruginosa*		
	Tomato	*Meloidogyne incognita*		
	Arabidopsis	*Pseudomonas syringae* pv. *maculicola*		
	Kiwi	*Sclerotinia sclerotiorum*		
	Tobacco	*Sclerotinia sclerotiorum*		
	Soybean	*Pseudomonas syringae* pv. *glycinea*		
P. ananatis	Pome fruit	*Penicillium expansum*	Agricultural water source	Degradation of mesotrione

Pantoea sp.	Potato	*Giberella pulicaris*	Wastewater treatment sludge	Biosorption of copper, chromium, cadmium
	Lettuce	*Escherichia coli*	Ghat forest soil	Biodegradation of phenol
	Spinach	*Escherichia coli*	Ornithogenic soil	Biosurfactant production

2. Conclusion

phosphate solubilization or nitrogen fixation. Number of Pantoea species are also involved in bioremediation of various pesticides and organic chemical compounds. This indicates the potential to degrade some recalcitrant and xenobiotic compounds. Some Pantoea strains also provide effective protection to plants against various bacterial and fungal diseases and post-harvest fruit rots. On the other hand, some of the species are recognized as a human pathogen and has led to controversy as limited documented cases of P. agglomerans bacteremia and infections have been reported. Most of the cases reported among immunocompromised patients or the pediatric population. Thus, Pantoea is a multifaceted bacterium that plays a significant role in agriculture as a plant growth promoter by producing hormone like IAA, inorganic pollutant degradation by producing potent enzymes and also protects some plants against pathogens by producing antibacterial and antifungal compounds. In some cases these also cause diseases in human beings. Therefore, this genus is very important for studies. In this review, the industrial, agricultural as well as ecological significance of the genus Pantoea is emphasized.

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