



REVIEW ARTICLE

# ***Pseudomonas* Species in Soil as a Natural Resource for Plant Growth Promotion and Biocontrol Characteristics - An Overview**

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## **ABSTRACT**

Plant growth-promoting *Pseudomonads* regulate plant growth by several direct and indirect mechanisms; direct mechanisms include producing phytohormones, increasing nutrient availability and indirect mechanisms include suppressing soil-borne plant pathogens by the production of siderophores, antibiotics, inducing systemic resistance and competing with pathogens. *Pseudomonas* spp. in soil has been reported from diverse ecological niches and has been well-documented as a model organism for regulating plant growth promotion. These bacteria are endowed with tremendous genetic and metabolic diversity and serve multiple ecological functions in the soil ecosystem. This versatile genus is one of the most commercially exploited bacteria in agriculture. The potential of the different species of *Pseudomonas* has not been realized sufficiently and requires emphasis on sustainable agriculture for the benefit of humankind. Research in the past decade has revealed that several species of *Pseudomonas* other than the common species such as *P. fluorescens*, *P. putida*, *P. aeruginosa*, have both plant growth promotion and biocontrol characteristics and have not been commercially exploited. According to the recent List of Prokaryotic names with Standing in Nomenclature (LPSN) there are 507 species of *Pseudomonas* and the present literature review brings out that 7.29% of them possess plant growth promotion (PGP) and biocontrol traits and thus can be utilized as biofertilizers in the field of agriculture. The role of different *Pseudomonas* spp. in the supply of plant nutrients and biocontrol of soil-borne plant pathogens are covered in this review.

**Key words:** Agriculture; *Pseudomonads*; Biocontrol; Rhizosphere; Soil

## **Introduction**

Plant-associated bacteria can be classified into beneficial, deleterious and neutral groups on the basis of their effects on plant growth. It is well documented that only 1-2% of bacteria promote plant growth in the rhizosphere and are referred to as plant growth-promoting rhizobacteria (PGPR), and *Pseudomonas* spp. is one of the predominant bacteria (Antoun and Kloepper, 2001). *Pseudomonads* are known mostly for their plant growth promoting abilities though a few cause plant disease. The genus *Pseudomonas* comprises bacteria found in diverse ecological habitats such as plant surfaces, water, soil, and sediments with the simple nutritional requirement. They play an important role in plant health management in the rhizosphere (Akansha and Das, 2016). The plant growth-promoting *pseudomonads* are rapid root colonizers utilizing

root exudates and interact directly and indirectly to improve plant growth and yield. Several studies have also shown their ability to suppress disease and induce resistance in plants. Their main mechanism of action involves the production of a diverse group of metabolites, including antibiotics, and volatile compounds like hydrogen cyanide (Couillerot *et al.*, 2009), competition for iron and other nutrients by the production of siderophore, niche exclusion (Akansha and Das, 2016), and induction of systemic resistance. Although some species of *Pseudomonas* are exploited commercially, several other species of *Pseudomonas* have these growth-promoting and biocontrol traits and are still unexplored. The present review discusses the methods employed by different species of *Pseudomonas* other than the well-known species in enhancing plant growth promotion and protection against soil-borne plant pathogens (Fig. 1).

## Plant growth-promoting traits of *Pseudomonas*

### Nitrogen fixers

The ability to fix atmospheric nitrogen is widely seen in phyla of Bacteria and Archaea, but was found earlier to be absent in the *Pseudomonas* genus. However, Yang (2019) reported that one of the species of root-associated Pseudomonad, *Pseudomonas stutzeri* A1501, can fix atmospheric nitrogen. This particular strain exhibits all the plant growth-promoting characteristics like broad utilization of carbon sources, nitrogen fixation, denitrification, degradation of aromatic compounds, biosynthesis of polyhydroxybutyrate and other functions that presumably give it an advantage in root colonization and to overcome environmental stresses. Genetic

information on *nif* genes suggested that this property was acquired by lateral gene transfer. The 49kb nitrogen fixation region consists of 59 genes constituting nitrogen fixation island, similar to that of other nitrogen fixers like *Wolinella succinogenes* and *Rhizobium leguminosarum*. The presence of *nif* genes in *P. stutzeri* raises the question of their origin. The rareness of nitrogen fixation properties in true pseudomonads suggests that *nif* genes were lost during evolution in most *Pseudomonas* species. Of late, many other nitrogen-fixing strains of *Pseudomonas* have been identified, like *P. migulae*, *P. putida*, *P. koreensis*, *P. entomophila*, *P. aeruginosa*, *P. sihuiensis*, *P. alcalignes*, *P. resinovorans* and *P. straminea* (Table-1).

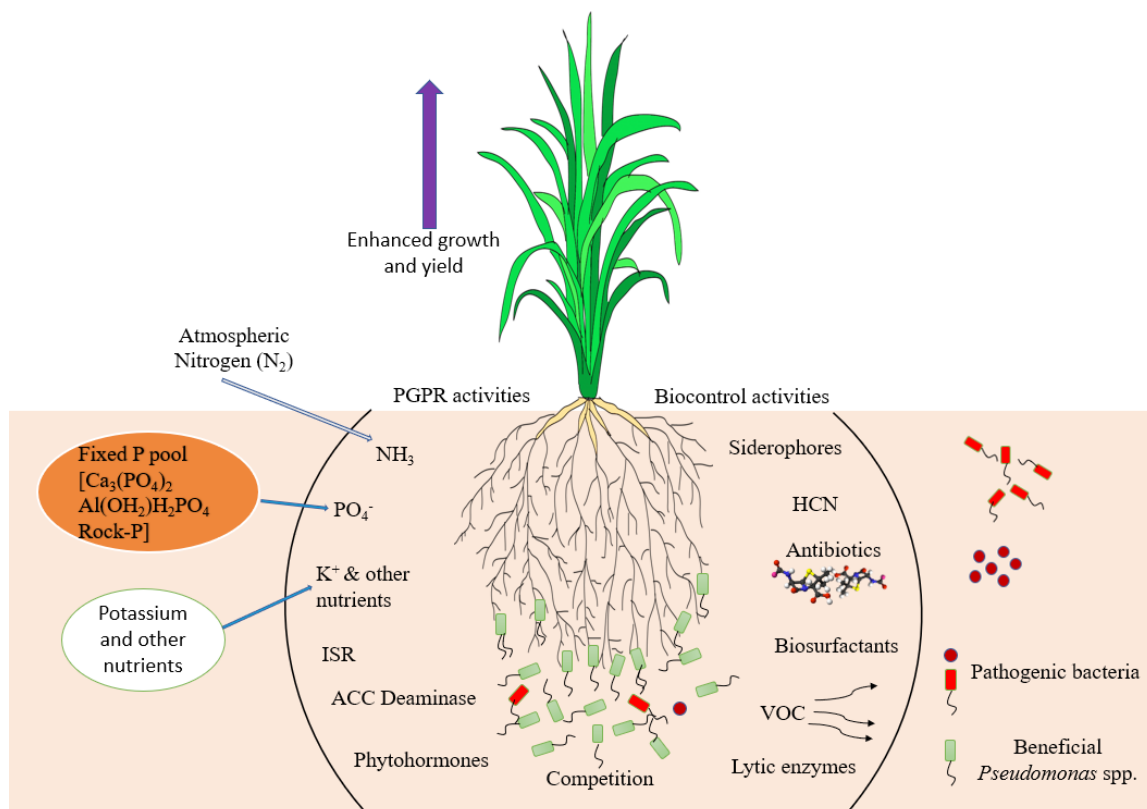
**Table 1. Growth promotion traits of *Pseudomonas* spp. in different crop plants.**

<i>Pseudomonas</i> spp.	Source	References
<b>Nitrogen Fixation</b>		
<i>P. migulae</i>	Himalayas	Suyal et al., 2014
<i>P. putida</i>	Rhizosphere of rice	Wickramasighe et al., 2021
<i>P. koreensis</i> & <i>P. entomophila</i>	Rhizosphere of sugarcane	Li et al., 2017
<i>P. aeruginosa</i>	Rhizosphere of sugarcane	Singh et al., 2021
<i>P. sihuiensis</i> ; <i>P. alcalignes</i> ; <i>P. resinovorans</i> ;	Rhizosphere of <i>Topinambur yacón</i>	Gabriela et al., 2021
<i>P. resinovorans</i> ; <i>P. straminea</i>	Rhizosphere of rice	Habibi et al., 2019
<i>Pseudomonas</i> spp.	Rhizosphere of Areca nut	Sutariati et al., 2020
<b>Phosphate solubilization</b>		
<i>P. corrugate</i>	Indian Himalayan region	Trivedi and Sa 2008
<i>P. plleroniana</i> ; <i>P. proteolytica</i> ;	Himalayan	Adhikari et al., 2021
<i>P. azotoformans</i>		
<i>P. luteola</i>	<i>Agav angustifolia</i> Haw.	Bautista-Cruz et al., 2019
<i>P. japonica</i>	Agricultural region of Erzurum	Alaylar et al., 2019
<i>P. rhodesiae</i>	Red lateritic soil	Maroniche et al., 2016
<i>P. prosekii</i>	Activated sludge and soil	Yu et al., 2018
<i>P. mediterranea</i>	Rhizosphere of tobacco	Gu et al., 2020
<i>P. pseudoalcaligenes</i>	Rhizosphere of rice	Jha & Subramanian 2014
<i>P. koreensis</i> ,	Rainfed agriculture field of Garhwal Himalaya	Gusain et al., 2015
<b>Phytohormone production</b>		
<i>P. fluorescens</i>	Fields of rice	Garcia et al., 2001
<i>P. mosselii</i>	Agave Americana rhizosphere	Adhikari et al., 2020
<i>Pseudomonas</i> spp.	Himalaya Kumaun region, India,	Chandra et al., 2019
<i>P. aeruginosa</i> (LJL-13)	Alfalfa grown under saline-alkali conditions	Liu et al., 2019
<i>P. fluorescens</i> P <sub>1</sub> ,		
<i>P. fluorescens</i> P <sub>3</sub> ,	Bacterial collection of Vali-e-Asr University of Rafsanjan	Zarei et al., 2020
<i>P. fluorescens</i> P <sub>8</sub> ,		
<i>P. fluorescens</i> P <sub>14</sub>		
<i>Pseudomonas</i> sp. strain S3	Rhizosphere of turmeric ( <i>Curcuma longa</i> );	Pandey and Gupta, 2020
<i>Pseudomonas</i> sp.	When grown in presence of organic acids and sugars	Panichikkal and Krishnankutty, 2020
<i>P. chlororaphis</i> PCL1606	Putative Fap-like fibre and Psl-like exopolysaccharide produced by PcPCL1606 in the biofilm formation process	Heredia-Ponce et al., 2021
<b>Biosurfactant production</b>		
<i>P. aeruginosa</i>	Rhizosphere of tea	Chopra et al., 2020
<i>P. aeruginosa</i>	<i>Parthenium hysterophorus</i>	Singh and Cameotra 2013

## Phosphate solubilizers

The ability of plant growth-promoting bacteria to convert insoluble form of phosphorus to a soluble form is an important trait, and as such, the use of these inoculants as biofertilizers provides a promising alternative to chemical fertilizers. The main P solubilization mechanisms employed by microorganisms include: (i) release of organic acids, siderophores, protons, hydroxyl ions and  $\text{CO}_2$  that dissolve complexes or mineral compounds (ii) production of extracellular enzymes (biochemical P mineralization) and (iii) the liberation of P during substrate degradation (biological P mineralization). Several reports of *Pseudomonas* species with phosphate solubilization potential have been reported. Nicholas *et al.* (2015) showed that endophytic *Pseudomonas* strains L111, L228, and L321 possess good phosphate solubilization activity and that the strain L321 expressed this trait under conditions of phosphate limitation, resulting in enhanced plant growth promotion of *Pisum sativum* plants, hence these *Pseudomonas* strains may be ideal biofertilizer candidates for commercial applications. Paul and Sinha (2017) found the antibacterial potential of a phosphate-solubilizing bacterium *Pseudomonas aeruginosa* isolated from river Ganga, effective in phosphate solubilization. Qian and Shanjiang (2019) screened and isolated five potential phosphate solubilizing bacteria from an alfalfa rhizosphere in heavy metal-contaminated

reclamation area in Shanxi Province, China. Based on morphological observations, 16S rRNA sequencing, cellular fatty acid composition analysis, and the BIOLOG test, three out of five strains were identified as *Pseudomonas* spp. The phosphate-solubilizing strain *Pseudomonas* sp. P34 was isolated from a wheat rhizosphere via wheat germ agglutinin by Liu *et al.* (2019). The results indicated that this strain could survive within the rhizosphere for a long time and colonize new spaces, resulting in the elongation of wheat roots. Attarzadeh *et al.* (2019) reported that *Pseudomonas fluorescens* is effective in increasing the concentration of nutrients in *Echinacea purpurea* under drought conditions resulting in increased relative water content and leaf area index, reduced ion leakage, and thus increased biological yield. Phosphate solubilizing *Pseudomonas* is also effective when co-inoculated with other phosphate solubilizing bacteria (PSB). Blanco-Vargas *et al.* (2020) co-inoculated phosphate-solubilizing *Pseudomonas* sp. (A18) and *Serratia* sp. (C7) isolated from soils of Colombia and demonstrated that application twice a week for two months increased *Allium cepa* total dry weight compared to uninoculated control. Similarly, several species of Pseudomonads like *P. corrugate*, *P. palleroniana*, *P. proteolytica*, *P. azotoformans*, *P. luteola*, *P. japonica*, *P. rhodesiae*, *P. prosekii*, *P. mediterranea*, *P. pseudoalcaligenes* and *P. koreensis* are capable of phosphate solubilization in soil (Table 1).



**Fig 1. Schematic illustration of important mechanisms known for plant growth promotion by *Pseudomonas* spp.**

### Phytohormone producers

Auxins and cytokinins are involved in plant growth and development like cell elongation, cell division, tissue differentiation, and apical dominance. Some soil microorganisms can also synthesize auxins and cytokinins, which may also be involved in root growth stimulation and plant stress tolerance. The genetic mechanism of auxin biosynthesis and regulation by *Pseudomonas* and some other bacteria are well studied; in these bacteria, several physiological effects have been correlated to the biosynthesis of the bacterial phytohormone. *Pseudomonas* use the plasmid-encoded genes to produce indole-3-acetic acid via the indole-3-acetamide pathway. They also possess the indole-3-pyruvic acid pathway, which is chromosomally encoded. They can conjugate free auxins or hydrolyze conjugated forms of auxins and cytokinins, as they have genes encoded for them.

Several species of *Pseudomonas* like *P. fluorescens*, *P. putida*, *P. extremorientalis*, *P. chloraphis*, *P. aurantica* and *P. mosselii* produce growth regulators that cause plants to produce greater amounts of fine roots that increase the absorptive surface for uptake of water and nutrients. Sharma *et al.* (2017) studied the growth-promoting traits of indigenous fluorescent *Pseudomonas* spp. isolated from the apple rhizosphere and observed that all the isolates produced plant growth regulators viz., auxins, gibberellins, and cytokinins. *Pseudomonas fluorescens* G20-18 was reported to synthesize cytokinins (Grokinsky *et al.*, 2016) and *P. fluorescens* Rt6M10 to synthesize ABA in the rhizosphere of *Vitis vinifera* (Salomon *et al.*, 2014). Egamberdieva (2011) reported that *P. putida*, *P. extremorientalis*, *P. chlororaphis* and *P. aurantiaca* were able to produce IAA in 4% NaCl conditions. *Pseudomonas* sp. was also able to increase the plant biomass of *Sulla carnosa* by producing IAA under high salt conditions (200-400 mM NaCl) Hidri *et al.* 2016.

### Potassium and other nutrients uptake

Potassium (K) is an essential nutrient and an important constituent of all living cells. Normally, soils contain K in larger amounts, but most of the K is in the unavailable form for the plant uptake. Potassium releasing microorganisms can convert the insoluble form into soluble forms for plant uptake. Bacteria such as *Bacillus mucilaginosus*, *B. edaphicus*, and *B. circulans*, *Acidotherobacillus ferrooxidans*, *Paenibacillus* spp., *Burkholderia* and *Pseudomonas* can release potassium minerals. Potassium releasing bacteria are present in all soils, but their diversity, number, and the ability for potassium solubilization vary depending on soil and environmental conditions. These bacteria can produce organic, inorganic acids

and polysaccharides, dissolve silicate minerals, and release K through acidolysis, complexolysis, chelation, and exchange reactions (Hidri *et al.*, 2016).

Research on isolation and identification has led to some potential potassium-solubilizing bacteria from the rhizosphere of different crops. Among them, *Pseudomonas* spp. was found to be predominant, such as *P. orientalis* from paddy soil (Khanghahi *et al.*, 2018), *Pseudomonas* spp. from tea plantation, sorghum, maize, bajra, and chilli soils (Bagyalakshmi *et al.*, 2017; Archana *et al.*, 2013). Verma *et al.* (2014) have identified drought-tolerant K-solubilizing microbes such as *Pseudomonas thivervalensis*, *Pseudomonas monteillii*, and *Pseudomonas lini*, among others from wheat crops growing in the central zone of India.

### ACC deaminase synthesis

Ethylene is an essential growth regulator required for the normal growth and development of plants. This plant hormone is produced by plants and is important in physiological changes in plants. Ethylene is not only a plant growth regulator but is also regarded as a stress hormone. Under stress like pathogenicity, salinity, drought, water logging and heavy metals, the level of ethylene is significantly increased, which negatively affects the overall plant growth. Ethylene in high concentration induces defoliation and disrupts other cellular processes that reduce crop yield (Bhattacharya and Jha, 2012). Plant growth-promoting rhizobacteria possess the enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase that facilitates plant growth by decreasing ethylene levels, inducing salt tolerance, and reducing drought stress in plants. Bacteria that produce ACC deaminase can relieve several forms of stress, such as effects of phytopathogenic microbes, polyaromatic hydrocarbons, heavy metals, high salt concentration, radiation, high light intensity, wound, insect predation, extremes of temperature, and floods (Ali *et al.*, 2014). Therefore, seed/root inoculation with ACC deaminase-producing rhizobacteria will result in plant root elongation, shoot growth promotion, and rhizobial nodulation enhancement, mycorrhizal colonization, and N, P, and K uptake in various crops.

Cheng *et al.* (2007) demonstrated that ACC deaminase and trehalose synergistically protect tomato plants against salt stress during the interaction with the PGPR *Pseudomonas* sp. UW4. *Pseudomonas fluorescens* strain TDK1 enhanced the saline resistance in groundnut plants due to its ACC deaminase activity, resulting in increased yield compared with the groundnut treated with *Pseudomonas* strains not having ACC deaminase activity. Akhgar *et al.* (2014) isolated an indigenous



strain of ACC-degrading *Pseudomonas fluorescens* in the rhizosphere of canola grown in saline soils, indicating that these bacteria may contribute to salinity tolerance. Aslam and Ali (2018) reported that ACC-deaminase activity in halotolerant *Pseudomonas* and other bacteria isolated from the rhizosphere and phylloplane of *Suaeda fruticosa* stimulated the growth of maize under saline conditions.

### Biofilm formation

Soil microbes have an important role to play in soil fertility. Soil surfaces allow the establishment of biofilms, where multispecies interact with each other and increase their survivability by modifying their growth and gene expression and this helps to withstand adverse environmental conditions (Ahmad *et al.*, 2017). Biofilms help the microbes to tolerate antibiotics, toxic chemicals and desiccation however, microbes differ in their ability to form biofilms both *in vitro* and *in situ* (Burmolle *et al.*, 2014). Rhizobacteria interact positively and negatively in mixed-species biofilms (Ren *et al.*, 2015). Some studies have also shown that certain strains of bacteria that are unable to form biofilm individually can promote biofilm formation in mixed

cultures, indicating a unique mode of cooperation in the biofilm mode (Klayman *et al.*, 2009). Several scientists have explored compatibility between *Pseudomonas* and other bacterial strains both in planktonic and biofilm mode of growth. Ansari and Ahmad (2019) observed that the interaction between the indigenous PGPR strains of *Pseudomonas fluorescens* FAP2 and *Bacillus licheniformis* B642 was compatible with planktonic and biofilm modes of growth and significantly enhanced vegetative growth and other photosynthetic parameters compared to uninoculated control. The consortium could be used as an effective inoculum in the growth of wheat plant. Both isolates demonstrated multiple plant growth-promoting (PGP) traits and biofilm-related functions such as the production of EPS, alginate, cell surface hydrophobicity and swarming motility. Powers *et al.* (2015) demonstrated interspecies interaction between *Bacillus subtilis*, a common soil bacterium and *Pseudomonas protegens*; metabolites produced by *P. protegens* inhibited biofilm formation and sporulation of *B. subtilis*. The interactions among rhizobacteria depend on the nature of the strains under study, and their metabolic requirements and extracellular products.

**Table 2. Biocontrol traits of *Pseudomonas* spp. in different crop plants.**

<i>Pseudomonas</i> spp.	Biocontrol activity	Reference
<b>General biocontrol</b>		
<i>P. koreensis</i>	From Tobacco rhizosphere; against <i>Phytophthora nicotianae</i> and <i>Rhizoctonia solani</i>	Gu <i>et al.</i> , 2020
<i>P. protegens</i>	Against <i>Botrytis cinerea</i> , <i>Alternaria alternata</i> , <i>Aspergillus niger</i> , <i>Penicillium expansum</i> and <i>Neofusicoccum parvum</i> , <i>Phaeoanellomyces chlamydospora</i> and <i>Phaeoacremonium aleophilum</i> ,	Andreolli <i>et al.</i> , 2019
<i>P. chlororaphis</i> sub sp. <i>aurantiaca</i>	Against <i>Rhizoctonia solani</i> AG-1(IA); <i>Colletotrichum dematium</i> , <i>Colletotrichum gloeosporioides</i> , <i>Fusarium oxysporum</i> f.sp. <i>melonis</i> , <i>Fusarium subglutinans</i> and <i>Stemphylium lycopersici</i>	Tagele <i>et al.</i> , 2019
<i>Pseudomonas</i> spp.	Cotton and sugarcane rhizosphere; against <i>Fusarium moniliformae</i> , <i>Fusarium oxysporum</i> and <i>Fusarium solani</i>	Zain <i>et al.</i> , 2019
<i>P. aeruginosa</i> PS24	<i>Rhizopus microsporus</i> , <i>Fusarium oxysporum</i> , <i>Aspergillus niger</i> , <i>Alternaria alternata</i> , and <i>Penicillium digitatum</i>	Uzair <i>et al.</i> , 2018
<i>P. segetis</i> strain P6	Isolated from the <i>Salicornia europaea</i> rhizosphere; strain P6 reduced soft rot symptoms caused by <i>Dickeya solani</i> , <i>Pectobacterium atrosepticum</i> and <i>P. carotovorum</i> on potato and carrot.	Rodríguez <i>et al.</i> , 2020
<i>Pseudomonas</i> strains (B11, T19, T24, and T75)	Against <i>Phalaris minor</i> and <i>Avena fatua</i> (weeds)	Dar <i>et al.</i> , 2020
<i>P. pseudocaligenes</i> AVO110	Isolated by the enrichment of competitive avocado root tip colonizers, controls avocado white root rot disease caused by <i>Rosellinia necatrix</i>	Pliego <i>et al.</i> , 2019
<i>P. donghuensis</i> strain SVBP6	From an agricultural plot in Argentina; against the phytopathogenic fungus <i>Macrophomina phaseolina</i> ; 7-hydroxytropolone is the main active metabolite responsible for the broad-spectrum inhibition of different phytopathogenic fungi.	Muzio <i>et al.</i> , 2020
<i>P. chlororaphis</i> PCL1606	Protect avocado plants against white root rot produced by the phytopathogenic fungus <i>Rosellinia necatrix</i>	Polonio <i>et al.</i> , 2017
<i>P. protegens</i> SN15-2	Isolated from tomato roots; inhibit the growth of <i>Ralstonia solanacearum</i>	Lou <i>et al.</i> , 2018
<b>Siderophore production</b>		
<i>P. geniculata</i> , <i>P. beteli</i> , <i>P. aeruginosa</i>	Isolated from rhizosphere of black pepper <i>Arachis hypogaea</i> L. (peanut)	Lou <i>et al.</i> , 2018 Gupta <i>et al.</i> , 2020

<i>P. koreensis</i>	Bacteriology Laboratory, Sakha Agricultural Research Station, Kafr El-Sheikh, Egypt.	Ghazy and El-Nahrawy, 2021
<i>P. putida</i>	It produces pyoverdine, a siderophore which is involved in its biocontrol activity	Daura-Pich <i>et al.</i> , 2020
<b>Antibiosis</b>		
<i>P. parafulva</i>	Isolated from rice rhizosphere and shows biocontrol ability against <i>R. solani</i> ; can produce antibiotic phenazine-1-carboxylic acid (PCA)	Zhang <i>et al.</i> , 2019
<i>Pseudomonas</i> sp.	Rhizosphere of rice; 2,4-diacetylphloroglucinol producer	Takeuchi <i>et al.</i> , 2015
<i>P. fluorescens</i>	Control Common scab of potato, caused by <i>Streptomyces scabies</i> ; through phenazine-1-carboxylic acid (PCA) production	Arseneault <i>et al.</i> , 2016
<b>VOCs</b>		
<i>Pseudomonas</i> sp	Against <i>Fusarium solani</i>	Gutiérrez-Santa <i>et al.</i> , 2020
<b>Induced systemic resistance</b>		
<i>P. simiae</i> WCS417	Upon colonization of <i>Arabidopsis</i> roots, WCS417 evades local root immune responses while triggering an induced systemic resistance (ISR) in the leaves.	Yu <i>et al.</i> , 2021
<i>P. putida</i> , <i>P. fluorescens</i> and <i>P. fluorescens</i>	Show host specificity in their ability to induce ISR in different plant species; in radish, WCS374 and WCS417 are potent elicitors of ISR, whereas WCS358 are not. Conversely, in <i>Arabidopsis thaliana</i> , WCS417 and WCS358 are able to trigger ISR,	Stringlis <i>et al.</i> , 2019
<i>P. simiae</i> WCS417r (formerly known as <i>P. fluorescens</i> WCS417r) and <i>P. fluorescens</i> SS101	Ability to induce systemic resistance in <i>Arabidopsis thaliana</i>	Pangesti <i>et al.</i> , 2017
<i>Pseudomonas</i> spp. Ps168	Isolated from soil and rhizosphere samples collected in Peru from Andean crops; induce systemic resistance to <i>Alternaria alternata</i> in tomato plants.	Ogata-Gutiérrez <i>et al.</i> , 2017

## Biosurfactants

Phytoremediation can be accelerated by the synergistic use of plants and microbes (Al-Awadhi *et al.*, 2009). Microorganisms associated with roots form a dynamic root-soil interface influenced by exudates, allowing increased availability of contaminant compounds and thereby helping plants adsorb and remove the pollutants (Compant *et al.*, 2010). Among heavy metals, Mn, Cu, Cr, Hg, Zn, Fe, Cd, Pb, As, etc., are probably the most toxic and are easily assimilable, and at high concentration, they are likely to interfere with key metabolic pathways (Narayanan and Devarajan, 2012). Rhizospheric microorganisms can also degrade organic pollutants such as petroleum hydrocarbons, chlorinated solvents, polycyclic aromatic hydrocarbons, and pesticides *via* their degradative pathways. The advances in environmental bioremediation have led to the application of bacterial biosurfactants in bioremediation due to their high biodegradability, low toxicity, and ecological acceptability. Biosurfactants are microbial surface-active agents, which are also excellent emulsifiers, foaming and dispersing agents, containing hydrophobic (non-polar) and hydrophilic (polar) parts that reduce surface tension and interfacial tensions between individual molecules at the surface and interface, respectively (Pacwa *et al.*, 2011). Microbial biosurfactants such as rhamnolipids, sophorolipid, and surfactin can effectively solubilize, emulsify, and mobilize both heavy metals and organic compounds.

During the application of biosurfactants on heavy metals, chemical interactions occur between the amphiphiles and the metal ions, that create complexes with metals at the soil interface, followed by desorption and removal of the metal from the soil surface, whereas for organic compounds such as hydrocarbons, the application of microbial surfactants increases the bioavailability of organic compounds such as hydrocarbons and mobilizes them by pseudo-solubilization and emulsification (Okoro and Akpabio, 2015). El-Sheshtawy and Doheim (2014) studied two types of microorganisms, *P. aeruginosa* and *B. subtilis*, suitable for the production of biosurfactants. The rhamnolipid biosurfactant produced by *P. aeruginosa* had also exhibited antimicrobial activity against different species of microorganisms.

## Biocontrol traits of *Pseudomonas*

### Siderophore producers

Iron is a micronutrient required by the microbes, and being highly insoluble is often a limiting factor in the rhizosphere. Siderophores are specific ferric iron-chelating agents secreted under low iron stress. Siderophores sequester available iron and make it unavailable to the competitors. They are also known to impart induced systemic resistance to plants and have been implicated in the biocontrol of several plant diseases (Miethke and Marahiel, 2007). Some microorganisms, including *Pseudomonas*, produce siderophores for iron acquisition to have a competitive advantage over other microbes.

Siderophores bind to ferric iron in the root zone and are then taken up by outer membrane receptors. Siderophores include a chemically diverse group of molecules classified into four main types, based on the functional groups involved in iron chelation: catecholate, phenolate, hydroxamate, and carboxylate. Some siderophores have mixed functional groups. Their different affinity to ferric iron depends on their structure. In the case of *Pseudomonas aeruginosa* two types of siderophores are produced, pyoverdine and pyochelin (Kramer *et al.*, 2020), and gene clusters involved in pyoverdine biosynthesis have been identified, which are responsible for the synthesis of the chromophore (pvc) and peptide (pvd) (Dumas *et al.*, 2013) moieties of the siderophore, respectively. Homologous systems regulating pseudobactin and pyoverdine utilization in *Pseudomonas putida* and *Pseudomonas fluorescens* that activate the transcription of several iron utilization genes (Ying-Ning *et al.*, 2018). Some *Pseudomonas* spp. can also use siderophores produced by other species. Villegas *et al.* (2002) used *Pseudomonas putida* WCS358, *P. fluorescens* WCS374, and siderophore negative mutants of these strains to assess the role of siderophores in potato growth stimulation. Siderophore negative mutants used the siderophores produced by their respective wild types; however, *P. putida* was able to use the siderophore produced by *P. fluorescens* strain, but *P. fluorescens* could not use the siderophore produced by *P. putida* (Table 2).

Pathogenic strains either do not produce siderophores or if produced, are of lower affinity, thus they have to compete for iron (Konstanze *et al.*, 2017). Thus, there seem to be siderophores mediated competition that is not well understood. Many natural environments are characterized by large pools of precipitated iron, and any soluble iron that is sequestered by siderophores is replenished by the dissolution of these precipitated iron sources. Other alternate functions of siderophores include transporting metals like zinc, manganese, copper and nickel and detoxifying the local environment by binding to toxic heavy metals without allowing them inside the cell. Siderophores can also regulate their own production, induce virulence factors, and protect cells from oxidative stress (Ellis *et al.*, 2000). *Pseudomonas* species known for the production of siderophores are *P. fluorescens*, *P. putida*, *P. aeruginosa*, *P. geniculata*, *P. beteli* and *P. korensis*.

### **Antibiotic producers**

The significance of antibiotics produced by plant growth-promoting rhizobacteria is well known. Some species of *Pseudomonas*, particularly fluorescent *Pseudomonas* are well known for the production of antibiotics. The compounds

produced are versatile and include antibiotics like phenazine-1-carboxylic acid, mupirocin, pyocyanin, pyrrolnitrin, and pyoluteorin. The phenazine family is nitrogenous heterocycle compounds produced by fluorescent pseudomonads. They are small molecules that can penetrate the cell wall of prokaryotes. Many phenazines exhibit antimicrobial activity, suppressing pathogenic microorganisms of plants, also playing an important role in the survival strategies of bacteria in the environment (Morrison *et al.*, 2016). The *P. aeruginosa* LV strain is a great producer of phenazine carboxylic acid (PCA). Phenazine-producing *Pseudomonas* contributes to the natural suppression of *Rhizoctonia solani*, causing sheath blight of rice (Karmegham *et al.*, 2020). Mavrodi *et al.* (2012) also reported that the frequency of wheat root colonized by these phenazine-producing pseudomonads is inversely related to annual precipitation; some of these pseudomonads showed strong inhibitory activity against *Rhizoctonia solani* AG-8 both *in vitro* and *in-situ*.

*Pseudomonas fluorescens* NCIMB 10586 produces a polyketide antibiotic called mupirocin in soil. Mupirocin comprises a monic acid (a heptaketide) containing a pyran ring, attached to 9-hydroxynonanoic acid *via* an ester linkage. It has broad-spectrum activity against Gram-positive than against Gram-negative bacteria (Gurney, 2011). The antibiotic acts by inhibiting bacterial isoleucyl-tRNA synthetase (Sandra *et al.*, 2014). A biocontrol strain of *Pseudomonas chlororaphis* PA23 by producing an arsenal of metabolites including pyrrolnitrin (PRN), phenazine (PHZ), hydrogen cyanide (HCN), and degradative enzymes was able to suppress the growth of the fungal pathogen *Sclerotinia sclerotiorum* as well as the nematode *Caenorhabditis elegans* (Nandi *et al.*, 2015). The antibiotic 2,4-diacetylphloroglucinol is a phenolic metabolite with antibacterial, antifungal, anthelmintic, and phytotoxic properties produced by *Pseudomonas* spp. controlled soil-borne plant pathogens in wheat plants grown in raw soil. Antibiotic production is a known trait of biocontrol mechanism in only some of the species of Pseudomonads.

### **Volatile organic compound producers**

Volatile organic compounds (VOCs) produced by rhizobacteria can stimulate growth, control plant pathogens, and induce systemic disease resistance in plants (Tahir *et al.*, 2017). Many bacteria regulate plant growth by emitting from a distance invisible volatile compounds that promote or inhibit plant growth without any contact. Around 846 different VOCs are produced by nearly 350 different bacterial species, including *Pseudomonas*, *Bacillus*, *Stenotrophomonas*, *Serratia*, and *Arthrobacter* (Lemfack *et al.*, 2014). *Pseudomonas* spp. are

distributed in diverse environments and is one of the most potent PGPR; of these, species such as *P. fluorescens*, *P. putida*, *P. rhodesiae*, *P. montellii* and *P. taiwanensis* have mechanisms that are beneficial to plants with determining effect on plant growth (Hafiz *et al.*, 2017). VOC production in bacteria can vary significantly and can indicate its varying regulatory effect on plants as a response to messages communicated between plant and microorganisms, but some VOCs help maintain rhizosphere competency (Bailly and Weisskopf, 2014).

Jishma *et al.* (2017) used five different *Pseudomonas* spp. isolated from the rhizosphere to assess the production and release of VOCs with impact on seedling growth of *Vigna radiata*. The study results indicated the production of 20 different VOCs from *P. fluorescens*, *P. putida*, *P. taiwanensis*, *P. montellii* and *P. rhodesiae* and most of the compounds were hydrocarbons like undecane, nonadecane, hexacosane, tetradecane, heptacosane, octadecane, heptadecane, hexadecane, and dodecane. The properties of these compounds include plant growth promotion, induction of induced systemic resistance and antimicrobial activity. Park *et al.* (2015) reported that a strain of *Pseudomonas fluorescens* SS101 produced 13-tetradecadien-1-ol, 2-butanone, and 2-methyl-n-1-tridecene enhanced the growth of *Nicotiana tabacum*. Hernández-León *et al.* (2015) analyzed the antifungal and plant growth-promoting (PGP) effects of diffusible organic compounds and VOCs produced by *Pseudomonas fluorescens* UM16, UM240, UM256, and UM270. These rhizosphere strains showed a high degree of antagonism against the phytopathogen *Botrytis cinerea* and significantly increased the biomass and chlorophyll content in *Medicago truncatula*. All the four *P. fluorescens* strains could protect *M. truncatula* plants from *B. cinerea* infection by producing either diffusible organic compounds or VOCs, thereby reducing stem disease symptoms and root browning. The VOCs emitted were mostly sulfur-containing compounds, including dimethyl disulfide, but strain UM270 was the only one that produced dimethyl hexadecylamine, a compound with antifungal and PGP activities.

### Inducing systemic resistance

Plant growth-promoting microorganisms colonize plants, and some may lead to induced systemic resistance (ISR) and protection of plants against various pathogens. ISR provides defensive immune capacity that protects plants and is generated in response to an external stimulus. The attributes of ISR include increased growth, production of antioxidants and proline, and modulation of phenols with antimicrobial and antioxidant properties, cell

wall reinforcement, and lignin deposition, tolerance to physiological stress and increased production of phytoalexins, defence enzymes and pathogenesis-related proteins (Jain *et al.*, 2014). Bas *et al.* (2010) reported that ISR generally primes defenses and is independent of the salicylic acid (SA) signalling pathway, and does not cause major alterations in the expression of defense-related genes. PGPR-primed plants do not have elevated expression of defence genes, once pathogens attack them, but instead show more rapid or stronger activation of defense response activated by functional jasmonate (JA) pathway (Vander *et al.*, 2009).

Substances involved in ISR are siderophores, antibiotics, N-acyl-L-homoserine lactone (AHL), and volatile compounds, partly the same as those involved in microbial antagonisms and are typically well studied in fluorescent *Pseudomonas*-pathogen interaction (Rachel *et al.*, 2018). *P. putida* WCS358 strain producing pseudobactin triggers ISR in tomato, whereas a mutant strain failed to do so (Shaikh *et al.*, 2020). *P. fluorescens* WCS374 and WCS417 produced siderophores that increased the suppression of disease by triggering of ISR (Berendsen *et al.*, 2015). Similarly, *P. fluorescens* CHAO producing diacetyl phloroglucinol (PhI) is involved through ISR against *Peronospora parasitica*. *P. fluorescens* WCS417 produced phytohormones act as the signalling molecules for the induction of ISR (Pangesti *et al.*, 2016). Inoculation of green gram plants with *P. fluorescens* Pf1 enhanced proline content, an ISR mediator (Sarvana Kumar and Duraisamy, 2010). Pea plants inoculated with fluorescent *P. aeruginosa* also suppressed *S. sclerotiorum* by decreasing oxalic acid production, alone or/and in consortia with other microbes (Jain *et al.*, 2011).

### Conclusion

*Pseudomonas* spp. are common soil organisms well known for exerting a wide range of plant beneficial effects. Many species of *Pseudomonas* have frequently been reported as plant growth-promoting rhizobacteria and biocontrol agents. *Pseudomonas* spp. are well-adapted to a wide range of environmental conditions. This wide environmental adaptability with many beneficial traits makes *Pseudomonas* spp. a suitable candidate for their application as biofertilizer or biocontrol agent. They easily colonize and multiply in the rhizosphere environment by rapidly utilizing root exudate. They play a major role in plant growth promotion by enhancing nutrient availability and producing phytohormones. They also protect plants against soil-borne plant pathogens by producing a wide spectrum of bioactive metabolites like antibiotics, siderophores, volatiles, hydrolytic enzymes, phytoalexins, and competing aggressively



with other microorganisms in the rhizosphere and inducing systemic resistance. They are easy to cultivate *in vitro* and mass-produced. Some of the PGP traits and biocontrol mechanisms such as nitrogen fixation, phosphate solubilization, phytohormone production, antibiosis and ISR are more common than other traits such as potassium release, ACC deaminase activity, biofilm formation and biosurfactant properties which are confined to some of the species of *Pseudomonas* indicating that knowledge regarding the growth-promoting traits and its presence in a particular strain becomes utmost important while selecting a PGPR strain of *Pseudomonas*. According to the List of Prokaryotic names with Standing in Nomenclature (LPSN) there are 507 species of *Pseudomonas* (Parte *et al.*, 2020). The literature review reveals that the plant growth-promoting traits and biocontrol characteristics are exhibited by nearly 37 different *Pseudomonas* species, 7.29% of the total known *Pseudomonas* species, which indicates that these beneficial microorganisms can be exploited in agriculture in future. However, their applicability for increasing crop productivity is limited. Hence the practical utility of these bacteria needs to be expanded through more focused research on crop productivity under different agro-ecological zones. This would help in utilizing the underutilized *Pseudomonas* spp. in sustainable agriculture for the benefit of humankind in the future.

## Statements and Declarations

All the authors of the manuscript declare that they do not have any conflict of interest

## Authors contribution statement

Anuroopa N: Conceptualization, Writing- Original draft preparation, Investigation, Data curation. Anshu B. Ram: Writing- Original draft preparation, Investigation, Data curation. Praveen R: Visualization, Data curation. Ashwin R: Data curation. Bagyaraj DJ: Writing- Reviewing and Editing, Supervision

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