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## *Pseudomonas fluorescens* as a plant growth-promoting rhizobacterium: mechanisms, applications, and prospects for sustainable agriculture

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#### ABSTRACT

Meeting the food demands of a global population projected to reach 9.38 billion by 2050 requires a substantial increase in agricultural production, even as roughly 38% of the world's 1.5 billion hectares of cropland face degradation and the intensive use of chemical fertilizers and pesticides continues to erode soil biodiversity and human health. Plant growth-promoting microbes (PGPM), particularly plant growth-promoting rhizobacteria (PGPR) such as *Pseudomonas* and *Bacillus*, offer a biologically based alternative that can enhance nutrient acquisition, suppress phytopathogens, and improve plant tolerance to abiotic stress. Among these, *Pseudomonas fluorescens* is one of the most extensively studied rhizobacteria owing to its aggressive rhizosphere colonisation, broad phytohormone and siderophore production, and capacity to suppress soil-borne and foliar pathogens through antibiosis, competition, lytic enzyme secretion, and induction of systemic resistance (ISR). This review synthesizes current knowledge of the taxonomy, secondary metabolite chemistry, direct and indirect plant growth-promoting mechanisms, biocontrol activity, crop-specific applications, and abiotic-stress-alleviating properties of *P. fluorescens*, and outlines the formulation, quality-control, and research needs that must be addressed to translate its laboratory potential into consistent field performance.

**Keywords:** *Pseudomonas fluorescens*, Plant growth-promoting rhizobacteria (PGPR), Biocontrol, Induced systemic resistance, Secondary metabolites, Sustainable agriculture

#### Introduction

Meeting the food demands of a global population projected to reach 9.38 billion by 2050 requires a massive scale-up in agricultural production. However, this necessity is severely constrained by widespread soil degradation, which currently affects roughly 38% of the world's 1.5 billion hectares of cropland. To counteract this, conventional farming has historically relied on intensive chemical fertilizers and synthetic pesticides. While these agrochemicals initially boosted productivity, their prolonged and excessive use has resulted in severe biodiversity loss, the elimination of beneficial soil biota, and health risks from toxic residues on crops. Consequently, there is an urgent global mandate to transition toward eco-friendly, sustainable agricultural alternatives.

Fungicides illustrate this dilemma well. As chemical pesticides used to prevent or suppress fungal diseases, they account for more than 35% of the global pesticide market, and their use is projected to keep increasing (Duarte Hospital *et al.*, 2023; Godfray & Garnett, 2014). Despite their role in protecting crop yield and quality, continuous and indiscriminate fungicide use has raised concerns about adverse effects on soil health and microbial diversity. Several studies have shown that fungicides can negatively influence beneficial soil microorganisms and inhibit key soil enzymes involved in nutrient cycling, including dehydrogenase, phosphatases, urease, and  $\beta$ -glucosidase (Muñoz-Leoz *et al.*, 2011), thereby impairing soil fertility and long-term agricultural sustainability.

Plant Growth-Promoting Microbes (PGPM), which include Plant Growth-Promoting Rhizobacteria (PGPR) such as *Bacillus* and *Pseudomonas* (Ex: Multiplex Bio Jodi) and Plant Growth-Promoting Fungi (PGPF) such as Arbuscular Mycorrhizal Fungi (AMF) (Ex: Multiplex Trishul) offer a promising biological alternative. These organisms aggressively colonise the plant rhizosphere, establishing robust densities of  $10^5$ – $10^7$  CFU per gram of root. PGPM enhance soil structure through exopolysaccharide production, facilitate nutrient acquisition through biological nitrogen fixation and mineral solubilization, suppress phytopathogens via direct antagonism and induced systemic resistance, and alleviate climate-driven abiotic stresses such as drought, salinity, and flooding through mechanisms including Osmoprotectant accumulation and ACC deaminase activity. PGPR promote plant health through several additional mechanisms, including competition with pathogens for nutrients and ecological niches, production of antimicrobial metabolites, secretion of pathogen-cell-wall-degrading enzymes, induction of systemic resistance, and degradation of environmental pollutants (Oleńska *et al.*, 2020). Common PGPR genera include *Azotobacter*, *Klebsiella*, *Enterobacter*,

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*Alcaligenes*, *Bacillus*, and *Pseudomonas* (Maçik *et al.*, 2020; de Andrade *et al.*, 2024; Ghadamgahi *et al.*, 2022).

Among these beneficial microorganisms, *Pseudomonas fluorescens* (Ex: Multiplex Sparsha) is one of the most extensively studied rhizobacteria because of its plant growth-promoting and biocontrol capabilities. It efficiently colonizes the rhizosphere and enhances plant growth through direct mechanisms, such as the production of phytohormones such as indole-3-acetic acid (IAA), phosphate solubilization, and siderophore-mediated iron acquisition and indirect mechanisms, including synthesis of hydrolytic enzymes and antimicrobial compounds and induction of systemic resistance against plant pathogens (David *et al.*, 2018). Several strains also degrade a wide range of pesticides and other xenobiotic compounds, making them valuable for both sustainable crop production and environmental remediation (Asim *et al.*, 2020; Bhatt *et al.*, 2021).

It should be noted that several *Pseudomonas* species are also considered opportunistic human pathogens (Singh *et al.*, 2021). *P. putida*, a producer of volatile organic compounds (Agisha *et al.*, 2019), and *P. fluorescens*, which promotes plant growth by increasing tolerance to water stress and by solubilizing phosphate and synthesizing siderophores (Zarei *et al.*, 2019), may occasionally cause skin and soft-tissue infections in humans. Consequently, regulatory restrictions apply to the production and sale of products derived from these species, requiring rigorous environmental and human-health assessment before product approval (Anderson *et al.*, 2018). Beyond plants, *Pseudomonas* has also shown activity against foodborne bacterial and fungal pathogens (Marrez *et al.*, 2019).

## Taxonomy and general characteristics

The genus *Pseudomonas*, part of the Proteobacteria, includes over 300 Gram-negative, rod-shaped species primarily found in plants, soil, and aquatic environments. Known for their rapid growth and metabolic versatility, they are used in bioremediation and industrial bio-manufacturing of various compounds (Glick & Nascimento, 2021; Rios *et al.*, 2018). *Pseudomonas* is notably associated with crops like maize, wheat, sugarcane, and rice, and was found to represent 64.2% of bacteria in the rhizosphere (Li *et al.*, 2018).

First described in 1894 and validated in 1980 (Haas & Défago, 2005; Kloepper *et al.*, 1980a) [1], *Pseudomonas* species are widely distributed across various environments. Advancements in phylogenomic technologies have led to significant revisions in its taxonomy, increasing the recognized species from about 250 in 2021 to over 300 by 2024. Of these, 43 were identified using whole-genome sequencing. This diversity highlights the genus' adaptability and beneficial effects on plants.

The genus *Pseudomonas* comprises one of the most diverse and taxonomically complex groups of Gram-negative bacteria, rod-shaped, motile, with more than 220–300 validly described species and new species continually being identified through advances in molecular taxonomy Table 1. (Peix *et al.*, 2009; Peix *et al.*, 2018). Species identification traditionally relied on morphological and biochemical characteristics; modern classification instead relies primarily on molecular approaches, including multilocus sequence analysis (MLSA) and whole-genome sequencing (Gomila *et al.*, 2015; Hesse *et al.*, 2018; Lalucat *et al.*, 2020).

**Table 1.** Selected biocontrol activities of *Pseudomonas* spp. across crops.

| Species                | Crop                                         | Effect                                                        | Reference                               |
|------------------------|----------------------------------------------|---------------------------------------------------------------|-----------------------------------------|
| <i>P. fluorescens</i>  | Rice, radish, eucalypt                       | ISR induction                                                 | Geels & Schippers, 1983                 |
| <i>P. fluorescens</i>  | Wheat and other crops                        | Strong ISR                                                    | Lamers <i>et al.</i> , 1988             |
| <i>P. fluorescens</i>  | Olive                                        | <i>Verticillium</i> wilt control                              | Maldonado-Gonzalez <i>et al.</i> , 2015 |
| <i>P. fluorescens</i>  | Flower bulbs, tomato                         | <i>Pythium</i> root rot, late blight control                  | de Souza <i>et al.</i> , 2003           |
| <i>P. fluorescens</i>  | General (model strain)                       | <i>Rhizoctonia</i> , <i>Pythium</i> control, ISR              | Naseby <i>et al.</i> , 2001             |
| <i>P. fluorescens</i>  | Sugar beet                                   | <i>R. solani</i> control                                      | Zachow <i>et al.</i> , 2015             |
| <i>P. fluorescens</i>  | Wheat                                        | Take-all disease control                                      | Nesemann <i>et al.</i> , 2015           |
| <i>P. protegens</i>    | Cotton                                       | <i>Rhizoctonia</i> , <i>Pythium</i> , <i>Fusarium</i> control | Howell & Stipanovic, 1980               |
| <i>P. protegens</i>    | Tobacco, wheat, cucumber, sugar beet, cotton | Black root rot, take-all, <i>Pythium</i> control              | Stutz <i>et al.</i> , 1986              |
| <i>P. protegens</i>    | Cocoyam                                      | <i>Pythium myriotylum</i> , <i>Rhizoctonia</i> control        | Perneel <i>et al.</i> , 2007            |
| <i>P. chlororaphis</i> | Wheat                                        | Take-all control                                              | Pierson & Thomashow, 1992               |
| <i>P. chlororaphis</i> | Tomato                                       | <i>Fusarium</i> crown/root rot control                        | Chin-A-Woeng <i>et al.</i> , 1998       |
| <i>P. koreensis</i>    | Lettuce, potato                              | <i>R. solani</i> control                                      | Adesina <i>et al.</i> , 2009            |
| <i>P. koreensis</i>    | Tomato, potato                               | <i>P. ultimum</i> , <i>P. infestans</i> control               | Hultberg <i>et al.</i> , 2010           |
| <i>P. mandelii</i>     | Potato                                       | <i>R. solani</i> , <i>Pythium</i> control                     | Michelsen <i>et al.</i> , 2015          |
| <i>P. mandelii</i>     | Olive                                        | <i>Verticillium dahliae</i> control                           | Gomez-Lama Cabanas <i>et al.</i> , 2018 |
| <i>P. putida</i>       | General (model strain)                       | ISR, pathogen competition                                     | Nelson <i>et al.</i> , 2002             |
| <i>P. putida</i>       | <i>Arabidopsis</i> , bean, tomato            | ISR induction                                                 | Van Wees <i>et al.</i> , 1997           |
| <i>P. syringae</i>     | Apple, pear, citrus                          | Postharvest disease control                                   | Janisiewicz & Marchi, 1992              |
| <i>P. syringae</i>     | Soybean                                      | <i>P. syringae</i> pv. <i>glycinea</i> control                | Völksch <i>et al.</i> , 1996            |
| <i>P. aeruginosa</i>   | Chickpea, pigeonpea                          | <i>Fusarium</i> wilt control                                  | Anjaiah <i>et al.</i> , 1998            |
| <i>P. aeruginosa</i>   | Tomato                                       | <i>Pythium</i> damping-off control, ISR                       | Buysens <i>et al.</i> , 1996            |
| <i>P. aeruginosa</i>   | Sweet melon                                  | Commercial biopesticide (China)                               | Huang <i>et al.</i> , 2009              |

## Secondary metabolites and antimicrobial compounds

*Pseudomonas* spp., particularly fluorescent pseudomonads, produce a wide range of secondary metabolites central to biocontrol and plant growth promotion. The major antimicrobial metabolites include hydrogen cyanide (HCN), phenazines (PHZ), 2,4-diacetylphloroglucinol

(DAPG), pyoluteorin (PLT), pyrrolnitrin (PRN), and cyclic lipopeptides (CLPs). These compounds suppress fungal and bacterial phytopathogens through inhibition of respiratory enzymes, disruption of cell membranes, generation of reactive oxygen species (ROS), and interference with pathogen growth. Several metabolites additionally contribute to biofilm formation, rhizosphere colonization, iron acqui

sition, quorum sensing, and induction of systemic resistance (ISR) (Ahemad & Kibret, 2014; Raaijmakers *et al.*, 2010; Weller, 2007). Approximately 6% of the *P. fluorescens* Pf-5 genome is dedicated to

secondary metabolite biosynthesis, underscoring the genus's exceptional capacity for antimicrobial compound production (Gross & Loper, 2009; Kumudini *et al.*, 2017).

**Table 2.** Major Secondary Metabolites Produced by *Pseudomonas* spp. and Their Biological Functions

| Secondary metabolite                                                                                 | Major biological functions                                                                                                                                                                             |
|------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 2,4-Diacetylphloroglucinol (DAPG)                                                                    | Broad-spectrum antibacterial and antifungal antibiotic; suppresses soil-borne fungal pathogens and induces induced systemic resistance (ISR).                                                          |
| Phenazines (PHZ)                                                                                     | Broad-spectrum antimicrobial compounds that generate reactive oxygen species (ROS), inhibit electron transport and DNA replication, suppress diverse pathogens, and improve rhizosphere fitness.       |
| Pyoluteorin (PLT)                                                                                    | Polyketide antibiotic exhibiting strong antifungal and antibacterial activity against several phytopathogens.                                                                                          |
| Pyrrolnitrin (PRN)                                                                                   | Broad-spectrum antifungal and antibacterial compound that disrupts fungal respiration and membrane integrity, contributing to disease suppression.                                                     |
| Hydrogen cyanide (HCN)                                                                               | Inhibits cytochrome <i>c</i> oxidase in target organisms, suppressing fungal, bacterial, and nematode pathogens; also contributes to nutrient mobilisation in the rhizosphere.                         |
| Cyclic lipopeptides (CLPs) ( <i>e.g.</i> , viscosin, amphisin, syringomycin, putisolvin, thanamycin) | Disrupt pathogen cell membranes; exhibit antibacterial, antifungal, and antiviral activities; promote biofilm formation, root colonisation, bacterial motility, and induced systemic resistance (ISR). |
| Mupirocin                                                                                            | Inhibits bacterial protein synthesis by targeting isoleucyl-tRNA synthetase; effective against Gram-positive bacteria, including <i>Staphylococcus</i> and <i>Streptococcus</i> spp.                   |

### Phenazines

Phenazines are redox-active, nitrogen-containing tricyclic pigments produced by *Pseudomonas* and some Gram-negative Proteobacteria (Mavrodi *et al.*, 2006). While over 100 phenazine structures exist, biocontrol strains mainly produce phenazine-1-carboxylic acid (PCA), phenazine-1-carboxamide (PCN), 2-hydroxyphenazine (2-OH-PHZ), and 2-hydroxyphenazine-1-carboxylic acid (2-OH-PCA). Pyocyanin (PYO) is specific to *P. aeruginosa* and plays a role in infections (Price-Whelan *et al.*, 2006). The biosynthesis involves a conserved seven-gene locus, *phzABCDEFG*, that synthesises PCA from chorismic acid, with tailoring enzymes (PhzO, PhzH, PhzS, PhzM) adding structural diversity. This process is regulated by quorum sensing and requires the GacS/GacA signal transduction system (Biessy & Fillion, 2018; Gross & Loper, 2009). Phenazines are effective against various pathogens, inducing oxidative stress and ISR (Ma *et al.*, 2016; De Vleeschauwer & Höfte, 2009), and play roles in biofilm formation and iron reduction (Mavrodi *et al.*, 2013). Production is mainly found in the *P. aeruginosa* group and the chlororaphis and *fluorescens* subgroups of *P. fluorescens* (Yang *et al.*, 2025).

### 2,4-Diacetylphloroglucinol (DAPG)

DAPG is a polyketide antibiotic primarily produced by *P. protegens* and *P. corrugata*, showing broad-spectrum activity against bacteria, fungi, oomycetes, and nematodes. It helps suppress diseases like take-all of wheat and black root rot of tobacco. Typically isolated from soils suppressive to take-all, DAPG disrupts cell membranes, induces ROS, and inhibits mitochondrial ATP synthesis. The conserved DAPG gene cluster includes *phlD*, a type III polyketide synthase responsible for phloroglucinol biosynthesis. Additionally, DAPG induces systemic resistance in *Arabidopsis* against various pathogens and stimulates root branching in tomato via auxin signaling.

### Pyoluteorin

Pyoluteorin is a hybrid polyketide–nonribosomal-peptide antibiotic, comprising a resorcinol ring attached to a dichlorinated pyrrole moiety, produced mainly by *P. protegens* and some *P. aeruginosa* isolates (Hu *et al.*, 2005; Ramette *et al.*, 2011). It suppresses seedling damping-off caused by *Pythium ultimum* in cotton and cress (Howell & Stipanovic, 1980; Maurhofer *et al.*, 1994) [2], and its 17-gene biosynthetic cluster (structural genes *pltABCDEFGHIJLM*; efflux genes *pltJKNOP*; regulatory genes *pltZ* and *pltR*) is present only in strains that also carry *phlD* (Gross & Loper, 2009). Its antimicrobial activity is

linked to disruption of cytosolic Ca<sup>2+</sup> homeostasis, ROS induction, and inhibition of biofilm formation (Kidarsa *et al.*, 2011; Yan *et al.*, 2017; Yang *et al.*, 2025).

### Pyrrolnitrin

Pyrrolnitrin is a chlorinated phenylpyrrole antibiotic produced by *Pseudomonas* spp. with broad-spectrum antifungal activity against important phytopathogens, including *Rhizoctonia solani*, *Fusarium* spp., *Botrytis cinerea*, *Pythium aphanidermatum*, and *Sclerotium rolfsii*. It suppresses fungal growth by disrupting the electron transport chain and osmotic signalling, effectively controlling damping-off diseases in crops such as cotton and cucumber. Pyrrolnitrin also served as the lead compound for the development of the commercial fungicides fenpiclonil and fludioxonil (Ligon *et al.*, 2000; Costa *et al.*, 2009; Kilani and Fillinger, 2016; Nyfeler and Ackermann, 1992; Yang *et al.*, 2025).

### Hydrogen cyanide (HCN)

Hydrogen cyanide (HCN) is a volatile secondary metabolite produced by several *Pseudomonas* spp. that inhibits cytochrome *c* oxidase, thereby suppressing the growth of fungal pathogens, nematodes, and certain insect pests. HCN contributes to the biological control of tobacco black root rot caused by *Thielaviopsis basicola* and has also been implicated in the suppression of root-knot nematodes, aphids, and termites (Blumer and Haas, 2000; Voisard *et al.*, 1989 [3]; Siddiqui *et al.*, 2006; Devi and Kothamasi, 2009; Kang *et al.*, 2019; Flury *et al.*, 2017).

### Siderophores

Siderophores are iron-chelating compounds produced by *Pseudomonas* spp. that contribute to biological control by competing with pathogens for iron, directly inhibiting pathogen growth, and inducing systemic resistance (ISR) in plants. The major siderophore produced is pyoverdine, while several strains also synthesize pyochelin, achromobactin, pseudomonine, corrugatin, and (thio)quinolobactin, enhancing their competitiveness and plant-beneficial effects (Meyer, 2000; Cornelis, 2010; Schalk *et al.*, 2020).

### Strain-specific bioactive molecules and toxins

Strain-specific metabolites: Certain *Pseudomonas* strains produce unique bioactive metabolites, including rhizoxins, sessilin, promysalin, and L-furanomycin, which exhibit antifungal, antibacterial, and antioomycete activities against a range of plant pathogens (Ligon *et al.*, 2000; Loper *et al.*, 2008; Li *et al.*, 2011; D'Aes *et al.*,

2014; Takeuchi *et al.*, 2015; Trippe *et al.*, 2013; Kaduskar *et al.*, 2017).

**Fit toxin:** Biocontrol strains belonging to the *Pseudomonas protegens* and *P. chlororaphis* subgroups produce the Fit toxin (FitD), a potent insecticidal protein that exhibits oral and injectable toxicity against lepidopteran larvae, contributing to the biological control of insect pests (Péchy-Tarr *et al.*, 2008; Ruffner *et al.*, 2012, 2015; Flury *et al.*, 2016, 2017).

### Regulation of secondary metabolite production

Regulation of secondary metabolites in *Pseudomonas* is complex; comprehensive reviews are provided by Haas and Keel (2003) and Sonnleitner and Haas (2011). Most biocontrol-relevant antibiotics are produced only when the GacS/GacA two-component system, widely conserved among Gram-negative bacteria, is active; mutations in *gacS* or *gacA* abolish biocontrol activity in most strains. Upon interaction with bacterial signal molecules presumed to be Krebs-cycle intermediates (Takeuchi *et al.*, 2009), GacS autophosphorylates and transfers a phosphate residue to GacA, activating transcription of small regulatory RNAs that relieve translational repression of biocontrol genes near ribosome-binding sites (Sonnleitner & Haas, 2011). Spontaneous *gacA/gacS* mutants can accumulate in culture, particularly among strains producing many secondary metabolites, and are recognisable by larger, flatter, more fluorescent colonies resulting from pyoverdine overproduction (Duffy & Défago, 2000; Yan *et al.*, 2018).

## Plant growth-promoting mechanisms

### Direct mechanisms

*Pseudomonas fluorescens* promote plant growth through several direct mechanisms that improve nutrient availability, stimulate root development, and enhance productivity:

- **Biological nitrogen fixation**, contributing to overall nitrogen supply;
- **Solubilization of insoluble phosphorus and potassium**, and mobilization of micronutrients such as zinc and manganese, via organic acids and phosphatase enzymes that convert insoluble phosphorus into plant-available forms (Bonotto *et al.*, 2025; Richardson *et al.*, 2009; Rodríguez & Fraga, 1999);
- **Production of phytohormones**, particularly indole-3-acetic acid (IAA), which stimulates root elongation, lateral root formation, root hair development, and overall biomass, alongside gibberellins and cytokinins (Bonotto *et al.*, 2025; Spaepen *et al.*, 2007);
- **ACC deaminase activity**, which lowers stress-induced ethylene levels and promotes root development; and
- **Siderophores** These are high-affinity iron-chelating compounds produced by *Pseudomonas* spp. that enhance plant iron uptake under iron-limited conditions while restricting iron availability to pathogens, thereby suppressing disease development (Neilands, 1995; Haas and Défago, 2005). A landmark study by Kloepper *et al.* (1980a, 1980b) [1] demonstrated that *Pseudomonas* strain B10 controlled take-all and *Fusarium wilt* through the production of the siderophore pseudobactin. By sequestering ferric iron ( $\text{Fe}^{3+}$ ), pseudobactin deprived pathogens such as *Fusarium oxysporum* f. sp. *lini* and *Gaeumannomyces graminis* var. *tritici* of the iron required for growth, converting disease-conducive soils into disease-suppressive soils. This study established iron competition as a major mechanism of biological control by fluorescent *Pseudomonas* and laid the foundation for the use of PGPR in sustainable disease management (Kloepper *et al.*, 1980a, 1980b) [1].

Collectively, these traits make *P. fluorescens* an efficient PGPR with the potential to improve nutrient-use efficiency, reduce fertilizer inputs, and support sustainable agricultural production (Mehmood *et al.*, 2023).

### Indirect mechanisms

Beyond direct growth promotion, *P. fluorescens* protects plants against biotic and abiotic stress through several indirect mechanisms, primarily mediated by:

- Production of antibiotics such as DAPG, phenazines, pyoluteorin, pyrrolnitrin, and HCN;
- Secretion of lytic enzymes chitinase,  $\beta$ -1,3-glucanase, protease, cellulase, lipase, and amylase that degrade fungal cell walls;
- Production of volatile organic compounds (VOCs) and biosurfactants (e.g., rhamnolipids);
- Induction of systemic resistance (ISR) in host plants; and
- Competition with pathogens for nutrients and ecological niches (Mehmood *et al.*, 2023).

Successful rhizosphere colonisation allows *P. fluorescens* to establish a protective microbial barrier around plant roots, limiting pathogen invasion. ISR itself is predominantly regulated through jasmonic-acid- and ethylene-dependent signalling, resulting in enhanced expression of defence-related genes, accumulation of pathogenesis-related (PR) proteins, cell-wall strengthening, and increased synthesis of phytoalexins and phenolic compounds (Pieterse *et al.*, 2014), improving resistance against a broad spectrum of fungal, bacterial, viral, nematode, and insect pests. The combined effect of antimicrobial metabolite production, hydrolytic enzyme secretion, competitive colonisation, and ISR activation makes *P. fluorescens* one of the most effective biological control agents available for integrated disease management (Compant *et al.*, 2005; Haas & Défago, 2005; Keel *et al.*, 1992; Lugtenberg & Kamilova, 2009).

### Rhizosphere competence

The success of *Pseudomonas* spp. as PGPR depends on rapid colonisation of roots and internal plant tissues, efficient utilisation of root exudates, strong competitiveness within the rhizosphere, production of antibiotics, siderophores, and volatile compounds, and high adaptability to environmental stress (Mehmood *et al.*, 2023).

### ISR as a broad-spectrum defence mechanism

*Pseudomonas* species are well-known plant growth-promoting rhizobacteria (PGPR) that colonize the rhizosphere and stimulate plant growth in various ways, including improved seed germination, enhanced seedling vigour, increased biomass, and higher crop productivity across multiple cropping systems (Udaya Shankar *et al.*, 2009). *Pseudomonas fluorescens* can induce systemic resistance (ISR), which activates the plant's natural defences against a wide range of pathogens, including fungi, bacteria, viruses, and nematodes. Unlike direct antimicrobial activity, ISR prepares the plant for a quicker and more robust defense response when faced with pathogen attacks. Although it shares similar characteristics with systemic acquired resistance (SAR), ISR is triggered by beneficial rhizobacteria instead of pathogen infections (Udaya Shankar *et al.*, 2009).

### Role in viral disease management

Seed treatment with *Pseudomonas fluorescens* in combination with *Serratia marcescens* significantly reduced the infection of Cucumber mosaic virus (CMV) in cucumber (*Cucumis sativus*) and tomato (*Lycopersicon esculentum*) under screen-house conditions. The observed decrease in virus titers in plants treated with plant growth-promoting rhizobacteria (PGPR) suggests that *Pseudomonas* restricts virus multiplication by activating the host's defence mechanisms rather than by directly inhibiting the virus (Raupach *et al.*, 1996; Udaya Shankar *et al.*, 2009).

### Multiple, complementary mechanisms of disease suppression

Taken together, the literature indicates that *Pseudomonas* suppresses plant pathogens through several complementary mechanisms operating simultaneously: siderophore-mediated competition for iron; synthesis of antibiotics that inhibit pathogenic microorganisms; secretion of small antimicrobial metabolites; and production of hydrolytic enzymes that interfere with pathogen development. These combined mechanisms contribute to improved plant health and enhanced disease resistance, positioning *Pseudomonas* spp. (Ex; Multiplex Sparsha) as promising components of Integrated Pest Management (IPM) programs and sustainable crop production systems more broadly (Udaya Shankar *et al.*, 2009).

### Biocontrol mechanisms

*Pseudomonas fluorescens* is one of the most extensively studied PGPR and has emerged as an effective biological control agent against a wide range of soil-borne and foliar plant pathogens. Since pioneering studies in the late 1970s, *fluorescent Pseudomonas* spp. (Ex; Multiplex Sparsha) has attracted considerable attention for their exceptional rhizosphere competence, rapid growth, metabolic versatility, and efficient root colonisation (Weller, 1988), reflecting the genus's broad physiological and genetic adaptability across terrestrial and aquatic environments (Nowak-Thompson *et al.*, 1997).

Its biocontrol efficacy stems from multiple, complementary direct and indirect mechanisms: direct antagonism through production of DAPG, phenazines, pyrrolnitrin, pyoluteorin, HCN, cyclic lipopeptides, and siderophores (Haas & Défago, 2005; Keel *et al.*, 1992); secretion of extracellular hydrolytic enzymes (chitinases, proteases, cellulases,  $\beta$ -1,3-glucanases) that degrade pathogen cell walls; induction of systemic resistance, priming plants for a faster, stronger response to attack (Cartieaux *et al.*, 2003); and competitive exclusion of pathogens from nutrients and ecological niches via efficient root-exudate utilization and high-affinity siderophore production (Weller *et al.*, 2002). Its excellent rhizosphere colonisation ability and persistence following seed or soil inoculation further contribute to field-level effectiveness. Numerous studies demonstrate that *P. fluorescens* effectively suppresses diseases caused by *Fusarium*, *Rhizoctonia*, *Pythium*, *Phytophthora*, and *Sclerotium*, among other economically important pathogens, while simultaneously promoting growth and productivity, making it one of the most promising microbial agents for integrated disease management and eco-friendly crop protection. Only a limited number of bioactive compounds play a clearly established role in *Pseudomonas* biocontrol: HCN, DAPG, phenazines, pyrrolnitrin, pyoluteorin, 2-hexyl-5-propyl-alkylresorcinol (HPR), siderophores, and cyclic lipopeptides—each typically associated with specific phylogenetic subgroups (Gross & Loper, 2009; Haas & Défago, 2005; Mishra & Arora, 2018; Olorunleke *et al.*, 2015; Raaijmakers & Mazzola, 2012).

**Table 3.** Crop-specific response of *Pseudomonas*

| Crop / Crop Group | <i>Pseudomonas</i> Application                            | Major Growth-Promoting / Biocontrol Effects                                                                                                                                                      | References                                                                                                                                                                                                                                  |
|-------------------|-----------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Coconut and cocoa | <i>Pseudomonas</i> sp. with <i>Aspergillus niger</i>      | Increased IAA and GA production and improved yield                                                                                                                                               | Iyer (1983)                                                                                                                                                                                                                                 |
| Black pepper      | <i>P. fluorescens</i> and other <i>Pseudomonas</i> spp.   | Improved N, K and P uptake; controlled foot rot and slow decline; inhibited nematodes; suppressed <i>Phytophthora capsici</i> through antibiotics, HCN and inhibition of sporangia and zoospores | Diby & Paul (2003); Sarma <i>et al.</i> (2010); Jisha & Alagawadi (1996); Paul & Sarma (2006); Défago <i>et al.</i> (1990); Thomashow & Weller (1995)                                                                                       |
| Tomato            | <i>Pseudomonas</i> spp.                                   | Controlled root and stem rot, <i>Fusarium wilt</i> , bacterial wilt, early and late blight, and bacterial canker through hydrolytic enzymes, HCN, siderophores, antibiotics and ISR              | Moataza (2006); Voisard <i>et al.</i> (1989); Lemanceau & Alabouvette (1993); Chin-A-Woeng <i>et al.</i> (2001); Tran <i>et al.</i> (2007); Amkraz <i>et al.</i> (2010); Saharan & Nehra (2011); Joseph (2017); Clough <i>et al.</i> (2022) |
| Okra              | <i>P. fluorescens</i>                                     | Produced IAA, HCN and ammonia; solubilized phosphate; suppressed <i>Fusarium solani</i> ; improved germination and root and shoot growth                                                         | Yadav <i>et al.</i> (2022)                                                                                                                                                                                                                  |
| Cucumber          | <i>Pseudomonas fluorescens</i> CV6 and <i>P. stutzeri</i> | Improved plant growth; provided 85.71% protection against damping-off; enhanced salt tolerance through synergistic association and biofilm formation                                             | Loper & Buyer (1991); Maleki <i>et al.</i> (2010); Saharan & Nehra (2011); Voisard <i>et al.</i> (1989); Díaz-Rodríguez <i>et al.</i> (2025)                                                                                                |
| Pepper            | <i>Pseudomonas</i> spp.                                   | Suppressed <i>Phytophthora capsici</i> and improved phosphorus availability and plant growth                                                                                                     | Islam <i>et al.</i> (2006); Saharan & Nehra (2011)                                                                                                                                                                                          |
| Zucchini          | <i>Pseudomonas</i> sp.                                    | Accelerated flowering and increased female flower production, resulting in earlier harvest                                                                                                       | Novello <i>et al.</i> (2021)                                                                                                                                                                                                                |
| Pea               | Fluorescent <i>Pseudomonas</i>                            | Promoted growth and provided biocontrol under low-temperature conditions                                                                                                                         | Saharan & Nehra (2011); Trivedi <i>et al.</i> (2008)                                                                                                                                                                                        |

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| Crop / Crop Group             | <i>Pseudomonas</i> Application                                                   | Major Growth-Promoting / Biocontrol Effects                                                                                                                                                                 | References                                                                                                                                                                                                                                                                                                                                                                  |
|-------------------------------|----------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Rice                          | <i>P. fluorescens</i>                                                            | Controlled bacterial leaf blight, sheath blight, blast and root nematodes; improved germination, nutrient uptake and yield through ISR, IAA production, phosphate solubilization and siderophore production | Rabindran & Vidhyasekaran (1996); Ramakrishnan <i>et al.</i> (1998); Nandakumar <i>et al.</i> (2001); Vidhyasekaran <i>et al.</i> (2001); Vasudevan <i>et al.</i> (2002); Raja <i>et al.</i> (2006); Mirza <i>et al.</i> (2006); Ashrafuzzaman <i>et al.</i> (2009); Ramezanpour <i>et al.</i> (2010); Muthukumar & Tamilselvi (2013); De Vleeschauwer <i>et al.</i> (2008) |
| Wheat                         | <i>Pseudomonas</i> spp.                                                          | Improved root and shoot growth and nutrient uptake; suppressed take-all, common root rot and spot blotch                                                                                                    | Srivastava <i>et al.</i> (1999); Wang <i>et al.</i> (1999); Kita <i>et al.</i> (2004); Gaur <i>et al.</i> (2004); Sharma <i>et al.</i> (2011); Saharan & Nehra (2011)                                                                                                                                                                                                       |
| Barley                        | <i>Pseudomonas gessardii</i>                                                     | Solubilized potassium and improved nutrient availability, chlorophyll, biomass and beneficial metabolites                                                                                                   | Díaz-Rodríguez <i>et al.</i> (2025)                                                                                                                                                                                                                                                                                                                                         |
| Cotton                        | Fluorescent <i>Pseudomonas</i> spp.                                              | Suppressed <i>Rhizoctonia solani</i> -induced damping-off through antifungal metabolites and rhizosphere colonization                                                                                       | Elad & Baker (1985); Saharan & Nehra (2011)                                                                                                                                                                                                                                                                                                                                 |
| Chickpea                      | <i>P. fluorescens</i>                                                            | Improved growth, biomass, pod number, grain yield and protein yield; enhanced IAA production and phosphate solubilization                                                                                   | Rokhzadi <i>et al.</i> (2008); Wani <i>et al.</i> (2007); Saharan & Nehra (2011)                                                                                                                                                                                                                                                                                            |
| Groundnut                     | <i>P. fluorescens</i>                                                            | Improved pod yield, nodulation, nutrient uptake and root growth; suppressed collar and stem rot                                                                                                             | Dey <i>et al.</i> (2004)                                                                                                                                                                                                                                                                                                                                                    |
| Soybean                       | <i>Pseudomonas</i> spp.                                                          | Controlled red crown root rot; improved root and shoot growth through VOCs, antibiotics and ACC deaminase activity                                                                                          | Win <i>et al.</i> (2022); Ramesh <i>et al.</i> (2009); Saharan & Nehra (2011)                                                                                                                                                                                                                                                                                               |
| Blackberry                    | <i>P. fluorescens</i> N21.4                                                      | Improved flowering, yield, fruit quality, phenolics, flavonoids and plant defense responses                                                                                                                 | García-Seco <i>et al.</i> (2013)                                                                                                                                                                                                                                                                                                                                            |
| Onion                         | <i>P. fluorescens</i> , <i>P. putida</i> , <i>P. protegens</i> and other species | Increased bulb weight and dimensions; improved mineral profile and reduced cadmium accumulation                                                                                                             | Novello <i>et al.</i> (2021)                                                                                                                                                                                                                                                                                                                                                |
| Potato                        | <i>P. fluorescens</i> and <i>P. putida</i>                                       | Enhanced root colonization, nutrient uptake and yield through phytohormone production and pathogen suppression                                                                                              | Burr <i>et al.</i> (1978); Schippers <i>et al.</i> (1987); Kloepper <i>et al.</i> (1988, 1989); Saharan & Nehra (2011)                                                                                                                                                                                                                                                      |
| Radish                        | Fluorescent <i>Pseudomonas</i> spp.                                              | Improved root development, nutrient uptake, growth and yield                                                                                                                                                | Kloepper & Schroth (1978); Kloepper <i>et al.</i> (1988); Saharan & Nehra (2011)                                                                                                                                                                                                                                                                                            |
| Sugar beet                    | <i>P. fluorescens</i> and <i>P. putida</i>                                       | Enhanced nutrient acquisition and growth through rapid root colonization and suppression of harmful microorganisms                                                                                          | Suslow & Schroth (1982); Kloepper <i>et al.</i> (1988); Saharan & Nehra (2011)                                                                                                                                                                                                                                                                                              |
| Tobacco                       | <i>P. fluorescens</i> CHA0                                                       | Induced systemic resistance against tobacco necrosis virus through salicylic acid and PR proteins                                                                                                           | Maurhofer <i>et al.</i> (1994)                                                                                                                                                                                                                                                                                                                                              |
| Sugarcane                     | Fluorescent <i>Pseudomonas</i> spp.                                              | Improved fresh and dry biomass through effective plant colonization and growth promotion                                                                                                                    | Muleta <i>et al.</i> (2009); Saharan & Nehra (2011)                                                                                                                                                                                                                                                                                                                         |
| Alfalfa and birdsfoot trefoil | <i>P. fluorescens</i> strains                                                    | Suppressed seedling diseases and improved plant establishment and biomass production                                                                                                                        | Bagnasco <i>et al.</i> (1998); Bajsa <i>et al.</i> (2005); De La Fuente <i>et al.</i> (2002, 2004); Höfte & Altier (2010); Quagliotto <i>et al.</i> (2009); Yanes <i>et al.</i> (2005)                                                                                                                                                                                      |

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| Crop / Crop Group | <i>Pseudomonas</i> Application      | Major Growth-Promoting / Biocontrol Effects                                      | References                                         |
|-------------------|-------------------------------------|----------------------------------------------------------------------------------|----------------------------------------------------|
| Olive             | Fluorescent <i>Pseudomonas</i> spp. | Showed antagonistic activity against olive knot disease                          | Zadeh <i>et al.</i> (2008); Saharan & Nehra (2011) |
| Lettuce           | Fluorescent <i>Pseudomonas</i> spp. | Improved nutrient uptake, root development and biomass                           | Chabot <i>et al.</i> (1993)                        |
| Carnation         | <i>Pseudomonas</i> strain WCS417    | Controlled <i>Fusarium wilt</i> by inducing phytoalexins and systemic resistance | Van Peer <i>et al.</i> (1991)                      |

## Abiotic stress management

### Salinity tolerance: *P. fluorescens* MSP-393

The ability of PGPR to withstand adverse environmental conditions is essential for their successful deployment in sustainable agriculture, particularly in salt-affected soils. *P. fluorescens* MSP-393, isolated from the saline coastal agricultural belt of southern India, is a salt-tolerant PGPR with biocontrol activity against bacterial blight of rice caused by *Xanthomonas oryzae* pv. *oryzae*; unlike many rhizobacteria, it retains root-colonization ability and growth-promoting function even under high salinity (Paul *et al.*, 2006).

Two-dimensional gel electrophoresis coupled with MALDI-TOF mass spectrometry showed that salt stress altered the expression of 22 proteins (20 upregulated, 2 downregulated; 15 identified), primarily associated with osmotic adaptation, membrane integrity, protein folding, transport, energy metabolism, and cellular survival, indicating a coordinated molecular response to high osmolarity (Paul *et al.*, 2006). Among the induced proteins, glutamine synthetase supports synthesis of glutamate, an important osmotic-balance compatible solute; acyl carrier protein and ABC transporters contribute to membrane stability and nutrient/ion transport; and upregulation of the SurE survival protein, 60-kDa chaperonin, DNA/RNA helicases, ribosomal proteins, and methionyl-tRNA synthetase enhances protein folding, nucleic acid stability, and overall metabolic resilience. Conversely, repression of the ABC iron-siderophore transporter and the ribose transport protein (RbsA) suggests that the strain conserves energy by reducing non-essential transport during salt stress, redirecting resources toward adaptation. Despite these adjustments, MSP-393 retained its capacity to produce siderophores, antibiotics, HCN, and other biocontrol factors, ensuring continued pathogen suppression and growth promotion under saline conditions (Paul *et al.*, 2006). These findings indicate that osmolyte accumulation together with induction of stress-responsive proteins forms the molecular basis of salt tolerance in this strain, and highlight the potential of salt-tolerant *P. fluorescens* strains for improving crop productivity in salt-affected soils as climate-resilient

## Conclusion

*Pseudomonas fluorescens* is among the most extensively characterized plant growth-promoting rhizobacteria, combining direct growth-promoting mechanisms—phytohormone production, nutrient solubilization, and siderophore-mediated iron acquisition—with a broad indirect biocontrol repertoire built on antibiotics, lytic enzymes, competitive rhizosphere colonization, and induction of systemic resistance. Its documented efficacy spans a wide range of crops and pathogens, and several strains additionally confer tolerance to salinity, drought, and other abiotic stresses, positioning *P. fluorescens* as a strong candidate for reducing dependence on chemical fertilizers and fungicides. Realizing this potential at scale will require closing the gaps identified above—particularly around field validation, formulation stability, and quality standardization—alongside continued molecular and omics-based research to refine strain selection and deployment strategies for next-generation sustainable agriculture.

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