Essay

# *Pseudomonas* spp. beneficial in agriculture

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## Abstract

Bacteria of the genus *Pseudomonas* inhabit a wide variety of environments, which is a reflection of their diverse metabolic capacity, this has allowed them to adapt to variable environmental conditions, also, this genus is considered ambivalent due to the fact that some species establish beneficial relationships with plants and others pathogenic relationships with plants, animals and humans. In the present work, we focus on the positive impact that this bacterial genus has in the agricultural field, due to its capacity as a plant growth-promoting bacterium (PGPB), being one of the best options as a plant and soil inoculant, to improve plant growth and disease management, through the wide range of metabolites that the beneficial strains are capable of producing, bacteria of this genus have been identified with diazotrophic capacity, producing antibiotics, auxins, siderophores, cellulolytic enzymes, organic acids for phosphorus solubilization and promotion of induced systemic resistance against phytopathogens, which makes them ideal in agricultural production either for biocontrol or biofertilization, likewise, their use does not affect the environment or the health of farmers.

**Keywords:** beneficial microorganisms, biocontrol, biofertilizers, suppressive soils.

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*Pseudomonas* are aerobic, gram-negative, chemoheterotrophic, motile, bacillus-shaped bacteria, belonging to the class Gammaproteobacteria and the family Pseudomonadaceae that includes approximately 191 different species (Kumar *et al*., 2017), due to their metabolic versatility and genetic plasticity, they are ubiquitous in different terrestrial and aquatic ecosystems. Currently, the genus has become relevant in the agricultural field due to the influence exerted by these bacteria on growth promotion, induced systemic resistance (ISR) in plants and the control of phytopathogens, through different mechanisms of action, among which are the production of various antimicrobial compounds such as 2,4-diacetylphloroglucinol (Kankariya *et al*., 2019) and cellulolytic enzymes (Kumar *et al*., 2017), among other metabolites, they produce phytohormones; they also improve the acquisition of nutrients through the production of siderophores (Wendenbaum *et al*., 1983).

They are particularly suitable as biological control agents and biofertilizers since: i) they use a wide range of root exudates as a source of nutrients (Lugtenberg *et al*., 1999); ii) they are abundantly present in soils, particularly in the rhizosphere (Haas and Keel, 2003); iii) they have a high rate of reproduction, compared to other bacteria in the rhizosphere, which allows them to maintain a high population density; iv) they have a wide range of metabolites through which they exert antagonistic or inhibitory activity against phytopathogens; v) they have diazotrophic capacity, producer of auxins, siderophores and solubilization of phosphorus; vi) they are easy to culture *in vitro*; vii) they can be reintroduced by seed inoculation (Lugtenberg *et al*., 1994; Rhodes and Powell, 1994); viii) they are susceptible to genetic modification with the appropriate techniques; and ix) they are capable of stimulating induced systemic resistance (ISR) (Van Loon *et al*., 1998; Chin-A-Woeng *et al*., 2003; Khan *et al*., 2016; Schwanemann *et al*., 2020), so they play an important role in promoting plant growth and biocontrol (Figure 1).

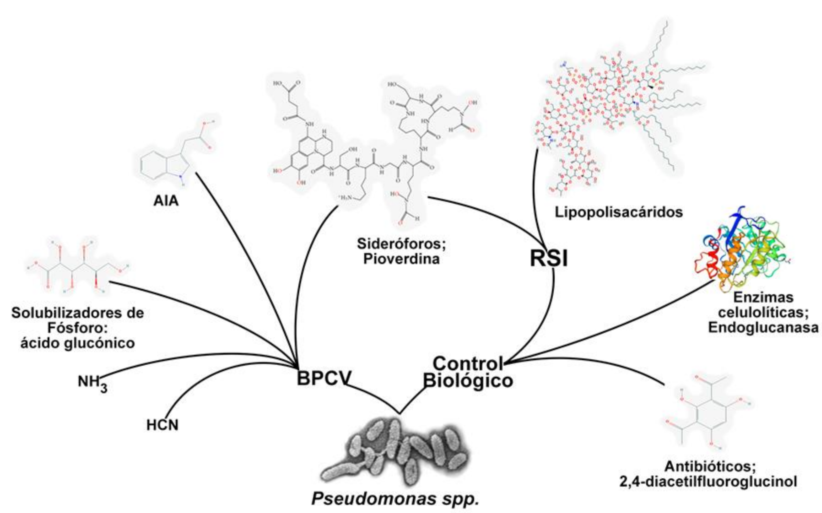


**Figure 1. General description of *Pseudomonas* spp. as PGPB and biological control agent.** Of the image structures NCBI PubChem (https://pubchem.ncbi.nlm.nih.gov).

*Pseudomonas* spp. have a wide metabolic repertoire, which allows them to act as plant growth-promoting bacteria (PGPB), due to the production of phytohormones such as indoleacetic acid (IAA), phosphorus solubilizers such as gluconic acid, the fixation of atmospheric nitrogen to ammonia

(NH3) and the production of hydrocyanic acid (HCN); likewise, they have the capacity for biological control by stimulating induced systemic resistance (ISR) by means of lipopolysaccharides on the cell surface and the production of siderophores, such as pyoverdine; in addition to the secretion of cellulolytic enzymes and the wide range of antibiotics such as pyoluteorin.

## Role in biological control

This genus has an exceptional capacity to produce a wide variety of antibiotics, some of them of the polyketide type such as 2,4-diacetylphloroglucinol (DAPG), mupirocin and pyoluteorin (Bender *et al*., 1999; Kankariya *et al*., 2019), as well as pyrrolnitrin, compounds derived from phenazine, and cyclic lipopeptides such as orphamide A, Pseudofactin and viscosin (Figure 2) (Quan *et al*., 2010; Jang *et al*., 2013; Ma *et al*., 2016; Malviya *et al*., 2020), the production of these compounds is modulated by exogenous, biotic or abiotic factors, such as the addition of fertilizers, the carbon source and the minerals that influence their synthesis. For example, the addition of glucose to the growth medium of *Pseudomonas* significantly increases the production of DAPG, while the supplementation of the culture medium with phosphate represses its synthesis (Kumar *et al*., 2017; Kankariya *et al*., 2019).

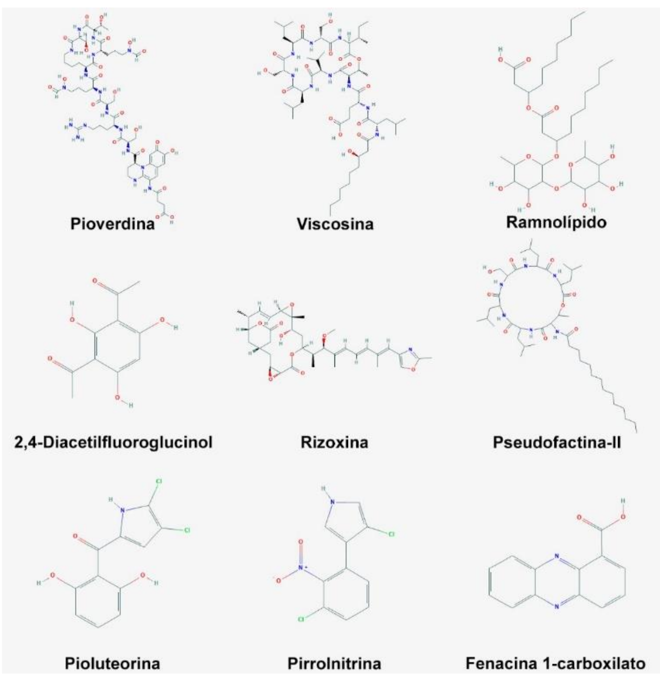


**Figure 2. Metabolic arsenal produced by *Pseudomonas* spp.** Of the image structures NCBI PubChem (https://pubchem.ncbi.nlm.nih.gov).

DAPG is a phenolic-type antibiotic, a broad spectrum of inhibition against bacteria, fungi, nematodes has been reported, it has been associated with suppressive soils and is a key component in the biocontrol of root and seedling diseases; such as black root rot in tobacco plants, control of phytopathogenic fungi such as *Thielaviopsis basicola*, *Pythium ultimum*, *Gaeumannomyces graminis* var tritici (Keel *et al*., 1990; Bender *et al*., 1999; Weller *et al*., 2007; Kankariya *et al*., 2019; Keswani *et al*., 2020); likewise, it has been observed that, at low concentrations, it has beneficial effects on plant growth.

DAPG production appears to be specific to *P. fluorescens*, *P. protegens*, *P. chlororaphis* and *P. brassicacearum* (Ramette *et al*., 2011; Gutiérrez-García *et al*., 2017). Suppressive soils are defined as those in which a pathogen cannot establish itself or persist, or if it establishes itself, it causes little damage to the plant (Baker and Cook, 1991), this type of soil provides a good example of how the rhizosphere stimulates and maintains edaphic microorganisms as a defense against soil-borne pathogens.

The mechanisms through which these microorganisms carry out their action in suppressive soils are: competition for nutrients, induction of systemic resistance, production of antibiotics and siderophores, among others (Jara and Elizondo, 2011), with *Pseudomonas fluorescens* being one of the most important groups of antagonistic microorganisms (Weller *et al*., 2002; Weller *et al*., 2007; Jara and Elizondo, 2011), as in the case of the monoculture of peas and flax, where evidence of DAPG production by *P. fluorescens* in the roots of these crops has been documented (Weller *et al*., 2002).

The mechanism of action of DAPG is not very specific and depends on its concentration. It has been observed that it alters the ionophore channels, damaging the cell membrane and organelles; in the mitochondria, it interrupts the membrane potential and generates an increase in the production of reactive oxygen species, in the chloroplast, it inhibits photosynthesis and in bacteria, it alters the integrity of the cell membrane (Kwak *et al*., 2011; Troppens *et al*., 2013; Kankariya *et al*., 2019; Julian *et al*., 2021).

Phenazine-derived antibiotics include a large family of tricyclic compounds with nitrogen, synthesized from the shikimic acid pathway, some phenazines have been reported to exhibit antibiotic, antifungal, insecticidal, antitumor, chemopreventive against certain types of cancer, antiplasmodial, antimalarial and antiparasitic activities (Smirnov and Kiprianova, 1990; Guttenberger *et al*., 2017).

The synthesis of these compounds is widely distributed in this genus, particularly *P. synxantha* strain 2-79 was one of the first bacteria identified in the production of phenazine-1-carboxylate (P1C) (Figure 2) (Biessy and Filion, 2018), *P. aureofaciens* strain 30-84 produces P1C, 2-hydroxyphenazine-1-carboxylate (OHP1C) and 2-hydroxyphenazine (2OHP) (Pierson and Thomashow, 1992) and *P. chlororaphis* PCL1391 produces P1C and phenazine-1-carboxamide (P1CN), which have been observed to suppress stem and root rot in tomato, caused by *F. oxysporum* f. sp. *radicis-lycopersici* (Turner and Messenger, 1986; Smirnov and Kiprianova, 1990; Chin-A-Woeng *et al*., 2003; Mavrodi *et al*., 2006; Ramette *et al*., 2011), another phenazine derivative, pseudobacterin-2, produced by *P. aureofaciens* strain BS1393, isolated in 1991 from the rhizosphere of barley in Voronezh, Russia, has been shown to be harmless to insects, fish, animals and humans, for which it was authorized in the Russian Federation in 1999 for its use against a wide range of phytopathogenic bacteria, fungi such as *Rhizoctonia*, *Fusarium* and the oomycete *Phytopthora* (Thomashow, 2013).

Its mechanism of action is based on altering the redox state of key metabolites inside the cell, through its dissemination or insertion into the cell membrane, acting as a reducing agent, which triggers the uncoupling of oxidative phosphorylation, as well as the production of superoxide radicals and hydrogen peroxide, which are toxic to the organism (Chin-A-Woeng *et al*., 2003).

Pyrrolnitrin (PRN) is a secondary metabolite derived from tryptophan, it has strong antifungal activity against a wide range of fungi, including Deuteromycetes, Ascomycetes and Basidiomycetes (Ligon *et al*., 2000), is produced by most strains of *Pseudomonas*, PRN was reported for the first time in 1964, from *Pseudomonas pyrrocinia*, which was isolated by Imanaka, Kousaka, Tamura and Arimase, since that time, this compound has been produced using different strains and is of great importance in the agricultural, pharmaceutical and industrial fields (Pawar *et al*., 2019), its efficacy has been proven against different types of gram-positive bacteria and against phytopathogenic fungi such as *R. solani*, different types of *Fusarium* such as *F. graminearum*, *F. culmorum*, *F. sambucinum*, *Pyrenophora triticirepentis*, *Thielaviopsis brassicola*, *Verticillium dahlia* and *Alternaria* spp., in addition, control of damping-off in cotton and cucumber, yellow leaf spot in wheat, dry rot in potatoes, and sunflower wilt has been reported (Quan *et al*., 2010; Pawar *et al*., 2019).

The mechanism of action of PRN is the attack on the cell membrane, by combination with phospholipids, affecting its permeability, which results in osmolar deregulation, at low concentrations, it uncouples oxidative phosphorylation and at high concentrations, it inhibits the electron transport chain, it also inhibits the synthesis of proteins and nucleic acids (Nose and Arima, 1969; Lambowitz and Slayman, 1972).

Cyclic lipopeptides (CLPs) are characterized by being synthesized by a non-ribosomal multi-enzymatic system, they are structurally diverse metabolites, they are made up of a fatty acid residue of 5 to 16 carbons and an amino acid chain length that ranges from 7 to 25 units, of which 4 to 14 form a lactone ring, based on the length and composition of the fatty acid and amino acid residues, they are classified into seven groups: viscosins, syringomycins, amphisins, putisolvins, tolaasins, syringopeptins, orphamides, and xantholysins (Raaijmakers *et al*., 2006; Gross and Loper, 2009; Geudens and Martins, 2018; Keswani *et al*., 2020).

Antagonistic activity against different phytopathogenic fungi and bacteria has been reported, as well as insecticidal activity for viscosin produced by *P. fluorescens* strain HS 870031 (Khan *et al*., 2016) and orphamide A, produced by *P. Protegens* (Loper *et al*., 2016), the action mechanism of CLPs is based on the formation of pores in the membranes, which coincides with the amphipathic nature of this type of metabolite. This membrane disturbance produces an ionic imbalance, directly affecting the formation of pH gradients, breaking the balance of $H^+$, $Ca^{2+}$ and $K^+$ (Aiyar *et al*., 2017; Geudens and Martins, 2018), which induces changes in calcium-mediated signaling and leads to cell death.

**Cellulolytic enzymes**

Another of the mechanisms used by phytopathogen biocontrol microorganisms is the synthesis of enzymes capable of degrading the cell wall, such as β-1,3-glucanase (Figure 1), chitinases, cellulases and proteases, which exert an direct inhibitory effect on the growth of pathogens, these enzymes have been detected in different strains of *P. aeruginosa* and *P. fluorescens* that have been shown to have chitinolytic activity (Neiendam and Sørensen, 1999; Kumar *et al*., 2017).

### Systemic resistance induced (ISR) by *Pseudomonas* spp.

The ISR is a state of defense that the plant develops against specific chemical or biotic stimuli (Van Loon *et al*., 1998), these defense mechanisms allow restricting or blocking the ability of pathogenic microorganisms to produce diseases, which are regulated by a network of physical interconnections and chemical signaling pathways, where jasmonic acid (JA) and ethylene (ET) participate, which results in partial or complete resistance against subsequent attack by pathogens.

The characteristics of this type of induced resistance are its long-distance action, long-lasting resistance, host specificity, and protection against a wide range of pathogens (Chin-A-Woeng *et al*., 2003; Kumar *et al*., 2017). It operates through signals produced by wounds, where the phytohormones JA and ET participate, this type of resistance is associated with the detection of molecular patterns present in bacteria, such as lipopolysaccharides (LPS), specifically the O antigen, as demonstrated in the study conducted with LPS of *P. fluorescens* WC417r against *Fusarium oxysporum* f. sp. *dianthi* in carnation, where purified LPS of the bacterial strain were applied to plant roots, triggering ISR (Van Peer and Schippers, 1992; Preston, 2004). It has also been observed that the CLP orphamide acts as an inducer of ISR, stimulating the expression of genes related to the defense against the fungus *Cochliobolus miyabeanus* in rice plants (Ma *et al*., 2017), similarly, pyoverdine, which is an iron-chelating siderophore (Figure 2), promotes ISR, as has been reported for *P. putida* WCS358 in the suppression of bacterial wilt in *Eucalyptus urophylla* caused by *Ralstonia solanacearum*, where foliar application of the purified metabolite pseudobactin 358 or the bacterium significantly reduced bacterial wilt, after inoculation with *R. solanacearum* (Ran *et al*., 2005).

The induction of resistance depends on the colonization of the root system by the inducing bacteria, which must be in sufficient numbers to trigger the ISR, which is achieved by adding bacterial suspensions to the soil before sowing, or at transplantation, or by covering seeds with high concentration of bacteria (Van Loon *et al*., 1998; Pieterse *et al*., 2001).

## Function of *Pseudomonas* spp. as plant growth-promoting bacteria

### Siderophore production

$Fe^{3+}$ is fundamentally found in nature forming part of salts and hydroxides with very low solubility, a direct mechanism that contributes to the acquisition of this nutrient is the production of siderophores, *Pseudomonas* spp. produce pyoverdine (Figure 2), siderophore synthesized from ornithine, it contains a dihydroxyquinoline derivative. The structure of the peptide differs among *Pseudomonas*, more than 40 different structures have been described, while the chromophore remains highly conserved and is bound to a peptide chain exhibiting two hydroxamate groups and one hydroxycarboxylate group, this type of chromopeptide siderophores are very characteristic of this genus and are of considerable importance in the agricultural field since they mediate iron uptake (Wendenbaum *et al*., 1983; Sah and Singh, 2015), by binding to $Fe^{3+}$, they convert the insoluble form into soluble, which facilitates absorption by plants and bacteria.

### Phosphorus solubilization

Phosphorus is an essential macroelement in plant growth and development, naturally this element is in an insoluble form, not assimilable by plants, therefore, the solubilization and remineralization of phosphorus is an important feature in PGPB, where thanks to the synthesis of low molecular weight organic acids, such as gluconic (Figure 1) and citric acids, which have the ability to chelate this element and thus facilitate its assimilation (Rathinasabapathi *et al*., 2018).

### Phytohormone production

Plants modulate their hormones during their life cycle, a very important aspect that can alter this process is biotic or abiotic stress, PGPB synthesize significant amounts of plant hormones, which allows them to modulate the growth and development of their hosts. Indole 3-acetic acid is one of the auxins produced by *Pseudomonas* spp., it plays a very important role in cell division, differentiation, seed germination, control of vegetative growth, induction of lateral and adventitious roots, photosynthesis, synthesis of pigments and secondary metabolites (Kumar *et al*., 2017).

## Conclusions

To understand the complexity of the interaction between plants and microorganisms, it is imperative to know all the biomolecules that their bacterial symbionts are capable of producing and how they can affect plant growth and development, modulating immune responses against phytopathogens and the acquisition of nutrients from the environment, in the particular case of *Pseudomonas*, a wide metabolic repertoire is known, which has been correlated with different functions, among which their phytopathogen biocontrol capacity stands out, thanks to the metabolic arsenal that they can synthesize, this type of microorganism represents one of several microbial species of agricultural interest that can impact food production, reducing the use of fertilizers and agrochemicals, given its metabolic characteristics and characteristics of interaction with the plant.

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