Unlocking the strength of plant growth promoting *Pseudomonas* in improving crop productivity in normal and challenging environments: a review

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**ABSTRACT**

The widespread use of biofertilizers, rather than chemical fertilizers, is significantly more likely to accomplish sustainable agriculture production globally. Plant growth-promoting rhizobacteria (PGPR) are chemical-free alternatives to conventional crop protection in agriculture. *Pseudomonas* spp. are unique among the PGPR genera in terms of root colonization, nitrogen fixation, production of exopolysaccharides, siderophores, hydrogen cyanide (HCN), and phytohormones, solubilization of phosphorus, potassium, and zinc, biofilm formation, antioxidant activities, stress adaptation abilities, and positive interactions with other microbial communities. They also aid plant development by promoting biotic and abiotic stress tolerance, as well as supporting host plant nutrition. *Pseudomonas* is regarded as an environmentally acceptable alternative to harmful chemical fertilizers because of its active growth-promoting actions. However, to achieve this goal, workers must first get a complete understanding of the numerous processes used by *Pseudomonas*, allowing them to fully exploit the bacteria potential in the future. Therefore, the present review has been undertaken to discuss the fundamental processes used by *Pseudomonas* spp. to promote plant development and reduce environmental stresses. In addition, we described some reported *Pseudomonas*-based biofertilizers worldwide and the presence of potential genes in the genome of different *Pseudomonas* strains to understand the mechanism of *Pseudomonas* mediated plant growth promotion at the molecular level.

**Introduction**

Agriculture is important for human and animal food security on the globe (Alawiye and Babalola 2019). By 2050, the world’s population is predicted to exceed 8 billion people, posing a huge challenge for agricultural systems to produce enough food to feed this growing global population (Prosek and Ivanova 2018). As a result, the farming sector has grown reliant on technology and chemical inputs to feed the rising population and meet the ever-increasing demand for grains and organic food (Mueller et al. 2012). For decades, agrochemicals (mainly chemical fertilizers and pesticides) are applied indiscriminately in agriculture have resulted in a loss of soil and plant health to improve productivity and reduce the continual risk of plant-pathogen infections. On the other hand, chemical fertilizers are costly, harm the soil, impair its water-holding capacity and fertility, induce nutritional imbalances, and produce excessive amounts of water contamination (Sprent and Sprent 1990).

Hence, there is a great need for solutions that allow for food production without the use of excessive agrochemicals (Cedeño et al. 2021). Rhizosphere management is the practice of increasing nutrient efficiency in the soil to boost plant growth and productivity (Zia et al. 2020). The rhizosphere is the soil’s surface area immediately surrounding a root that is directly impacted by plant root exudates (Hartmann et al. 2008). Root exudates include a range of organic acids, amino acids, sugars, and other little compounds that operate as significant chemo-attractants for soil bacteria. Thus, depending on the plant species or even variety, the roots might produce significant variances in the chemical content of the exudates, attracting a specific microbial diversity (Olanrewaju et al. 2019). Plant growth-promoting rhizobacteria (PGPR), invade and multiply in the rhizosphere environment within the plant microbiome (Compant et al. 2019), gaining momentum in agricultural practices, as conventional chemical fertilizers. In sustainable agriculture, PGPR play an important role, improving crop yield, soil fertility, increasing biodiversity and association with other helpful microorganisms, and limiting pathogen growth and infection (Vázquez et al. 2020). Many strains of beneficial soil microorganisms have been isolated for their potential in rhizosphere management to boost plant yield and are now being exploited in biotechnology to improve food security and agricultural sustainability (Reed and Glick 2013). In China, the top 5 most used strains in Chinese biofertilizer products are *Bacillus subtilis, Paenibacillus mucilaginosus, B. amyoliquefaciens, B. licheniformis, and B. megaterium* (Ma 2019). Whereas, in other counties, *Pseudomonas*-based biofertilizers are *Pseudomonas fluorescens* and *P. putida* in Vietnam, *P. fluorescens* in Cuba, *P. striata* in India, *P. azotoformans* and *P. chlororaphis* in Sweden, and *P. fluorescens* in Sri Lanka, etc. (Table 1). In some situations,
combining two or more compatible microbes of different species (or strains) can provide advantageous additive or synergistic consequences, because the lack of activities in one introduced microbe can be compensated by the action of the other (Louca et al. 2018).

_Pseudomonas_ is a genus with over a hundred different species that houses the most diverse group of bacteria on the earth (Hesse et al. 2018a). The _Pseudomonas_ genus belongs to the proteobacteria subclass gamma. This proteobacteria's acceptance can be measured by its ability to thrive in a variety of environments, including freshwater, terrestrial, and marine ecosystems. They also have a close association with higher life forms, and it is one of the most researched bacterial species (Selvakumar et al. 2015). _Pseudomonas_ which shows their abundant presence in the rhizosphere (Muleta et al. 2009) and their outstanding growth-promoting characteristics, such as better root colonization, enzyme and metabolite production, nutrient solubilization, indole acetic acid (IAA), and siderophore production, acting as a biocontrol agent, and inducing systemic resistance against diseases, have attracted a lot of attention (Podile and Kishore 2006). Many _Pseudomonas_ species, such as _P. aeruginosa_, _P. chlororaphis_, _P. fluorescens_, _P. putida_, and _P. syringae_ are well-known for their ability to promote plant development and reduce a range of plant diseases (Raaijmakers and Mazzola 2012; Singh et al. 2021). There is a need for a complete discussion and clarification of the role of _Pseudomonas_ spp. to make better use of these naturally occurring microbes for improving plant growth and decreasing environmental stresses.

Therefore, this review mainly focuses on exploring deeper into the various characteristics of plant growth promoting (PGP) _Pseudomonas_ strains that can boost agricultural output in both normal and stressful situations. The knowledge gathered from this review will aid us in understanding the value of _Pseudomonas_-based biofertilizers in agriculture and overcoming the issues related to chemical fertilizer use.

### _Pseudomonas_ in combination with other _Pseudomonas_ strains, PGPR species, or plant mutualists

Several plants may form mutualistic connections that result in enhanced nutrition, hormone levels, and resistance to abiotic and biotic stresses. These benefits can be provided by bacteria or fungus; relying on the mutualist species, the connection can occur on the leaf or root area, or within the plant (endophytes). Numerous researches have investigated the impact of applying many mutual beneficial organisms to soils at the same time on plant defense (Senthilaraja et al. 2010). The impact of introducing a large number of mutualistic organisms to soils at the same time on plant defense has been studied extensively (Whipps 2001). Several _Pseudomonas_ isolates (Seevinas et al. 2012) to many other mutualistic bacteria (Domenec et al. 2006) or mutualistic fungus were among the species that contributed (Jaderlund et al. 2008). When a large number of agents are utilized, the probability of at least one of them will be highly adapted to the specific environment in which the organisms are delivered increases. Disease control by the plant can be improved when imported mutualists have distinct impacts on induced defense responses (Domenec et al. 2006).

The most commonly investigated combination of _P. fluorescens_ and other PGPR is _Bacillus_ spp., but _Rhizobium_ spp., _Burkholderia_ spp., and _Serratia_ spp. are also explored regularly. The rhizosphere is colonized by many _Bacillus_ strains drawn by root exudates (Feng et al. 2018). It secretes compounds that promote the quantity of native plant beneficial species after establishing biofilm on plant roots (such as _Pseudomonas_ spp.). They share extracellular matrix and vital metabolites by establishing a densely linked biofilm, which improves their rhizosphere fitness (Sun et al. 2021). A combination of _P. fluorescens_ and _Bacillus_ has been associated with increased control of _Fusarium_ disease by inducing the defense-related enzymes peroxidase (POD) and polyphenol oxidase (PPO) (Sundaramoorthy et al. 2012). The number of studies that have examined the effects of mixing _Pseudomonas_ and other PGPR introductions has shown that they enhance biological control (Combes-Meynet et al. 2011). In addition, studies have shown that inoculating with _P. fluorescens_ only is more efficient than mixing _Pseudomonas_ with the other PGPR strains. (Stockwell et al. 2011). Many _Pseudomonas_ species link with plants as plant endophytes (Ryan et al. 2008) and rhizosphere colonizers, promoting plant health by antagonizing plant-pathogenic bacteria (biocontrol) and the development of plant disease tolerance (Haas and Defago 2005).

### _Pseudomonas_ as a biofertilizer

Microbial biofertilizers are helpful microorganisms that interact with the rhizosphere or endosphere of plants to improve soil fertility and stimulate nutrient absorption to boost yield (Okur 2018). Biofertilizers are gaining importance as an ecologically responsible and cost-effective way to enhance crop yield and soil fertility (Glick 2020). When applied to the seed, plant surface, and soil, these microbial inoculants inhibit the rhizosphere and the interior of the plant, encouraging plant development (Raghuvanshi 2012).

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**Table 1. List of some _Pseudomonas_-based biofertilizer products.**

| Type of biofertilizer | Biofertilizer name | _Pseudomonas_ strain(s) | Manufacturer's country | Reference(s) |
|-----------------------|-------------------|------------------------|------------------------|--------------|
| Nitrogen fixer         | BioGro            | _P. fluorescens_       | Vietnam                | Uribe et al. (2010) |
| Phosphate solubilizer | Fofofina          | _P. fluorescens_       | Cuba                   | Uribe et al. (2010) |
| Phytostimulator        | Amase             | _P. azotoformans_      | Sweden                 | Mehnaz (2016); Macik et al. (2020) |
| Phytostimulator        | Bio Gold          | _P. fluorescens_       | Sri Lanka              | Mehnaz (2016); Macik et al. (2020) |
| Biocontrol             | Cedemon           | _P. chlororaphis_      | Mustafa et al. (2019)  |
| Biocontrol             | Cedrex            | _P. chlororaphis_      | Mustafa et al. (2019)  |
| Biocontrol             | Ceral             | _P. chlororaphis_      | Mustafa et al. (2019)  |
| Liquid PSA             | Laboratorios BioAgro S.A. | _P. aurantiaca_ | Argentina              | Celador-Lera et al. (2018) |
| AbiTEP GmbH           | FSB 24 fl, BactoflA 10 | _P. fluorescens_       | Germany                | Odoh et al. (2019) |
| Greenmax AgroTech      | Biomax            | _P. fluorescens_       | India                  | Odoh et al. (2019) |
| Amka Products (Pty) Ltd | Organicos       | _Pseudomonas spp._     | South Africa           | Adeleke et al. (2019) |
| Cleveland biotech      | Ammmite A100     | _Pseudomonas spp._     | United Kingdom         | Odoh et al. (2019) |
They not only contribute nutrients to the soil, which improves soil fertility and agricultural yield, but they also defend the plants against pests and diseases. They have been proven to improve root system development, lengthen root system life, destroy hazardous compounds, boost seedling survival, and shorten the flowering time (Youssef and Eissa 2014). Another advantage is that after 3–4 years of continuous usage of biofertilizers, they are no longer required because parental inocula are adequate for growth and multiplication (Bumandalai and Tserennadmid 2019). Some of the commonly used *Pseudomonas*-based biofertilizer products in different countries are represented in Table 1.

**Colonization in plants**

Colonizing the plant root and rhizosphere efficiently is the first and most crucial stage in utilizing biocontrol agents (BCAs) to protect plants from soil-borne illnesses (Figure 1). Insufficient rhizosphere colonization can limit or diminish the beneficial effects of biocontrol microbes, leading to disease control inadequacy. The viability of *Pseudomonas* species populations that inhibit bacterial wilt disease in tomatoes improved as diversity increased (Hu et al. 2016). Additionally, the total viable bacterial population on bean root tips was enhanced when two different biocontrol *Pseudomonas* species consortia for anthracnose was applied (Bar-das et al. 2009). Positive control of numerous colonization-related biological processes, including biofilm production, growth, and migration, by connections between microbes within the consortium, could elucidate these favorable microbial colonization effects. Efficient colonization of bacterial strains such as *P. koreensis*, *P. aeruginosa* Z5, and *P. aeruginosa* B18 plays a significant role in eliminating plant diseases and increasing crop improvement in diverse crops, according to previous studies (Yasmin et al. 2014; Li et al. 2017; Singh et al. 2021). Singh et al. (2021) also reported the presence of colonization gene i.e. minCDE, lysC, and yjbB in genome of *P. aeruginosa* B18, assists its part in antifungal activity against *Sporisorium scitamineum* and growth improvement in sugarcane (Table 2).

**Differential gene expression in Pseudomonas inoculated crops**

Several previous researches revealed differential expression of defense-related genes in crops infected with *Pseudomonas* strains. For example, inoculation of the rhizospheric strain *P. koreensis* MU2 elevated the salt-resistant genes GmST1, GmSALT3, and GmAKT2, resulting in a considerable reduction in the abscisic acid (ABA) and jasmonic acid (JA) whereas increasing the salicylic acid content in soybean. Furthermore, the inoculation of *P. koreensis* MU2 boosted root and shoot length, plant biomass, and total chlorophyll in soybean plants (Adhikari et al. 2020). Singh et al. (2021) observed higher expression of *SuGLU*, *SuSOD*, *SuCHI*, and *SuCAT* genes (associated with biocontrol and stress response) in leaf tissues of smut susceptible sugarcane variety after inoculation with antagonistic strain *P. aeruginosa* B18 compared to control. Pathogen-related protein 1a (PR1a) was shown to be upregulated in *Solanum lycopersicum* treated with *P. aeruginosa* D4 when compared to the control (Durairaj et al. 2017). Shang et al. (2021) investigated the relative levels of expression of defense signaling marker genes (PR1 a/c, PR2, EFE26, H1N1, and ACC oxidase) in root and soil samples to increase an understanding of tobacco plants in response to pathogenic *Ralstonia solanacearum* after infecting *Pseudomonas* strains and results demonstrated that *Pseudomonas* strains aided tobacco plants in resisting *R. solanacearum* invasion by inducing systemic resistance (Shang et al. 2021).

**Pseudomonas exerts both direct and indirect plant-beneficial actions**

The growth-promoting mechanisms of *Pseudomonas* spp. are well-known. Production of growth regulators (phytohormones), mineral solubilization, siderophores production, phosphate solubilization, and protection of the plant from biotic and abiotic stresses by enzymes like 1-aminoacyclopropane-1-carboxylate (ACC) deaminase, chitinase, and production of osmolytes and exopolysaccharides are just a few of the important growth-promoting mechanism (Glick et al. 2007; Hayat et al. 2010; Przemieniecki et al. 2015) (Figure 2). All of the above-mentioned growth-promoting features may be uncommon among strains belonging to a single genus. Whereas, most *Pseudomonas* spp. were found to be positive for these primary growth-promoting characteristics (Indiragandhi et al. 2008). In contrast to many agrochemicals, antagonistic secondary metabolites generated by *Pseudomonas* strains against phytopathogens are biodegradable compounds (Bhattacharyya and Jha 2012).

(A)#Direct mechanisms

**Phytohormone production**

Bacteria, both free-living and symbiotic, promote plant growth by producing chemicals that are functionally identical to phytohormones generated by the plant. Some of the substances implicated in the control of biological processes essential for plant growth and development include auxins, cytokinins, gibberellins, ABA, and ethylene (Shah and Daverey 2020).

(l)#Auxins

Auxins are powerful compounds produced naturally by plants that participate in nearly all aspects of plant physiology, particularly cell division, expansion, differentiation, and stress relief (Paque and Weijers 2016). Whereas auxins are crucial plant growth regulators, IAA and the genes that govern its production are found in fungi and bacteria (Mat-suda et al. 2018). The indole-3-pyruvate (IPyA) pathway is preferred by beneficial rhizobacteria, but the indole-3-acetamide (IAM) pathway is preferred by pathogenic plant-linked bacteria (Ma et al. 2011). At low concentrations, bacterial auxins support the extension of primary plant roots, while at higher concentrations, auxins promote the production of lateral and adventitious roots that can increase mineral absorption and enhance the development of root exudates, which support bacterial growth (Verbon and Liberman 2016). Patten and Glick (2002) found enhanced root development in *Brassica napus* with *P. putida* strain GR12-2 when compared to plants injected with an IAA-deficient *P. putida* mutant. Auxins produced by bacteria may also defend against the detrimental effects of a range of environmental circumstances, including, salt, drought, and soil pollution (Kudoyarova et al. 2019). When compared to control
plants under Cd stress, switchgrass infected with *P. grimontii* Bc09, *P. veronii* E03, and *P. fluorescens* Oj24 yielded higher biomass and IAA while accumulating less Cd (Table 3) (Begum et al. 2019). Sugarcane plants inoculated with IAA-producing *P. aeruginosa* B18 grew better under smut pathogen stress (Table 4) and comprehensive genomic study also revealed the presence of trpABCDEG genes linked to IAA production in its genome (Singh et al. 2021) (Table 2).

(ii)#Cytokinin

Cytokinins are involved in many aspects of plant growth and development, such as embryogenesis, root and shoot apical activity control, vascular growth, root elongation, branching root, and nodule development, and apical dominance in response to environmental changes (Osugi and Sakakibara 2015). Under salt stress, cytokinin-producing bacteria like *Pseudomonas* spp. boosted root and shoot growth along with proline content in *Glycine max* tissues, according to Naz et al. (2009) (Table 3). Plant growth-promoting cytokinins are produced by rhizobacteria linked with *Coleus forskohlii*, including *P. putida* MTP40 and *P. putida* MTP50 (Patel and Saraf 2017). As biocontrol agents in Arabidopsis, cytokinins regulated the *P. fluorescens* strain G20-18 against *P. syringae* infection (Table 4) (Grobkinsky et al. 2016). The mechanisms of cytokinin production in bacteria are largely unknown. MiaA is likely to encode a tRNA (2)-isopentenyl pyrophosphate transferase, similar to tRNAIPTs, that are involved in the synthesis of cytokinins (Stringlis et al. 2018).

(iii)#Gibberellins

Seed dormancy, germination, quiescence, flowering, fruit ripening, root growth stimulation, and root hair abundance are all regulated by this set of compounds (Binenbaum et al. 2018). GAs, similar to auxins and cytokinins, are generated by bacteria and fungi as well as plants. To date, 136 chemical structures have been identified as naturally occurring gibberellins, the most prevalent of which is GA3 (gibberellic acid). In various investigations, bacteria-produced gibberellins have been demonstrated to boost plant growth and yield (Oleńska et al. 2020). Bacteria gibberellin production was affected by higher levels of glutamic acid, threonine, glycine phenylalanine, arginine, and proline, all of which could have a huge impact on inoculated crop growth (Kang et al. 2017). Gibberellin-like substances were found in the cell-free media of *P. fluorescens* (Lenin and Jayanthi 2012), *P. aeruginosa* (Katzenelson and Cole 1965), *P. monteilii* (Pandya and Desai 2014; Sandhya et al. 2010), and *P. koreensis* MU2 (Kang, Khan et al. 2019). *P. koreensis* MU2 inoculation improved shoot length (27%), shoot fresh (29%) and dry (33%) weight of GA deficient mutant waito-c (Kang, Adhikari et al. 2019).

(iv)#Abscisic acid

Abscisic acid (ABA) is a hormone that primarily inhibits growth and metabolic actions in crops, such as seed growth and maturation, initiation of seed and bud dormancy, senescence, protein, and suitable osmolyte synthesis, and regulation of the plant’s ability to stay alive in harsh and challenging situations (Shu et al. 2018). The ABA-synthesizing *P. putida* MTCC5279 coupled with *Cicer arietinum* gave salt and drought tolerance to their host plants by changing morpho-physiological and biochemical properties and regulating the activity of stress-responsive genes (Tiwari et al. 2016) (Table 3).

Figure 1. Effective colonization of antagonistic *Pseudomonas* strain in plants (A) Fungal pathogen, (B–C) Dual culture plate and agar well diffusion assay showing inhibition of fungal pathogen by antagonistic *Pseudomonas* strain, (D) Confocal laser scanning microscopy (CLSM) showing green fluorescent protein (GFP)-tagged *Pseudomonas* strain, and (E–F) Colonization of GFP-tagged *Pseudomonas* strain in root and leaf tissues of plants.
ACC deaminase, which lowers plant ethylene and ACC levels in plants, resulting in increased bacterial colonization/competitiveness (Conforte et al. 2010), bacterial nodulation ability (Nascimento et al. 2016), plant growth enhancement (Glick et al. 2007), and plant endurance to stresses (Nascimento et al. 2013).

### Phosphorus solubilization

Phosphorus (P) is an essential macronutrient for crop biological development and growth (Soetan et al. 2010). It could be found in soil in amounts of 400–1200 mg/kg. Despite a high concentration level, it has a very low soluble concentration, making it unavailable to plants. Phosphate solubilizing microorganisms (PSM) are well-known for their ability to transfer phosphorus from an insoluble to a soluble state, hence encouraging plant growth. Acidification, chelation, and exchange reactions are all common mechanisms for this conversion. P-solubilizing characteristics were found in *Pseudomonas* species obtained from soil and rhizospheres of diverse crops (Mishra et al. 2014; Li et al. 2017; De Boer et al. 2019). Ma et al. (2011) observed an increment in biomass yield and phosphorus intake in *Triticum aestivum* that had been treated with *Pseudomonas* spp. and Srivastava and Srivastava (2020) revealed that *Arabidopsis thaliana* infected with the phosphorus solubilizing bacteria *P. putida* MTCC 5279 thrived effectively in salt stress and P deficiency conditions with higher acidic and alkaline phosphatases activity, as well as significantly higher biomass. In *P. putida*, phosphate specific transport (pst) is employed for free inorganic phosphate transport, and it is made up of *pstABC* genes with a two-component phosphate uptake signal transduction system that comprises *phoP/phoR* (Table 2) (Gupta et al. 2014). Singh et al. (2021) reported presence of *pstABC* and *phoBDHRU* genes in *P. aeruginosa* B18 genome (Table 2).

### Potassium solubilization

Potassium (K) is a necessary nutrient for plant development. If there is inadequate potassium, the plants’ roots will be underdeveloped, they will grow more slowly, the seeds formed will be few, and the productivity will be decreased (Mcafee 2008), and the plants will become more susceptible to diseases and pests (Troufflard et al. 2010). Many microbes in the rhizosphere are critical for the release of potassium from different insoluble potassium components present in soil and surrounding systems. Several studies have found

### Table 2. Plant growth-promoting and stress-related genes in *Pseudomonas* strains’ genomes.

| PGP- traits       | *Pseudomonas* strains | Gene                      | References               |
|-------------------|-----------------------|---------------------------|--------------------------|
| Phosphorus        | **metabolism**        | **P. psychrotolerans** CS1 | **phoBHRU**              | Kang et al. (2020)  |
|                   |                       | **P. putida**             | **pstABC**               | Gupta et al. (2014) |
|                   |                       | **P. aeruginosa**         | **psxABC**               | Singh et al. (2021) |
|                   | **Nitrogen**          | **P. psychrotolerans** CS1 | **nprB**                 | Kang et al. (2020)  |
|                   |                       | **P. aeruginosa**         | **ntrB**                 | Singh et al. (2021) |
|                   | **Plant hormones**    | **P. chlororaphis subsp.** | **nirQ**                 | Zhang et al. (2020)  |
|                   |                       | **P. aeruginosa**         | **nibB**                 | Singh et al. (2021) |
|                   | **Siderophore**       | **P. psychrotolerans** CS1 | **Fes**                  | Kang et al. (2020)  |
|                   |                       | **P. putida**             | **Pvd**                  | Gupta et al. (2014) |
|                   |                       | **P. aeruginosa**         | **Fes**                  | Lamont et al. (2006) |
|                   |                       | **P. aeruginosa**         | **Ftva**                 | Duan et al. (2013)  |
|                   |                       | **P. psychrotolerans** CS1 | **PvdYII**               | Nelkner et al. (2019) |
|                   |                       | **P. putida**             | **acdS**                 | Singh et al. (2021) |
|                   |                       | **P. aeruginosa**         | **acdS**                 | Singh et al. (2021) |
|                   |                       | **P. aeruginosa**         | **acdS**                 | Singh et al. (2021) |
|                   |                       | **P. psychrotolerans** CS1 | **acdS**                 | Singh et al. (2021) |
|                   |                       | **P. putida**             | **acdS**                 | Singh et al. (2021) |
|                   |                       | **P. aeruginosa**         | **acdS**                 | Singh et al. (2021) |
|                   | **Biofilm formation** | **P. aeruginosa**         | **Efp**                  | Singh et al. (2021) |
|                   |                       | **P. aeruginosa**         | **Efp**                  | Singh et al. (2021) |
|                   |                       | **P. psychrotolerans** CS1 | **Efp**                  | Singh et al. (2021) |
|                   |                       | **P. putida**             | **Efp**                  | Singh et al. (2021) |
|                   |                       | **P. aeruginosa**         | **Efp**                  | Singh et al. (2021) |
|                   | **Root colonization** | **P. aeruginosa**         | **minCDE**               | Singh et al. (2021) |
|                   |                       | **P. chlororaphis subsp.** | **yijB**                 | Singh et al. (2021) |
|                   |                       | **P. psychrotolerans** CS1 | **xerC**                 | Zhang et al. (2020)  |
|                   |                       | **P. aeruginosa**         | **xerD**                 | Singh et al. (2021) |
|                   |                       | **P. putida**             | **xerD**                 | Singh et al. (2021) |
|                   |                       | **P. aeruginosa**         | **xerD**                 | Singh et al. (2021) |
|                   |                       | **P. psychrotolerans** CS1 | **xerD**                 | Singh et al. (2021) |
|                   |                       | **P. putida**             | **xerD**                 | Singh et al. (2021) |
|                   | **Phenazine**         | **P. aeruginosa**         | **phzA, B**              | Gupta et al. (2014) |
|                   |                       | **P. putida**             | **phzF**                 | Gupta et al. (2014) |
|                   | **Superoxide dismutase** | **P. aeruginosa**         | **SODA**                 | Singh et al. (2021) |
|                   |                       | **P. putida**             | **sodBC**                | Gupta et al. (2014) |
|                   | **Peroxidase**        | **P. putida**             | **oxrR**                 | Gupta et al. (2014) |
|                   |                       | **P. psychrotolerans** CS1 | **CopABCD**              | Kang et al. (2020); Cooksey (1993) |
**Pseudomonas** to be potassium-solubilizing bacteria (Yadav et al. 2017).

**Zinc solubilization**

In plants, zinc is directly implicated in carbohydrate metabolism, cytochrome production, and superoxide radical removal; it also functions as a cofactor in a variety of enzyme activities, ribosomal fraction stabilization, growth-promoting hormone production, cell membrane integrity, floral tissue formation, and pollen tube growth, etc. (Kamran et al. 2017). Reduced plant growth, wilting of floral parts, reduced leaf size, and poor seed quality, pollen development, and root growth are all symptoms of zinc deficiency (Cakmak 2000). Zinc deficiency can be alleviated by using zinc solubilizing rhizobacteria (ZSR), which are effective at mobilizing zinc complexes in the soil and so resolving plant zinc deficiency (Khan et al. 2019). Applying specific *Bacillus, Pseudomonas,* and *Serratia* species resulted in greater zinc mobilization in wheat (7–12%) and soybeans, according to numerous research (Lefevre et al. 2014). In pot experiments, Goteti et al. (2013) observed that bacterizing maize seedlings with a Zn-solubilizing *Pseudomonas* strain boosted Zn uptake and concentration substantially. Sunithakumari et al. (2016) reported that *Stenotrophomonas, Mycobacterium, Enterobacter, Pseudomonas,* and *Xanthomonas,* among other rhizobacteria isolated from banana, chili, bean, groundnuts, maize, sorghum, and tomato plants, have substantial *in vitro* Zn solubilization capacities. Zinc solubilizing properties and improved Zn absorption were reported after *Pseudomonas* strains were inoculated into rice plants (Joshi et al. 2013).

**Siderophore production**

Bacteria produce siderophores which are small organic molecules that improve iron absorption in iron-deficient conditions. Like PGPR, *Pseudomonas* sp. confronts its ion requirement by consuming siderophores formed by several other rhizosphere microorganisms. To boost the quantity of iron available in its native habitat, *P. putida* employs heterologous siderophores produced by other microorganisms (Rathore 2015). In host plants, bacterial siderophores influence iron homeostasis, immune function, and growth (Hesse et al. 2018b). For example, the siderophore pyoverdine analog (apo-pyoverdine) of *P. fluorescens* strain C7R12 impacts the expression of roughly 2000 genes in *A. thaliana* (Trapet et al. 2016). Many genes involved in the production of iron-mobilizing phenolic compounds were discovered to be positively activated in *A. thaliana* colonized by *P. fluorescens* WCS417. Bacterial strains that can produce a large number of siderophores were less inhibited by elevated copper concentrations, and the fraction of siderophore-synthesizing strains grew in lockstep with the ion gradient (Hesse et al. 2018b). Similarly, *P. aeruginosa* ZGKD3, Cd (II), and Zn (II) boosted overall siderophore production, such as pyoverdine (Shi et al. 2017). Gupta et al. (2014) found acrAB, _flu, fpvA, mbtH,* and _pvd* genes in *P. putida* genome. Kang et al. (2020) found entFS, _fepBCDG,* and _fes* genes in *P. psychrotolerans* CS51 genome, participating in siderophore synthesis.

**Biological nitrogen fixation**

Biological nitrogen fixation (BNF) is the mechanism through which nitrogen-fixing bacteria use a complex enzyme system called nitrogenase to convert atmospheric elemental nitrogen into plant usable forms (Masson-Boivin and Sachs 2018). Nonsymbiotic nitrogen fixation, which involves members of the *Arthrobacter, Acetobacter, Clostridium, Azotobacter, Bacillus,* and *Pseudomonas* genera (Dinnage et al. 2019), and symbiotic nitrogen fixation, which involves members of the Rhizobiaceae family with leguminous plants (Martins et al. 1999). Li et al. (2017) reported *P. koreensis* and *P. entomaphila* strains as a nitrogen-fixing strain in sugarcane. The fixation of elemental nitrogen by beneficial soil microbes like PGPR accounts for a large portion of the elemental nitrogen that enters the soil under natural settings (Ji et al. 2019). Thus, plant-microbe interactions via BNF play a significant role in the formation of organic fertilizers (Kuypers et al. 2018). The gene _nifU_ is required for nitrogen fixation and is involved in the construction of the Fe-S

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**Figure 2.** Plant growth-promoting mechanisms of *Pseudomonas* strains.
Table 3. List of Pseudomonas strains in abiotic stress management in various crops.

| Abiotic stress | Concentration | Pseudomonas strains | Bacterial traits | Crops | Conditions | Plant responses to inoculants | References |
|----------------|---------------|---------------------|------------------|-------|------------|-------------------------------|------------|
| Drought        | –             | *P. chlororaphis*   | Secretion of volatile compounds 2R, 3R butanediol | Arabidopsis | Pots | Increased plant growth | Cho et al. (2008) |
|                | –             | *P. putida*         | Production of EPS | Sunflower | Pots | Improved plant life, biomass, and the ratio of root adherent soil/root tissue | Sandhya et al. (2009) |
|                | –             | *P. aeruginosa*     | Production of EPS | Okra | Pots | Increment of water and moisture content in the soil | Yadav et al. (2018) |
|                | –             | *P. aeruginosa*     | Production of EPS and catalase | Maize | Pots | Increment of water and moisture content in the soil | Naseem and Bano (2014) |
|                | –             | *P. aeruginosa*     | Production of EPS and P-solubilization | Maize | Pots | Increased soil aggregates constancy | Putrie et al. (2013) |
|                | –             | *P. syringae, P. putida, P. stutzeri, and P. monteilli* | Production of IAA, gibberellic acid, siderophore, HCN, and ammonia, and P-solubilization | Maize | Pots | Increased normal weight diameter of root-adhering soil and soil aggregates firmness | Sandhya et al. (2018) |
|                | –             | *P. fluorescens*    | EPS production and P-solubilization | Wheat | Pots | Improved plant growth and biomass, relative water content, and nutrient uptake | Khan et al. (2017) |
|                | –             | *P. libanensis*     | P-solubilization, ACC deaminase activity, and production of IAA, siderophore, and ammonia | Wheat | Laboratory and pots | Increased plant growth and physiological parameters | Kour et al. (2019) |
|                | –             | *Pseudomonas sp.*   | Auxin production | Wheat | Pots | Enhanced vegetative growth and yield | Raheem et al. (2018) |
|                | –             | *P. putida*         | Gibberellic's production | Wheat | Pots | Antioxidant activity | Kang et al. (2014) |
| Salt           | 100 mM NaCl   | *P. simiae*         | Biofilm | Soybean | Pots | Increased shoot and root length, leaf area, and trifoliate leaf count | Vaishnav et al. (2016) |
|                | 200 mM NaCl   | *Pseudomonas sp.*   | – | Soybean | Laboratory | Enhanced root and shoot growth and biomass with a higher number of lateral roots | Kasotia et al. (2016) |
|                | 120 mM NaCl   | *P. putida*         | Production of gibberellins, ABA, JA, and salicylic acid | Soybean | Pots | Increased shoot length, fresh weight, and chlorophyll content | Kang et al. (2014) |
|                | 200 mM NaCl   | *P. putida*         | IAA production and P-solubilization | Soybean | Pots | Phosphorus and nitrogen acquirement, nodule formation, and root system physiology | Egamberdieva et al. (2017) |
|                | 100 mM NaCl   | *P. simiae*         | IAA and siderophore production, and phosphate solubilization | Soybean | Pots | Improved soybean seed germination and growth | Vaishnav et al. (2016) |
|                | 100 mM NaCl   | *P. simiae*         | – | Soybean | Laboratory | Increment in chlorophyll and proline content and decrease in accumulation of root Na+ | Vaishnav et al. (2015) |
|                | 600 mM NaCl   | *Pseudomonas sp.*   | Production of β-1-3 glucanase, chitinase, siderophore, HCN, pyocyanin, and IAA, and phosphate solubilization | Sunflower | Pots and field | Increased plant growth | Tewari and Arora (2016) |
|                | 100 mM NaCl   | *P. fluorescens*    | Production of siderophore and IAA K+/Na+ ratio | Sunflower | Pots | Decreased accumulated Na+ and increased biomass and K+ content | Shilev et al. (2012) |
|                | 150 mM NaCl   | *P. anguilliseptica* | Biofilm formation and EPS production | Faba bean | Pots | | Mohammed (2018) |

(Continued)
Table 3. Continued.

| Abiotic stress | Concentration | Pseudomonas strains | Bacterial traits | Crops | Conditions | Plant responses to inoculants | References |
|----------------|---------------|---------------------|------------------|-------|------------|-------------------------------|------------|
| 100 mM NaCl    | P. extremorientalis and P. aeruginosa | IAA production | Wheat | Laboratory | Protection of root by improving biofilm constancy | Egamberdieva (2009) |
| 171 mM NaCl    | P. aeruginosa and P. aurantiaca | Phosphate solubilization, production of IAA, HCN, ammonia, phenol, and free amino acids | Groundnut | Pots | Increased leaf area | Ghori et al. (2015) |
| 100 mM NaCl    | Pseudomonas sp. | ACC deaminase activity, phosphate solubilization, and IAA production | Groundnut | Pots | Preserved ion homeostasis and increased seedling growth | Sharma et al. (2016) |
| 100 mM NaCl    | P. Chlororaphis and P. putida | IAA production | Cotton seed | Pots | Improved seed germination and seedling growth | Egamberdieva et al. (2015) |
| –              | P. putida      | IAA production | Cotton seed | Pots and field | Increased germination rate and biomass | Yao et al. (2010) |
| 171 mM NaCl    | P. fluorescens and P. putida | Production of IAA and HCN and ACC deaminase activity | Rape seed | Laboratory | Increased seedling growth | Jalili et al. (2009) |
| 250 mmol NaCl  | P. putida      | ACC deaminase activity | Rape seed | Laboratory | Increased antioxidant enzymes activity and pathogenesis-related responses | Cheng et al. (2012) |
| 90 mmol NaCl   | P. putida      | ACC deaminase activity | Tomato | Pots | Improved Toc-GTPase expression and shoot growth | Yan et al. (2014) |
| 300 mM NaCl    | Pseudomonas sp. | Potassium solubilization | Wheat | Pots | Increased K uptake | Pirhadi et al. (2016) |
| 300 mM NaCl    | Pseudomonas sp. | Production of siderophore and phytohormones and cellulolytic activity | Beet | Pots | Improved root length and biomass (dry) | Piernik et al. (2017) |
| Heat           | –              | P. putida | Antioxidant activity | Wheat | Pots | Enhanced root and shoot length, dry biomass, tiller, spikelet, and grain formation | Ali et al. (2011) |
| Metal          | 400 mg kg\(^{-1}\) Zinc (Zn) | P. brassicacearum | Metal-chelating molecules | Brown mustard | Pots | Improved root accumulation and resistance to Zn | Adediran et al. (2016) |
|                | 1500 mg kg\(^{-1}\) Zn | P. aeruginosa | Production of IAA and siderophore and P- solubilization | Wheat | Pots | Enhanced P and N uptake, total soluble protein, and biomass | Islam et al. (2014) |
|                | 500 mg kg\(^{-1}\) Copper (Cu) | P. brassicacearum | Production of IAA and siderophore and ACC deaminase activity | Black medick | Pots | Increased growth, total dry biomass, root weight, and root nodules number | Kang et al. (2017) |
|                | 8.6 mg L\(^{-1}\) Arsenic (As), 4.2 mg L\(^{-1}\) Cadmium (Cd), 3.7 mg L\(^{-1}\) Cu, 14 mg L\(^{-1}\) Lead (Pb), and 18 mg L\(^{-1}\) Zn | P. koreensis | ACC deaminase activity, P- solubilization, and nitrogen fixation | Chinese silver grass | Pots | Improved biomass, height, number of culms, chlorophyll, and protein content | Babu et al. (2015) |

cluster (Smith et al. 2005). Kang et al. (2020) identified the norB gene in P. psychrotolerans CS51’s genome (Table 2).

**Exopolysaccharide production**

Exopolysaccharides (EPS) are biodegradable polymers with a large molecular mass that are formed by a wide range of bacteria, algae, and plants from monosaccharide residue and derivative (Sanlibaba and Cakmak 2016). EPSs are directly responsible for plant growth and crop production by preserving water content, accumulating soil particles, maintaining necessary interaction between plant roots and rhizobacteria, and supporting the host under stress situations (Panwar et al. 2016). Bacteria release EPS, which are responsible for bacterial adhesion to soil particles and root surfaces, typically in collaboration with other bacteria. EPS links soil particles to combined, improving water retention and cation exchange capacity while also stabilizing soil structures (Upadhyay et al. 2011). Environmental fluctuations, water, and nutrient absorption, and epiphytic colonization are all protected by the contained matrix of microcolonies that EPS creates (Balsanelli et al. 2014). In the legume-rhizobia symbiosis, they are also essential for complete biofilm generation and the development of functional nodules (Skorupska et al. 2006). Inoculating EPS-producing P. mendocina onto Lactuca sativa including an arbuscular mycorrhizal fungus,
Table 4. List of antagonistic *Pseudomonas* strains against different plant pathogens.

| Crops          | *Pseudomonas* strains | Pathogens                                      | Bacterial traits                                                      | Conditions            | Plant responses to inoculants                                      | References         |
|----------------|-----------------------|------------------------------------------------|-----------------------------------------------------------------------|-----------------------|-------------------------------------------------------------------|--------------------|
| Tomato         | *P. fluorescens*      | *Ralstonia solanacearum*                        | Antibiosis                                                           | Pots and field        | Improved plant growth                                              | Mohandas et al. (2010) |
|                | *P. fluorescens*      | *Fusarium oxysporum* f. sp. lycopersici         | Siderophore production                                               | Pots                  | Increased plant height and weight                                  | Kannan and Surendar (2009) |
|                | *P. fluorescens*      | *Fusarium oxysporum* f. sp. lycopersici         | IAA production and induced systemic resistance                      | Pots                  | Increased shoot length and protein content                         | Srivastava et al. (2010) |
|                | *Pseudomonas sp.*     | *Fusarium oxysporum* f. sp. lycopersici         | Siderophore and rhizomorph production and P-solubilization          | Pots and field        | Enhanced shoot length, and fresh and dry shoot weight              |                    |
|                | *Pseudomonas sp.*     | *Ralstonia solanacearum*                        | –                                                                    | Pots                  | Pathogen growth suppression and competition for resources          | Hu et al. (2016)     |
| Banana         | *P. fluorescens*      | *Fusarium oxysporum* f. sp. cubense             | –                                                                    | Pots and field        | Plant growth promotion                                              | Mohandas et al. (2010) |
|                | *P. fluorescens*      | *Fusarium oxysporum* f. sp. cubense             | Production of defense-related enzymes and induced systemic resistance | Pots and field        | Plant growth promotion                                              | Kavino and Manoranjitham (2017) |
|                | *P. aeruginosa*       | *Fusarium oxysporum* f. sp. cubense             | Chitinase and 2,4-diacyltlyphloroglucinol production                | Pots                  | –                                                                 | Wong et al. (2019)   |
|                | *Pseudomonas sp.*     | *Fusarium oxysporum* f. sp. cubense             | Production of stress-related enzymes, and pathogenesis-related proteins | Pots                  | Increased total leaf count, plantlets height, pseudostem diameter, and chlorophyl content | Mohd Fishal et al. (2010) |
| Rice           | *Pseudomonas sp.*     | *Xanthomonas oryzae*                            | Production of siderophore and IAA, P-solubilization, peroxidase, phenylalanine-ammonia lysis, and polyphenol-oxidase activity | Pots                  | Decreased diseased leaf area, increased root and shoot length, and plant dry weight |                    |
|                | *P. baetica*          | *Fusarium oxysporum*, *Alternaria sp.*, and *Curvularia sp.* | Production of pectinase and P-solubilization                         | Laboratory            | Increased growth of seedlings and root hairs formation              | Verma et al. (2018)  |
| Maize          | *P. putida*           | *Fusarium verticillioides*                      | –                                                                    | Laboratory            | Inhibition of fungal growth and colonization                        | Niu et al. (2017)    |
| Potato         | *P. fluorescens*      | *Ralstonia solanacearum*                        | Antibiosis                                                           | Laboratory – Pots     | Enhanced growth of plantlets height, and seedlings and root hairs formation |                    |
|                | *P. chlororaphis*     | *Phytophthora infestans*                        | Competition (siderophores) and antibiotic (phenazines and HCN)      | –                     | –                                                                 |                    |
|                | *P. aeruginosa*       | *Rhizoctonia solani*                            | Unknown mechanisms                                                   | –                     | Increased potato yield                                              | Mohabat et al. (2015) |
| Peanut         | *P. fluorescens*      | *Sclerotium rolfsi*                             | Antimicrobial compounds production                                  | –                     | –                                                                 | Lohitha et al. (2016) |
| Soybean        | *P. aeruginosa*       | *Macrophomina phaseolina* and *Sclerotinia sclerotiorum* | Chitinase β-1,3 glucanase, cellulase, ammonia, and siderophore production | Pots                  | Enhanced seed germination, seedling vigor index, and chlorophyl content | Thakkar and Saraf (2014) |
| Sugarcane      | *P. aeruginosa*       | *Sporisorium scitamineum*                       | Produced antimicrobial compounds, enzymes i.e. β-1,3-glucanase, chitinase, protease, and cellulase, ammonia, IAA, HCN, and siderophore, and ACC deaminase activity | Pots                  | Increased sugarcane growth                                         | Singh et al. (2021)  |
|                | *P. putida*           | *Colletotrichum falcatum*                       | IAA and HCN production and phosphate solubilization                | Pots                  | Increased sugarcane growth                                         | Kishore et al. (2017) |
|                | *P. monteilii*        | *Sporisorium scitamineum* and *Ceratocystis paradoxa* | Nitrogen fixation, IAA and siderophore production, ACC deaminase activity, and P-solubilization | –                     | –                                                                 | Li et al. (2017)    |
|                | *P. putida*           | *Sporisorium scitamineum* and *Ceratocystis paradoxa* | Nitrogen fixation, IAA, siderophore, ammonia, and HCN production, ACC deaminase activity, and P-solubilization | –                     | –                                                                 | Li et al. (2017)    |
|                | *P. koreensis*        | *Sporisorium scitamineum* and *Ceratocystis paradoxa* | Nitrogen fixation, IAA, siderophore, ammonia, and HCN production, ACC deaminase activity, and P-solubilization | –                     | –                                                                 | Li et al. (2017)    |
|                | *Pseudomonas sp.*     | *Sporisorium scitamineum* and *Ceratocystis paradoxa* | Nitrogen fixation, IAA, siderophore, ammonia, and HCN production, ACC deaminase activity, and P-solubilization | –                     | –                                                                 | Li et al. (2017)    |
|                | *P. plecoglossicida*  | *Ceratocystis paradoxa*                         | Nitrogen fixation, IAA, siderophore, and ammonia production, ACC deaminase activity, and P-solubilization | –                     | –                                                                 | Li et al. (2017)    |
|                | *P. taiwanensis*      | *Ceratocystis paradoxa*                         | Nitrogen fixation, IAA, siderophore, and HCN production, ACC        | –                     | –                                                                 | Li et al. (2017)    |

(Continued)
Reactive oxygen species (ROS; comprising superoxide $O_2^\cdot$, hydroxyl radical OH·, hydrogen peroxide $H_2O_2$, and others) are produced as a metabolic byproduct in plants and serve mainly as signaling molecules. Plants growing under stress produce more ROS, which causes DNA damage, redox state changes, abnormal protein formation, denaturation of membranous proteins, lipid peroxidation, membrane fluidity reduction, interference with enzymatic activity, and overall cell homeostasis, leading to cell damage and in extreme cases plant cell death (Halo et al. 2015). Enzymatic antioxidants i.e. ascorbate peroxidase (APX), catalase (CAT), superoxide dismutase (SOD), etc., and non-enzymatic antioxidants (ascorbic acid, glutathione, GSH, tocopherols, etc.) both contribute to mitigating ROS and hence defend plant cells from oxidative stress. In this context, PGPRs use their antioxidant enzyme system to protect plants from oxidative stress. Inoculating rice with *P. fluorescens* increases the activities of POD, APX, SOD, and CAT, which helps to alleviate salt stress (Singh et al. 2020). Singh et al. (2021) discovered multiple oxidoreductase genes i.e. KatE, osmC, and SODA in the genome of *P. aeruginosa* B18, indicating that this bacterium can boost plant development in the presence of smut pathogen (Table 2). Also, genes for SOD (sodBC), POD (osmC and oxyR), and CAT synthesis were discovered in the *P. putida* genome (Table 2) (Gupta et al. 2014).

**Production of cell-wall-degrading enzymes**

The synthesis of hydrolytic enzymes i.e. chitinases, cellulases, proteases, glucanases, and others capable of hydrolyzing polymeric materials such as cellulose, hemicellulose, chitin, cell wall proteins, and so on, was discovered to be capable of preventing a range of plant diseases. (Mabood et al. 2014). PGPR generates and excretes a variety of hydrolytic enzymes and these enzymes' defense-related actions have been demonstrated against a variety of phytopathogens. Chitin is a structurally important component of the fungal cell wall. PGPR attacks fungal cell walls by secreting chitinolytic enzymes, which cause chitin breakdown. In this way, chitinolytic bacteria *P. aeruginosa* B18 inhibits fungal pathogens like *S. scitamineum* sugarcane pathogen (Singh et al. 2021) and improves plant growth indirectly. Rhizobacteria that produce cellulase rapidly hydrolyze cellulose to glucose by the synergistic effects of enzymes such as glucanases, hydrolases, and glucosidas (Siqueira et al. 2020). By degrading cellulose wastes, cellulolic bacteria can provide a source of carbon in the soil rhizosphere, which enhances soil quality and preserves nitrogen balance (Behera et al. 2017). These bacteria that produce cellulose are also used in the biological biomass conversion to biofuels (Siqueira et al. 2020). Cellulase-mediated conversion techniques are deemed greener and more environmentally benign than chemical conversions. *P. fluorescens* LPK2 and *Sinorhizobium fredii* KCC5 generate beta-glucanases and chitinases to inhibit *Fusarium*
oxysporum and F. udum, causing Fusarium wilt disease (Ramadan et al. 2016). Numerous hydrolase genes such as bgIBX, floE2, gdhA, malQ, and ribA were recognized in the genome of P. aeruginosa B18 (Table 2) (Singh et al. 2021). Similarly, chitinase genes were found in the P. putida genome (Table 2) (Gupta et al. 2014).

**Volatile organic compounds (VOCs)**

VOCs formed by bio-control strains enhance plant growth, suppress bacterial, fungal, and nematode diseases, and establish systemic resistance in plants to plant pathogens (Raza et al. 2016). Volatile organic compounds (VOCs) produced by PGPR have been shown to boost plant development, ensuing in improved shoot biomass and changed stress reactions. More research is needed to understand how plants perceive volatile and the mechanisms that result from this perception (Bailey and Weiskopf 2012). Plants and other rhizosphere microorganisms interact with each other in the rhizosphere, PGPR produces VOCs with varying roles and functions (Bitas et al. 2013). VOCs have a dual direct and indirect influence during plant growth-promoting activities, as per a deep investigation (Santoyo et al. 2019), suggesting that rhizosphere VOCs can either directly or indirectly boost plant development by reducing the growth of plant pathogens. A putative VOCs produced by P. simiae AU improved soybean salt resistance by reducing root Na⁺ (100 mM NaCl) buildup and boosting proline and chlorophyll levels (Vaishnav et al. 2015). Hence, these VOCs cause increased phosphate accessibility in the rhizosphere, which benefits the plants that are affected (Kumari et al. 2018).

**Hydrogen cyanide**

HCN producing traits have a significant impact on plant establishment by suppressing fungal infections (Aarab et al. 2019). HCN produced by PGPR works as a biocontrol agent but also contributes to geochemical processes in the substrate, like metal chelation. Many biocontrol PGPR are capable of producing hydrogen cyanide (HCN) (Santoyo 2012). Many strains of Pseudomonas species, including P. aeruginosa, P. koreensis, and P. entomophila, showed good HCN production as well as biocontrol effectiveness against various sugarcane diseases (Singh et al. 2021; Li et al. 2017). HCN produced by PGPR appears to work in combination with other biocontrol techniques employed by the same bacteria. The capacity of HCN to inhibit cytochrome c oxidase and other key metalloenzymes contributes to its toxicity (Nandi et al. 2017). Strain P. fluorescens CHA0 generates HCN, which adds significantly its biocontrol potential. Anaerobic regulator (ANR) and global activator (GacA) are necessary for the maximum expression of hcnABC genes involved in HCN biosynthesis in P. fluorescens (Blumer and Haas 2000). Nelkner et al. (2019) detected gene clusters (hcnABC) encoding HCN in P. brassicacearum 3Re2-7 genome (Table 2).

**Antibiosis**

Strains of Pseudomonas genera play an important role in suppressing harmful microbes by generating antibiotics. Over the last two decades, the synthesis of antibiotics by PGPR has been one of the most successful and well-studied bio-control techniques for a variety of plant diseases (Islam et al. 2016). Many Pseudomonas species synthesize a broad range of antimicrobial compounds i.e. phenazines, pyrrolnitrin, phenazine-1-carboxamide, phenazine-1-carboxylic acid (PCA), 2,4 diacetylphloroglucinol (DAPG), rhamnolipids, pyoluteorin, oomycin A, ecomycins, viscosinamide, cepaciamide A, pyocyanin, butyrolactones, N-butylnenzene sulphonamide, phenamonic acid, azomycin, cepafungins, FR901463, and Karalicine (Ramadan et al. 2016).

2,4-Diacetylphloroglucinol (DAPG), which is mostly generated by Pseudomonads, is one of the most extensively studied and effective antibiotics. DAPG causes membrane damage and inhibits the generation of zoospores in Pythium sp., as well as controlling bacterial canker disease in tomato plants (Lanteigne et al. 2012). Pseudomonads also synthesize phena/ne antibiotics with redox activity that can control phytopathogens such as Gaeumannomyces graminis and F. oxysporum. Overuse of antibiotic-producing PGPR for harmful microorganism growth enhancement and biocontrol has led to the establishment of the induced systemic resistance (ISR) mechanism in many plant pathogens, subsequently tolerance to particular antibiotics because of these strains’ increased dependence. Phenazines derived from Pseudomonas strains via functional group substitution on the core phenazine’s ring structure, i.e. PCA. For PCA synthesis, the phenazine biosynthetic operon (phzXY-FABC) is essential (Mavrodi et al. 2010). The phzO gene encoding monooxygenase in P. chlororaphis 30–84 converts few PCA to 2OHPCA (Pierson and Pierson 2010). The genome of P. aeruginosa PA01 contains numerous phenazine modifying genes that convert PCA into four additional phe/nazine derivatives: phenazine-1-carboxamide (PCN), 5-methyl-phenazine-1-carboxylic acid (SMPCA), and 1-hydroxy-phenazine (1OHPZ) via phzH, phzM, and phzS activities, respectively (Mavrodi et al. 2006). Gupta et al. (2014) discovered the phzE gene (responsible for phenazine synthesis) in the genome of P. putida (Table 2). Moreover, the PltB gene (responsible for pyoluteorin synthesis) from P. putida strain NH-50 was amplified and sequenced (Hassan et al. 2011).

**Induced systemic resistance**

Induced resistance is a physiological condition of enhanced defensive ability produced by specific environmental stimuli, which leads to the strengthening and stimulation of the plant’s innate defense mechanism against subsequent pathogenic attacks. Plants that have been bio-primed with PGPR develop systemic resistance to a variety of plant diseases (Nazzin et al. 2013). PGPR plays a role in activating ISR in a plant’s rhizosphere (Pieterse et al. 2014). Ethylene and jasmonate signaling are implicated in ISR; both of these hormones play an important role in strengthening plant defense responses against a wide range of phytopathogens (Bukhat et al. 2020). Several bacterial components, including homoserine lactones, DAPG, 2, 3-butanediol, LPS, acetoin, siderophores, cyclic lipopeptides, and flagella, are participating in ISR (Torres-Cortés et al. 2018). Rhizobacteria-mediated ISR initiation in crops stimulates the production of antimicrobial substances including benzoxazinoids and coumarin, further increasing the activation of ISR-triggering strains (Hu et al. 2018; Stringlis et al. 2018). Hence, over
thousands of generations, plant immune systems can be modified to recruit microbes for plant resistance. ISR has been researched in several rhizobacteria-inoculated plants and, as first established by Van Peer and Schippers (1992), protected plants against the fungal disease *Fusarium oxysporum* f. sp. *dianthi* by utilizing *P. fluorescens* strain WCS417r. Plant defense systems can be induced by pre-treatment with a suitable PGPR, allowing the plant to respond faster and more powerfully to a future pathogen attack. ISR does not specifically target pathogens but rather primes the plant against a variety of diseases, and it is not just produced at the site of induction.

**Biofilm production**

Biofilms are extracellular matrices that are made up of exopolysaccharides, proteins, nucleic acids, lipids, and microbes embedded in them (Zboralski, Filion 2020; Danhorn and Fuqua 2007). *Pseudomonas* is a well-studied biofilm-producing bacterium genus. Dekkers et al. (1998) have shown that lipopolysaccharides (LPS), particularly the O-antigen, can play essential roles in root tip colonization in *Pseudomonas* sp. Some of these organisms have clinical applications, but this ability also permits rhizospheric bacteria to cling to plant root surfaces (Danhorn and Fuqua 2007). Once linked to the plant roots, PGPR may more easily exert their helpful mechanisms towards the plant; PGPR with good biofilm formation boost their plant growth-promoting activities, even in the presence of environmental stress (Meena et al. 2017).

The creation of a biofilm matrix takes place in stages. Microorganisms initially stick to a surface in what is known as primary adhesion; these microorganisms contain distinct cellular features such as pili or flagella and enzymes known as adhesins that aid this adherence. Motility can assist bacteria to resist the hydrophobic forces that repel them off surfaces. In the second stage, the bacteria that successfully adhere begin to divide, spread around the initial spot, and establish microcolonies. The following stage involves the secretion of various exopolysaccharides by microbes such as alginites, celluloses, N-acetylglucosamines, and galactose. Finally, the microcolonies embedded in the exopolymer matrix begin to liberate themselves from the matrix, and the process may be repeated at a different location (Zboralski, Filion 2020). A biofilm frequently provides enhanced capacity to the microorganisms that are incorporated. Because its constituents may coordinate operate as osmoprotectants, biofilms formed by PGPR protect plants subjected to stress conditions such as drought and high salinity (Rojas-Solis et al. 2020). *P. aeruginosa* B18 genome contained genes that take part in biofilm development such as *efp*, *flgBCDEFGHl*, *hfg*, and *motA* (Table 2) (Singh et al. 2021). Biofilm-related genes were also reported in the genomes of *P. chlororaphis* subsp. *aurantiaca* JD37, *P. aeruginosa* PAO1, and *P. polymyxa* (Table 2) (Zhang et al. 2020).

**Pseudomonas sp. in the alleviation of biotic and abiotic stresses**

Several experiments conducted and analyzed by different scientists showed that *Pseudomonas* spp. inoculation can promote plant development in both normal (Zahir et al. 2004; Cummings 2009; Hayat et al. 2010) and stressful environments (Glick et al. 2007; Nadeem et al. 2016). This tremendous performance of *Pseudomonas* spp. was due to their particular characteristics and environmentally friendly traits which enable them to survive under stress conditions and exhibit their potential regarding agricultural and environmental issues (Figure 3).

*P. aureofaciens*, *P. aeruginasa*, *P. brassicacearum*, *P. chlororaphis*, *P. fluorescens*, and *P. putida* are the most commonly reported *Pseudomonas* species that include plant beneficial rhizospheric strains (Nadeem et al. 2016). Some research suggests that rhizobacterial colonization causes changes in ROS and secondary product metabolism, which may help the plant guard against or mitigate the impact of pathogen infections (Rashid and Chung 2017). *Pseudomonas* strains implicated in phytopathogen inhibition generate antimicrobial compounds i.e. HCN, PCA, and pyrurolnitin, reducing iron accessibility, along with cell-wall degrading enzymes that help in the breakdown of pathogen cell walls, preventing harmful pathogens growth and disease suppression (Bhattacharyya and Jha 2012; Mabood et al. 2014; Li et al. 2017; Singh et al. 2021). One of the most varied bacterial complexes in the genus *Pseudomonas* is the *P. fluorescens* complex, including more than 50 species that are adequately recognized and a considerable number of unidentified isolates (Garrido-Sanz et al. 2017). This complex’s strains have been isolated from a variety of plant-related habitats, and many species can be considered beneficial since they are defined as PGPR or reduce phytopathogen consequences (Raaijmakers et al. 2009).

**Abiotic stress**

Abiotic stress harms plant morphological, physiological, and biochemical functioning, which is harmful to plant health. Drought, salt, and heavy metal stress are the most common abiotic stressors that crops endure across the world. Plant growth and development are influenced by soil quality, nutrition, and physicochemical qualities. Similarly, the availability of macro and micronutrients in easily palatable forms is an important factor that influences plant growth at all stages. Different growth-promoting *Pseudomonas* strains have been shown to have favorable impacts on dry biomass, germination, growth performance, yield, and nutrient absorption under salt, drought, and heavy metal stress tolerance in diverse crops in previous studies *via* various mechanisms (Table 3). For example, *P. aeruginosa* MCCB0035, *Pseudomonas* sp., and *P. libanensis* improved the growth of okra (Yadav et al. 2018), maize (Sandhya et al. 2010), and wheat (Kour et al. 2019) plants under drought stress, *Pseudomonas* sp., *P. anguilliseptica* SAW24, and *P. extremorientalis* enhanced sunflower (Tewari and Arora 2016), faba bean (Mohammed 2018), and wheat (Egamberdieva 2009) growth under salt stress, whereas *P. aeruginosa* and *P. brassicacearum* improved growth of wheat and black medick under Zn and Cu stress (Islam et al. 2014; Kong et al. 2017) (Table 3).

**Biotic stress**

Similarly, a variety of harmful diseases produced by fungi, bacteria, viruses, and nematodes are severe biotic limitations that result in reduced crop development and yield outputs. PGPR can be effectively managed in the agro-farming system
to control most of the listed biotic stresses, boost yields, and decrease the use of chemical fertilizers (Glick 2020). This is referred to as biocontrol, and it is achieved through competition, antibiosis, and ISR. *Pseudomonas* strains such as *P. aeruginosa* B18, *P. fluorescens*, *Pseudomonas sp.*., *P. putida* AA7, and *P. baetica* have been reported to be more efficient in providing pathogen protection and improving growth in different crops (Yasmin et al. 2016; Niu et al. 2017; Verma et al. 2018; Djaya et al. 2019; Singh et al. 2021) (Table 4).

**Conclusions and future perspectives**

This review is abundant with useful information demonstrating the ability of *Pseudomonas* strains to support the plant growth and development in a wide range of crops, as well as increasing the ability of crops to manage biotic and abiotic challenges. This tolerance is owing to the existence of certain characteristics in these strains, and understanding the probable action mechanisms of *Pseudomonas* and its positive interactions with plants is critical for increasing plant growth and output. In the future, plant growth-promoting *Pseudomonas* strains might be an efficient alternative to chemical fertilizers and pesticides for increasing agricultural production in an environmentally friendly and several promising ways. However, a variety of conditions exist, including, commercial formulation, host specificity, durability and survival, and variation in an extensive range of environmental circumstances, necessitating extensive research in this field to completely use them as sustainable agricultural approaches and meet future food demands sustainably.

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