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Bacterial siderophores: a biotechnological alternative for sustainable agriculture

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KEYWORDS

Biocontrol, biofertilizers, iron, siderophores, sustainable agriculture

HIGHLIGHTS

- This review integrates current knowledge on the biosynthesis, classification and regulation of bacterial siderophores, emphasizing their ecological and agricultural relevance.
- It explores how siderophore-producing plant growth-promoting rhizobacteria enhance plant iron acquisition and suppress phytopathogens through multiple molecular mechanisms.
- This work highlights the biotechnological potential of siderophores as sustainable tools to reduce agrochemical dependence and promote environmentally friendly crop management strategies.
- It underscores the need for functional and molecular studies to elucidate how siderophores promote plant immunity and to advance their biotechnological application in ecofriendly agriculture.

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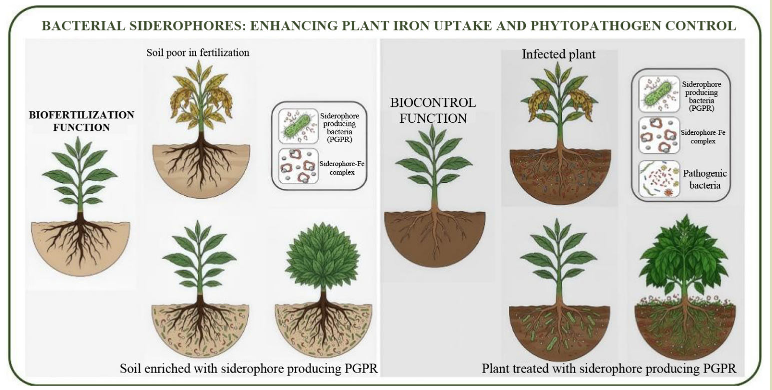
GRAPHICAL ABSTRACT



ABSTRACT

Iron is an essential element for all organisms due to its involvement in numerous cellular processes. Siderophores, which are small organic molecules produced by microorganisms, chelate iron and have significant biotechnological potential. Plant growth-promoting rhizobacteria (PGPR) that synthesize siderophores can improve plant iron uptake and contribute to the management of phytopathogens. Elucidating the biosynthesis and functional roles of siderophores in plant growth is important for developing ecological strategies that minimize agrochemical use, and mitigate pest and disease damage. This review examines the classification, biosynthesis, transport and regulation of bacterial siderophores, highlights prominent siderophore-producing PGPR, and discusses the mechanisms by which siderophores facilitate plant growth and phytopathogen suppression.

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1 Introduction

Agricultural productivity has increased considerably in recent decades. This is due to technologies from the green revolution and the expansion of land and water use. Progress in agriculture has aided global food security. It also offers business opportunities and is key for economic development, providing jobs for millions[1,2]. The world population in 2050 may reach 9.5 billion. This would mean a 70% increase in food demand. Meeting this need requires stable food security through sustainable agriculture[3–5]. Achieving this production goal requires supplementing soil with chemical fertilizers like nitrogen and phosphorus. These fertilizers can harm soil fertility and microbial diversity and can contaminate surface and groundwater[1,2,6]. Nutrient accumulation in the environment from excessive fertilizer use relates to changes in environmental and climate factors, such as temperature, precipitation, droughts and floods. It is also linked to the spread of pests and diseases resistant to chemicals. This would significantly affect crop yields[7,8].

The use of biofertilizers in agriculture helps meet growing demand for healthy, safe food with long-term sustainability. Biofertilizers also improve soil biodiversity[9,10]. Plant growth-promoting rhizobacteria (PGPR) live in the rhizosphere and roots. They offer important advantages, such as more nutrient availability and resistance to pathogen attack. This results in higher yields for important crops.

PGPR help plants grow through direct and indirect mechanisms. Direct benefits include nitrogen production or uptake, hormone and iron supply (via bacterial siderophores), and phosphate solubilization. Indirect benefits occur when PGPR control the growth of phytopathogens via antibiotics, siderophores, and lytic enzymes (Fig. 1) [1,11–14].

Siderophores are small organic compounds from microorganisms and plants that grow in low-iron conditions. They capture Fe^{3+} from land and water, making it available to microbes and plants. Siderophore production is related to the spread and virulence of pathogens. However, they also help plant growth in several ways. Phylogenetic analysis using

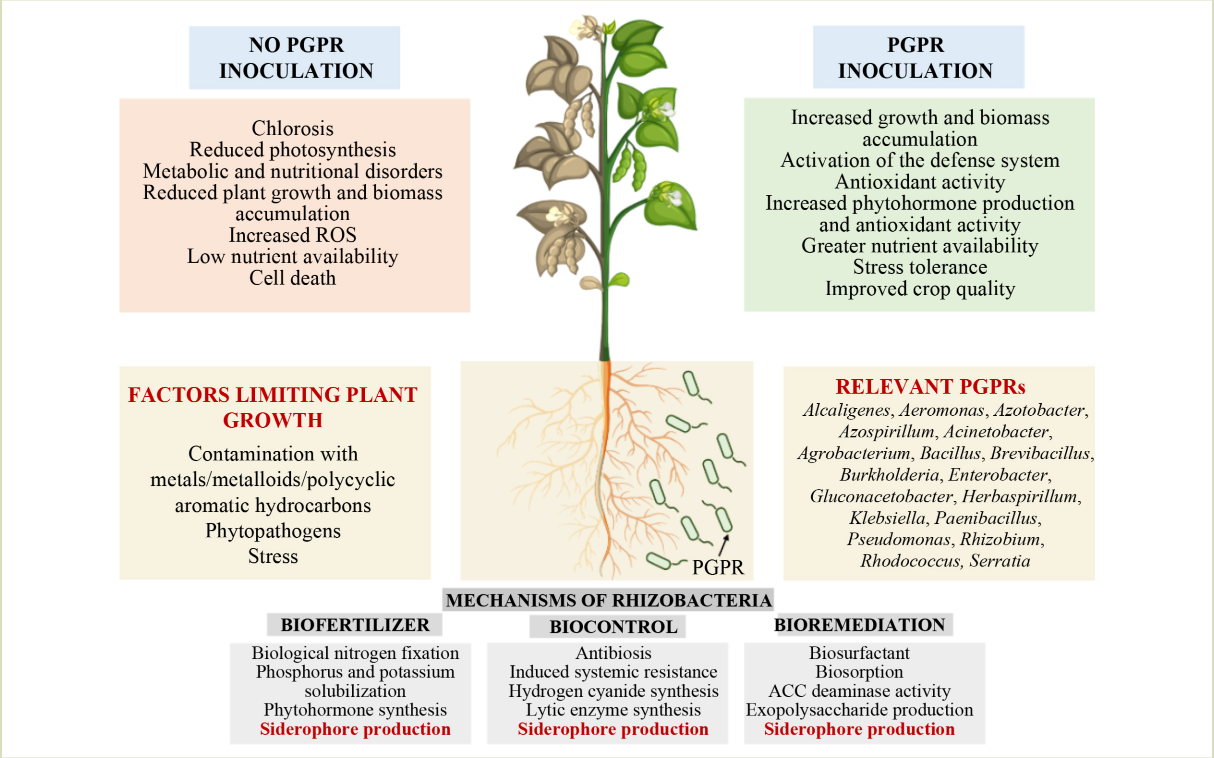

Fig. 1 Schematic representation of growth-promoting rhizobacteria (PGPR) mechanisms and their effect on promoting plant growth.

multilocus sequence typing groups siderophore-producing PGPR into the following bacterial orders: Enterobacterales, Pseudomonadales, Neisseriales, Burkholderiales, Rhodospirillales, Rhizobiales, Actinomycetales, and Bacillales (Fig. 2). The genera include: *Alcaligenes, Aeromonas, Azotobacter, Arthrobacter, Azoarcus, Azospirillum, Acinetobacter, Agrobacterium, Aneurinibacillus, Bacillus, Beijerinckia, Brevibacillus, Burkholderia, Enterobacter, Gluconacetobacter, Gluconobacter, Herbaspirillum, Klebsiella, Paenibacillus, Pseudomonas, Rhizobium, Rhodococcus, Saccharothrix, Serratia, Thiobacillus* and *Variovorax*[15–18].

This review details the synthesis, transport and regulation of bacterial siderophores and brings together various studies that have used or referenced beneficial siderophore-producing bacteria that positively affect plant growth and development.

2 Iron absorption

2.1 Role of iron in living organisms

Iron is the fourth most abundant element and the second most abundant metal on earth; it is essential for the life of all organisms, as it participates in cellular processes such as DNA synthesis, the tricarboxylic acid cycle, the electron transport chain, oxidative phosphorylation, nitrogen fixation and the biosynthesis of aromatic compounds[22,23]. Under physiological conditions, iron can exist in two interconvertible oxidation states, ferrous (Fe^{2+}) and ferric (Fe^{3+})[24,25]. Its biological functionality depends on its incorporation into proteins, either as a mono- or binuclear species, or in more complex forms as part of mixed iron/sulfur groups or in the heme group[24]. Its

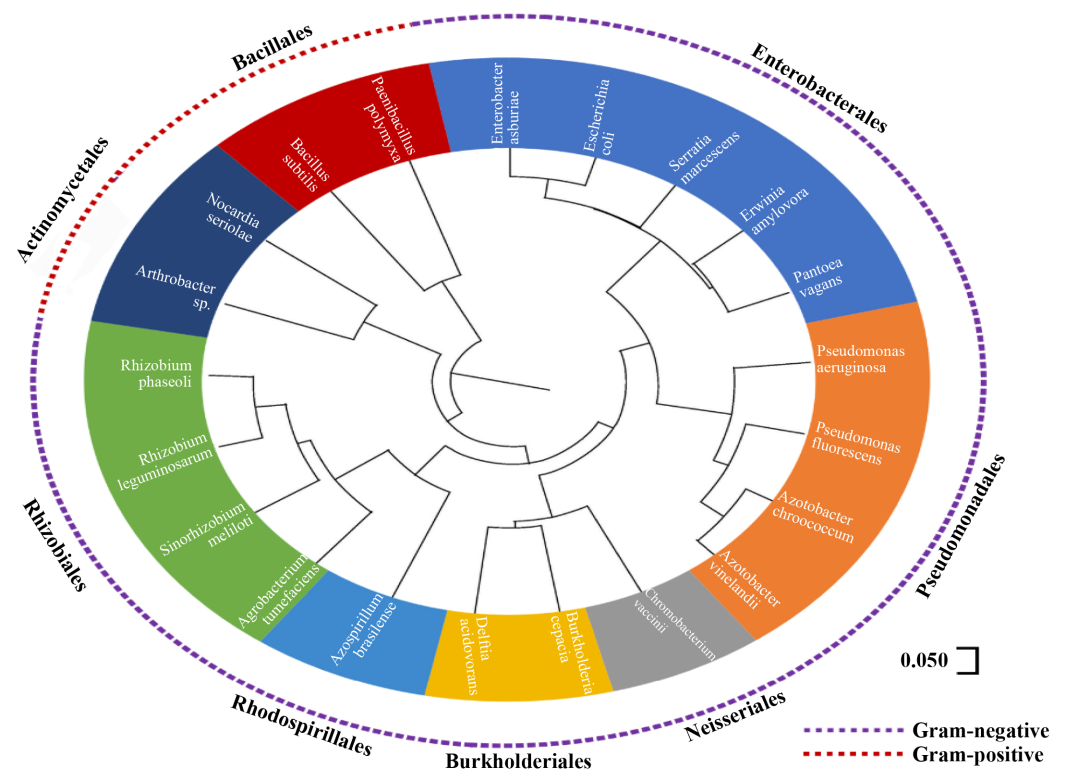

Fig. 2 Phylogenetic analysis of siderophore-producing, growth-promoting rhizobacteria associated with plant growth promotion. Phylogenetic analysis of siderophore-producing PGPR associated with plant growth promotion. Multilocus sequence typing analysis was performed with a concatenated sequence of four housekeeping genes (*gyrB*, *ftsZ*, *pyrH* and *recA*) for each species, using the services of the NCBI (The National Center for Biotechnology Information) to consult DNA sequence databases and the BLAST algorithm[19] for specific sequence identification. Sequence alignment and phylogenetic tree construction were performed using BioEdit version 7.2.5[20] and MEGAX version 10.2.2[21].

deficiency can reduce nucleic acid synthesis and also inhibit bacterial growth, causing morphological changes in bacteria[22].

The synthesis of iron-binding proteins reduces their availability, causing iron deficiency that limits bacterial growth and gives the host the time needed to eradicate the infection through various defense mechanisms. Meanwhile, an increase in free iron can cause toxicity due to the generation of reactive oxygen species[26].

Strict regulation of iron uptake prevents its accumulation to toxic levels that promote reactive oxygen species (ROS) production. A robust antioxidant stress response is also essential for maintaining iron homeostasis[27]. Plants require iron in the Fe^{2+} form for chlorophyll synthesis, enzyme function in cellular respiration and key metabolic processes such as the tricarboxylic acid cycle, oxidative phosphorylation and photosynthesis. Despite its abundance in soil, iron is often unavailable to plants due to its presence as poorly soluble ferric ion[1,12,28,29]. Ferric chlorosis, a nutritional disorder resulting from low iron availability, impairs plant growth and reduces crop productivity. Chlorosis is characterized by a contrast between green and yellowish tissue, reflecting chlorophyll deficiency[30]. Iron accessibility in soil decreases as redox potential and pH increase[31]. Certain PGPR can colonize the rhizosphere and enhance iron uptake by synthesizing and releasing siderophores, thereby increasing and regulating iron bioavailability under appropriate conditions[32].

2.2 Mechanisms of iron assimilation in bacteria

Ferrous iron is present in soil at low concentrations, in the range 10^{-10}–10^{-9} $mol{\cdot}L^{-1}$, whereas living organisms require levels between 10^{-7} and 10^{-5} $mol{\cdot}L^{-1}$[33,34]. To overcome the limited availability of Fe^{3+} in soil, bacteria have developed multiple iron uptake strategies. Siderophore production represents the primary iron chelation mechanism[1,35]. In addition, Gram-negative pathogenic bacteria can acquire iron by directly binding transferrin, lactoferrin or heme-containing proteins to specific substrate receptors located in the bacterial outer membrane. This process enables iron extraction through direct interaction between the bacterial receptor and the host protein[36]. This recognition is specific, for example, in *Actinobacillus pleuropneumoniae*, *Haemophilus influenzae*, *Neisseria gonorrhoeae* and *N. meningitides*, which take iron from human transferrin and lactoferrin [37–41].

The FeO system, first identified in *Escherichia coli*, is a mechanism for capturing Fe^{2+}, which is relatively more soluble at neutral pH than Fe^{3+} and can therefore be transported more easily across the outer membrane. However, the ferrous form only predominates under reducing or anaerobic conditions[22,38]. The heme group is an important source of iron and can be acquired by pathogenic bacteria through specific outer membrane transport proteins dependent on the TonB protein, which are coupled to ABC-type inner membrane transporters. Once inside the cell, the heme group is recycled by the bacteria and incorporated into their metabolism[38]. Heme utilization genes have been identified in pathogenic vibrios, such as *Vibrio anguillarum, V. cholerae,* and *V. vulnificus*[42–44].

Most bacteria possess iron uptake systems mediated by siderophores (from the Greek *sideros*meaning iron and *phores* meaning carrier)[34,35]. Siderophores are small molecules, between 500 and 1500 daltons in molecular weight, with a high affinity for ferric iron (Fe^{3+}) of 10^{-20}–10^{-30} $mol{\cdot}L^{-1}$, synthesized by many bacteria such as *Azospirillum*, *Azotobacter*, *Bacillus*, *Brevibacillus*, *Enterobacter*, *Mesorhizobium*, *Paenibacillus*, *Pseudomonas*, *Rhizobium* and *Serratia*[1,45–48]. Siderophores are widely recognized as key virulence factors of pathogenic bacteria[39,49–54]. However, bacterial siderophores also contribute to iron uptake that promotes plant growth by converting insoluble iron into soluble iron[1,29,34,45].

3 Siderophores

3.1 Synthesis of siderophores

Siderophores were discovered in the 1950s when ferrichrome A and mycobactin were identified in the fungi *Ustilago sphaerogena* and *Mycobacterium avium* subsp *paratuberculosis*, respectively[55,56]. To date, more than 500 different siderophores have been identified, demonstrating their importance, specificity and variety being classified into microbial siderophores and phytosiderophores[1,57,58]. Variations in siderophore structure produce differences in iron affinity, optimal pH, membrane compartmentalization, and the ability to evade lipocalin 2, a molecule produced by the host that is capable of inactivating certain siderophores[59].

Bacterial siderophores can be divided into three large families based on the chemical groups involved in iron binding: hydroxamates, carboxylates and catecholates/phenolates (Fig. 3)[59]. Each family of siderophores has distinctive characteristics that affect their affinity for iron, but all use negatively charged oxygen atoms to coordinate the binding with the ferric ion (Fe^{3+}). Mixed-type siderophores with uncommon iron-binding chemical groups such as amines or heterocyclic structures have also been characterized (Fig. 3), for example, aerobactin, anguibactin, mycobactin, pyoverdin and yersiniabactin[33,57,60–62]. Iron-binding groups are usually bidentate and form pseudo-octahedral and hexadentate coordination complexes around the ferric ion[46].

The four types of siderophores are recognized by the functional group involved in iron chelation. Mixed-type siderophores contain different chemical groups; hydroxamate in yellow, catecholate in red and carboxylate in green.

According to their chemical structure and metal-binding groups, the three families of siderophores have different characteristics[59] (Table 1).

Various studies show that bacteria can produce multiple types of siderophores. For example, *Pseudomonas aeruginosa* produces pyoverdine and pyochelin, *E. coli* produces enterobactin and aerobactin and *Streptomyces coelicolor* produces deferoxamine E, deferoxamine B, and coelichelin. The ability to produce multiple siderophores, each with different properties and affinities for binding metal ions, provides a survival and growth advantage in diverse environments[35,38].

Most siderophores are synthesized by non-ribosomal peptide synthetases (NRPSs) or by mixed NRPS-polyketide synthetase systems. Some bacterial siderophores, including staphyloferrin

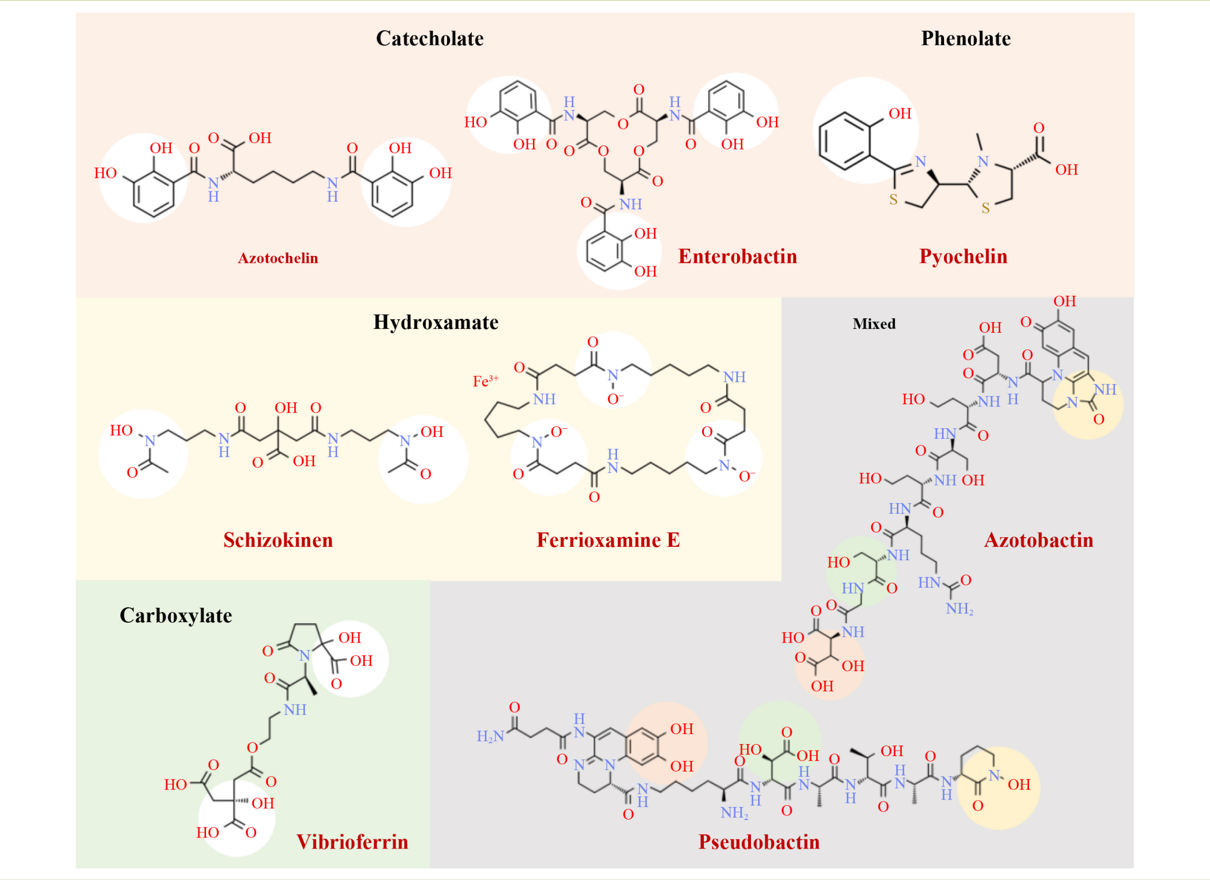

Fig. 3 Examples of the main classes of siderophores.

Table 1 Iron affinity of siderophores

Siderophore type	Iron affinity	Siderophore example
Catecholates	Medium	Enterobactin, bacillibactin and spirilobactin
Hydroxamates	Low	Shizokinen, rhizobactin and vicibactin
Carboxylates	Variable: high at acidic pH and low at physiological pH	Staphyloferrin and rhizoferrin

A and B in *Staphylococcus aureus*, petrobactin in *Bacillus anthracis* and alcaligin in *Bordetella pertussis*, are produced through NRPS-independent pathways[62,63]. NRPSs contain three core domains: an A domain responsible for substrate recognition, a peptidyl carrier protein that holds the activated substrate, and a C domain that catalyzes peptide bond formation. Additional domains may be present to facilitate cyclization or other modifications of the final compound[64].

The biosynthesis of siderophores in bacteria is induced by intracellular iron deficiency and is regulated by the Fur repressor (Fig. 4)[62]. Seven proteins are required for the synthesis of enterobactin in *E. coli*: EntABCDEFH. 2,3-dihydroxybenzoic acid (DHBA) is produced from chorismate by the synthesis of EntC, EntB and EntA. DHBA is the functional group of catecholate-type siderophores. Next, three DHBA molecules are condensed with three L-serine molecules through the synthesis of NRPSs, whose reactions are catalyzed by EntE, EntB, EntD and EntF[65–67]. After synthesis, siderophores are secreted into the extracellular medium by three main types of transporters: the major facilitator superfamily, the resistance-nodulation-division superfamily and the ABC superfamily[62].

At high iron concentrations, the Fur and Fe^{2+} complex is formed, which binds to the Fur box to prevent transcription of the siderophore operon genes. At low iron concentrations, Fe^{2+} is released from Fur proteins, allowing transcription of the siderophore synthesis and transport genes. (Adapted from Galvis et al.[50]).

A high concentration of iron causes the formation of the Fur and Fe^{2+} complex in the promoter region, which prevents the transcription of genes involved in transport, while at low concentrations, Fe^{2+} is released from Fur proteins, causing the transcription of iron transporter genes. At high iron concentrations, the Fur protein undergoes conformational changes and binds to the Fur box to prevent the transcription of siderophore genes. At low concentrations, the Fur protein does not bind to iron II, allowing the transcription of siderophore-related genes, synthesis of siderophore proteins and their transport to the extracellular space for iron uptake.

3.2 Transport of siderophores

Microorganisms deprived of iron secrete siderophores into the extracellular environment. These molecules form highly stable

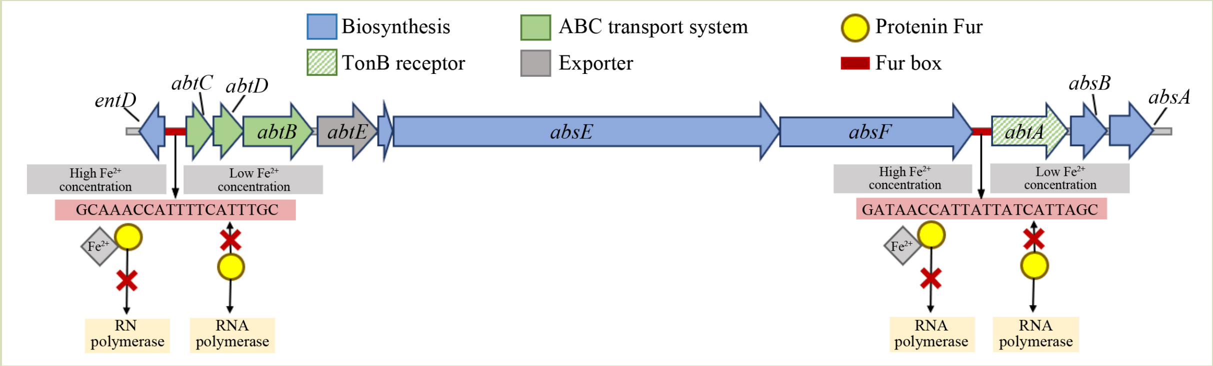

Fig. 4 Regulatory system for the expression of amphibactin synthesis proteins and transport to the extracellular space for iron uptake.

complexes with iron, which are then transported into the cell via specific transporters. In Gram-negative bacteria, the process initiates when the Fe^{3+}-siderophore complex binds to TonB-dependent transporters located in the outer membrane. The most extensively studied of these transporters are FepA (enterobactin), FhuA (ferricromcin) and FecA (ferric citrate) in *E. coli*, as well as FptA and FpvA in *P. aeruginosa*. The TonB system supplies the energy required for translocation of the ferri-siderophore complex into the periplasm. Once in the periplasm, the siderophore binds rapidly to a specific periplasmic binding protein and is subsequently transported across the inner membrane by an ATP-binding cassette (ABC) transporter. The ABC transporter system comprises two proteins: one functions as a permease to facilitate membrane passage, while the other provides the necessary energy for transport. Upon entry into the cytoplasm, iron is released from the siderophore complex by cytoplasmic reductases, which are generally not specific to the iron acquisition system. In *E. coli*, an alternative mechanism involves esterase enzymes that degrade the siderophore, thereby releasing iron into the cytoplasm[62, 65–67].

3.3 Regulation of siderophore systems

In Gram-negative bacteria, iron metabolism is primarily regulated by the Fur repressor. Under iron-rich conditions, the Fur protein binds to a conserved palindromic DNA sequence known as the Fur box, repressing transcription of iron uptake genes. When intracellular iron levels decrease, Fur dissociates from DNA, resulting in increased transcription of these genes. Thus, intracellular iron concentration directly modulates the expression of genes involved in iron metabolism[62,68–70]. In contrast, *E. coli* has a distinct regulatory system for ferric citrate acquisition that is activated by ligand binding at the cell surface[71]. While iron is essential for bacterial growth, excessive iron is toxic due to the generation of hydroxyl radicals via Fenton and Haber-Weiss reactions. Therefore, precise regulation of iron acquisition mechanisms is essential[72,73].

3.4 Social interactions mediated by siderophores

Some studies have reported that siderophore-producing bacteria can, in principle, affect both unwanted competitors and beneficial microorganisms, depending on environmental conditions and iron and nutrient dynamics. Control mechanisms may be due to competition for iron, in which siderophore production increases its availability to bacteria by capturing and transporting it with high affinity. It could also depend on the siderophore spectrum, in which different bacteria produce siderophores with specific affinities and receptors. To mitigate this effect, beneficial microorganisms could respond, for example, by (1) modifying the microenvironment (e.g., altering the local pH or competing for other nutrients), (2) effecting cooperative behavioral strategies, such as sharing siderophores to collectively access iron and compensate for loss, (3) increasing the production of their own siderophore, or (4) acting as cheaters, producing receptors for the siderophores of other bacteria. This network of iron interactions must be considered when using siderophore-producing bacteria as a biological control alternative, as the introduction of siderophores or the manipulation of iron availability could have collateral effects on the community[59,74,75].

Interactions within bacterial communities are important for plant resistance to pathogen infections. For example, facilitating metabolic interactions within inoculated bacterial consortia can promote the growth of pathogens if they can use the same metabolites. However, if metabolic interactions are more specific, they may benefit only members of the inoculated consortium and have no effect, or even negative effects, on pathogen growth through resource competition. Different studies have shown that siderophore-mediated interactions can be used as an effective strategy for designing functional microbial inoculants, where the interaction between siderophores can promote or limit pathogen invasion depending on the composition of the inoculum[76–79]. *Pseudomonas* spp. consortia have been used to suppress *Ralstonia solanacearum*, demonstrating that siderophore-mediated interactions significantly enhance the antagonistic effect of the consortium against the pathogen[80]. In another study, six combinations of bacteria efficient for mineral solubilization and siderophore production were tested and identified as *Erwinia persicina, Serratia marcescens*, *S. nematodiphila* and *S. surfactantfaciens*. It was observed that one of the combinations significantly increased the growth and physiological parameters of oat plants compared to other microbial consortia developed, the control and mineral fertilizers[81]. This shows that microbial consortia increased growth parameters compared to treatments with a single inoculant. Therefore, they can be used as potential biofertilizers and biocontrol agents to eradicate low yields in crops of agronomic interest.

3.5 Siderophores also have the ability to activate plant immunity

Several studies have shown that iron capture by siderophores is a unique mechanism that triggers typical plant immune responses. Transcriptomic analyses in bacteria demonstrated that 69 of 133 iron-sensitive genes were reprogrammed in plants with pattern- or effector-activated immunity, compared to the transcriptomes of bacteria grown in disease-susceptible plants. Bacterial genes that are repressed by iron were also repressed by plant immunity, indicating that a component of plant immunity is to repress genes involved in iron uptake[82]. The siderophore chrysobactin, produced by *Dickeya dadantii*, promotes systemic colonization of the bacterium in *Arabidopsis* sp. leaves and activates plant response to iron deficiency and the salicylic acid pathway, which can repress the jasmonic acid defense pathway necessary for plant defense against *D. dadantii*. In addition, chrysobactin causes the regulation of the iron storage gene FER (iron-binding ferritins), which is involved in defense against *D. dadantii*[82–84]. *Arabidopsis* sp. plants deficient in FER expression are more susceptible to *D. dadantii*, where FER gene expression is triggered by plant perception of iron depletion, rather than by the siderophore itself. In *Nicotiana tabacum*, overexpression of FER prevented paraquat-induced ROS damage, indicating that iron sequestration to limit the Fenton reaction is effective against some pathogens[82]. The siderophore deferrioxamine, produced by *Erwinia* spp., *Pantoea* spp., *Pseudomonas* spp. and *Streptomyces* spp., was used to study the immune response of *Arabidopsis thaliana*, observing an accumulation of callose in the leaves, which is related to the susceptibility or resistance of the plant and can be suppressed by microbial effectors[85].

4 Application of siderophores in agriculture

Low Fe absorption by plants in poor soils leads to a decrease in photosynthesis, causing chlorosis that affects agricultural production. Siderophores produced by PGPRs can supply iron and promote plant growth. In addition, PGPRs synthesize siderophores that can limit the development of pathogenic microorganisms through competition. Therefore, siderophores can be considered an ecological alternative to reduce the adverse effects caused by phytopathogens and agrochemicals[86].

4.1 Biofertilizers

Iron is a micronutrient necessary for chlorophyll biosynthesis, redox reactions and other important physiological activities in plants, and its deficiency significantly reduces the quantity and quality of crop production[34]. Bacterial siderophores form complexes with Fe^{3+} by dissolving minerals. They promote plant growth by increasing the release of soil iron[87]. Numerous studies have illustrated the role of siderophores as potential biofertilizers.

Microbial activity in the rhizosphere significantly influences iron uptake in plants such as maize and sunflower (*Helianthus annuus*), as demonstrated in both sterile and non-sterile soils. Under non-sterile conditions, plants exhibited robust growth and optimal iron concentrations in their roots. In contrast, sterile conditions that suppressed siderophore production led to poor growth and marked iron deficiency[34,88,89]. Studies on cumin (*Cuminum cyminum*) compared chemical Fe chelators and Fe siderophores for iron fertilizer application. Chemical chelators improved plant growth and yield, whereas Fe siderophores were more effective for seed enrichment[90]. Also, combining iron with siderophore-producing rhizobacteria has proven to be a favorable and cost-effective strategy for enhancing potato (*Solanum tuberosum)* crop yields[91]. Collectively, these findings indicate that microbial siderophores are a promising source of iron for plants.

In this regard, it is known if different *Pseudomonas* species can improve plant growth by producing the siderophore pyoverdine[34,57,92]. Pyoverdine from *Pseudomonas fluorescens* was used in an iron-deficient growth assay with *A. thaliana*, in which the siderophore was supplied directly to the medium in the form of apo-pyoverdine (iron-free siderophore), mimicking the bacterial product. Inoculation with the siderophore reversed the iron deficiency phenotype and restored the growth of plants maintained in the iron-deficient medium. This demonstrated that iron is incorporated more efficiently with pyoverdine than with EDTA, as indicated by the significantly higher iron content of plants enriched with Fe-pyoverdine. The production of the siderophore pyoverdine by *P. fluorescens* improves iron nutrition in a plant species belonging to iron absorption strategy I[35,84,85]. Another study using different siderophore-producing strains of *Pseudomonas japonica* demonstrated the potential of these bacteria as PGPR in iron- and zinc-deficient soils of maize crops, resulting in higher yields after inoculation[93]. *Pseudomonas putida*, which produces the siderophore pseudobactin, was tested as an inoculum in the soil of beet (*Beta vulgaris*), potato and radish

(*Raphanus sativus*) crops, resulting in increased plant growth and yield[87].

Other siderophore-producing PGPR, such as *Bacillus sporothermodurans* (syn. *Heyndrickxia sporothermodurans*) and *Streptomyces tendae* F4, improve the growth and quality of sunflower plants. Also, it was determined that the chelating agent EDTA is not superior to the hydroxamate siderophores synthesized by *S. tendae* F4 in terms of solubilizing metals for plant absorption[94,95]. *Bacillus subtilis*, which produces bacillibactin, a catecholate-type siderophore, could be considered a potential bioinoculant, as it promoted iron absorption and growth in sesame (*Sesamum indicum)*[96]. *Azospirillum brasilense* is also used as a biofertilizer, producing hydroxamate and catecholate siderophores that can trigger response mechanisms to Fe deficiency in cucumber (*Cucumis sativus)* plants, even under conditions of Fe sufficiency, preparing plants to better resist iron limitation[97]. Likewise, *A. brasilense* can contribute to the iron nutrition of hydroponically grown strawberry plants (*Fragaria* sp.). This study also demonstrated that hydroxamate siderophores are more efficient than catecholates in supplying iron to plants[98]. The endophytic bacteria *Arthrobacter sulfonivorans* and *Enterococcus hirae*, which produce two siderophores, are associated with improved wheat (*Triticum aestivum*) yields in soils with low iron availability[99].

Siderophores are a source of iron in saline soils, where its bioavailability is reduced for plants. Two studies determined the presence of siderophores in *Achromobacter denitrificans*, *Bacillus aryabhattai* and *Ochrobactrum intermedium*, and the use of *B. aryabhattai* as a biofertilizer in rice (*Oryza sativa*) crops with low productivity caused by high salinity and iron deficiency. After inoculation with *B. aryabhattai*, increased plant growth was observed, which could be due to improved iron absorption that favors nutrient availability and the production of indole-3-acetic acid and chlorophyll[100,101]. The iron chelating capacity of *Azotobacter vinelandii, Bacillus megaterium* and *B. subtilis* was also demonstrated under alkaline conditions, determining their potential as PGPRs due to their production of siderophores and ability to correct chlorosis in calcareous soils[102] (Table 2).

Table 2 Growth-promoting rhizobacteria PGPR producers of siderophores reported as biofertilizers

Siderophore		PGPR	Reference
Type	Name		
Catecholate	Spirilobactin	*Azospirillum brasilense*	[103]
	Aminochelin	*Azotobacter vinelandii*	
	Azotochelin	*A. vinelandii*	
	Protochelin	*A. vinelandii*	
	Enterobactin	*Enterobacter asburiae, Escherichia coli, Serratia marcescens* and *Streptomyces* sp.	[59]
	Agrobactin	*Rhizobium radiobacter* (syn. *Agrobacterium radiobacter*)	[103]
	Bacillibactin	*Bacillus subtilis*	[96,103]
Hydroxamate	Anfibactin	*Azotobacter chroococcum*	[14,49]
	Rhizobactine	*Bacillus* megaterium, *Pseudomonas* sp. and Sinorhizobium *meliloti*	[58]
	Desferrioxamine	*Pantoea vagans*	[103]
	Schizokinen	*B. megaterium* and *A. vinelandii*	[102,103]
	Vicibactin	*Rhizobium leguminosarum* and *R. phaseoli*	[104,105]
	Ferrioxamine B	*Arthrobacter* sp., *Chromobacterium* sp., *Erwinia* sp., *Nocardia* sp., *Pseudomonas* sp. and *Streptomyces* sp.	[106–110]
	Desferrioxamine E	*Pseudomonas stutzeri*	[62,111]
	Delftibactin	*Delftia acidovorans*	[112,113]
Mixed	Pyoverdine	*Pantoea* eucalypti, Pseudomonas *fluorescens*	[57,92,114,115]
	Crochelin	*A. chroococcum*	[14,116]

4.2 Biocontrol agents

The primary bacterial mechanisms that inhibit phytopathogen proliferation include the production of antibiotics, bacteriocins and siderophores. Siderophore-producing PGPR decrease the availability of iron near plant roots, thereby limiting pathogen access to this essential nutrient (Fig. 5). These bacteria offer an effective alternative for disease management by enhancing crop yields and protection while reducing reliance on environmentally harmful chemical pesticides[117].

The production of siderophores by growth-promoting rhizobacteria (PGPR) can protect plants from virulence factors synthesized by phytopathogens, promoting plant growth. The plus and minus signs represent the effect of siderophore production (left plant) or virulence factors (right plant) on plant health.

Numerous studies have demonstrated the role of siderophores, mainly from *Bacillus* sp. and *Pseudomonas* sp., as biological control agents[15,34,57]. In 1980, the first study was published that demonstrated the importance of siderophore production as a mechanism for controlling the pathogen *Erwinia carotovora* by several strains of *P. fluorescens* isolated from potato roots[118]. A recent study reports the high efficiency of *P. fluorescens* PSF02, a siderophore producer, as a biocontrol agent for *Fusarium oxysporum* in peanut plants (*Arachis hypogaea*)[119]. The siderophore pyoverdine was identified in *Pseudomonas*, and its production participates in the control of foot rot and wilt diseases in maize, wilt in potatoes, and growth deficiency in wheat and barley, caused by *Fujikuroi*, *F. oxysporum*, and *Gaeumannomyces graminis*, respectively[120–122]. The siderophores pyoverdine and pseudobactin are produced by *P. putida* and are associated with the induction of resistance in cucumber to diseases caused by *Colletotrichum orbiculare*, *Pseudomonas syringae* pv. *lachrymans* and *F. oxysporum* f. sp. *cucumerinum*[123,124]. The non-pathogenic strain *P. syringae* 7NSK2, which produces the siderophores pyoverdine and pioquelin, was used effectively to control *Pythium splendens*, which causes wilting in tomatoes (*Solanum lycopersicum*)[125].

Different isolates of *B. subtilis* have been used as antagonists of the phytopathogenic fungi *Cephalosporium maydis*, *F. oxysporum* and *Rhizoctonia solani*. The siderophores of these

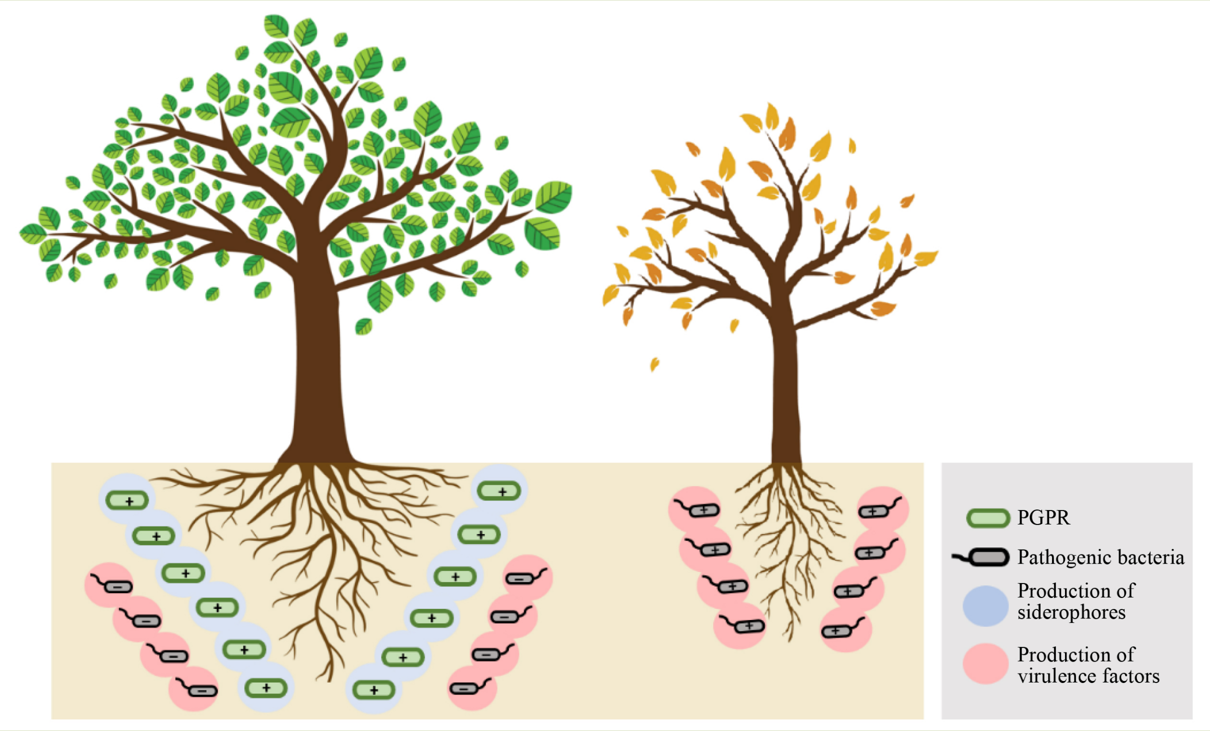

Fig. 5 Role of siderophores in pathogen control.

bacteria, such as bacillibactin, induce resistance to these diseases[126–128]. Through *in vivo* trials in banana (*Musa* spp.) plants and *in vitro*, the activity of *Bacillus siamensis* siderophores was verified, showing antifungal capacity against *F. oxysporum* greater than 70%[129]. Two hydroxamate-type siderophores were identified in *Paenibacillus triticisoli* that showed antimicrobial activity against *B. subtilis, E. coli* and *S. aureus* and, promoting the plant growth of *A. thaliana*[48].

Lysobacter enzymogenes synthesizes the siderophore spermine and is considered a new biocontrol agent for *Colletotrichum fructicola*, which causes pear anthracnose[130,131]. *Serratia plymuthica* AED38, which produces the siderophore serratiochelin C, has also been shown to have controlling activity against the fungus *Phytophthora cinnamomi*, which causes root rot in avocados (*Persea americana*)[132]. The production of the siderophore enterobactin by *S. marcescens* is associated with the pathogen resistance response of cucumber[133].

The direct use of purified siderophores from rhizobacteria has proven to be effective in controlling various phytopathogens, such as *Aspergillus niger* NCIM 1025, *A. flavus* NCIM 650, *Aspergillus calidoustus, Alternaria alternata, Botrytis cinerea, Candida albicans, F. oxysporum, Globisporangium ultimum, Pythium ultimum, P. cinnamomi, R. solani, Sclerotinia sclerotiorum, Talaromyces pinophilus, T. verruculosus,* and *P. syringae* pv. tomato, based on siderophores from *Pseudomonas* sp.[134–138], *Bacillus* sp.[128,139,140], *Alcaligenes faecalis*[141], *Brevibacillus brevis* GZDF3[17] and *S. plymuthica* AED38[132].

The interaction between bacteria is currently being studied, where the production of siderophores by one could enhance the antagonistic response of the other; however, depending on the species analyzed, the association may give rise to unwanted competing phenotypes. Therefore, it is necessary to better understand the nature and dynamics of the interactions between these bacteria in order to design consortia with predictable compatibility and high biocontrol potential[142] (Table 3).

Bacterial siderophores offer several advantages over common mineral fertilizers, such as specificity and efficiency in iron absorption, the use of micronutrients with a lower risk of overdose, and the stimulation of soil microbiota, with a potential dual effect: as antimicrobial agents and biofertilizers. Their potential use as a bio-input to reduce long-term costs and implement sustainable agricultural practices remains a challenge, as it requires purification, characterization and large-scale production. However, advances in synthetic biology, along with the use of bioinformatics tools and omic technologies, are opening new horizons for the industrial production of siderophores through biotechnology[148,149].

5 Conclusions

Rhizobacterial siderophores are now recognized as central to rational and sustainable agriculture. This analysis shows that these molecules mobilize iron for plant growth and act as biocontrol agents against phytopathogens. This dual role makes siderophores a viable ecological alternative to mineral fertilizers and synthetic pesticides, helping soil biodiversity and food safety.

However, implementing these molecules on an industrial scale is challenging. Though they are successful in medicine, such as

Table 3 Growth-promoting rhizobacteria (PGPR) producers of siderophores reported as biocontrol agents

Siderophore		PGPR	Reference
Type	Name		
Catecholate	Enterobactin	*E. coli*, *E. asburiae*, *S. marcescens* and *Streptomyces* sp.	[59,133]
Phenolate	Pyochelin	*Burkholderia* sp. and *Pseudomonas* sp.	[143,144]
Carboxylate	Vibrioferrin	*A. chroococcum* and *A. vinelandii*	[103,145–147]
Mixed	Pseudobactin	*Pseudomonas* sp.	[87,124]
	Pyoverdine	*P. eucalypti* and *P. fluorescens*	[57,92,114,115]
	Fusarinin	*P. triticisoli*	[48]
	Ornibactin	*Ba cenocepacia*	[59]

desferrioxamine B and cefiderocol, their use in agriculture is limited by knowledge gaps. It is important to understand how siderophore structures affect plants and learn how roots take up iron from bacteria. Without such studies, creating effective PGPR consortia will remain a trial-and-error process.

The horizon of siderophore biotechnology is now broadened by synthetic biology, omic technologies, and bioinformatics. These tools are key to optimizing large-scale production, enabling cleaner and more cost-competitive synthesis. Characterizing new membrane receptors and discovering chemical structures in unexplored habitats will lead to next-generation biofertilizers and innovations in bioremediation and diagnostics.

Compliance with ethics guidelines

Fabían Galvis and Javier Soto declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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