

Review

Microbial Metallophores in the Productivity of Agroecosystems

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Abstract: Microbial metallophores are low-molecular-weight chelating agents produced by microorganisms to acquire essential metal ions. Their biosynthesis, transport, and regulation involve complex processes, specialized enzymatic machinery, and intricate regulatory networks. This review examines the multifaceted roles of metallophores in microbial ecology and their potential applications in sustainable agriculture, emphasizing their key role in trace metal acquisition, nutrient cycling, and plant–microbe interactions. Furthermore, it explores the potential applications of metallophores in agriculture, bioremediation, and biotechnology, connecting their potential to the development of novel strategies for sustainable agriculture.

Keywords: metallophores; microbes; agroecosystem; siderophores; chalkophores; molybdo-phores



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1. Introduction

In recent years, among the green strategies implemented to mitigate the negative effects of agrochemicals on soil, water quality, and human health, the development of bioproducts based on beneficial microorganisms has gained significant attention in the academic, industrial, and governmental sectors [1]. Plant-growth-promoting bacteria (PGPB) and plant-growth-promoting fungi (PGPF) establish symbiotic relationships in the rhizosphere, phyllosphere or plant-endosphere, resulting in mutual benefits [2–4]. PGPB and PGPF promote crop growth and yield through both direct and indirect mechanisms, mediated by different types of symbiotic interactions with host plants. Direct mechanisms involve improving the plant’s nutritional status by enhancing root exploration, water uptake, nutrient availability and absorption, and overall plant physiology [5–7]. Indirect mechanisms include protection against abiotic and biotic stresses, such as biological control of phytopathogens through the activation of induced or acquired systemic resistance, as well as tolerance to extreme environmental conditions, heavy metal toxicity, and nutrient imbalances [6,8,9]. In both types of mechanisms, the ability to produce siderophores is

a key characteristic of many effective PGPB and PGPF strains, that can be used for the development of biofertilizers or biofungicides [10,11].

Metal ions such as copper, iron, manganese, molybdenum, nickel, vanadium, and zinc are essential trace elements required for the enzymatic functioning of microorganisms and plants [12]. However, these metals are often present in low concentrations in the soil and may be insoluble or biologically unavailable. Archaea, bacteria, fungi, and plants have evolved mechanisms to scavenge these metals by secreting chelating agents called metallophores, which sequester metal ions from other chemical species generally from the soil [13,14]. Once transported into cells, metal ions are released from metallophores, becoming bioavailable. Metallophores are low-molecular-mass organic molecules that facilitate the complexation and mobilization of metal ions through ligand reactions [15,16]. Their biosynthesis and exudation depend on the organism's internal metal ion concentrations [17]. Siderophores, the best-known and most extensively studied metallophores, are primarily involved in iron acquisition. These compounds, consisting of approximately 500 different chelators ranging from 400 to 1500 Da, exhibit a high affinity for Fe^{3+} but can also chelate other metallic micronutrients or toxic ions, forming stable complexes with elements such as aluminum, cadmium, copper, gallium, indium, lead, and zinc [18–21]. The best-known siderophores are pyoverdine, pyochelin, and pyocyanin from *Pseudomonas* strains, as well as enterobactin from *Escherichia coli* and *Salmonella typhimurium* [22–24]. Siderophores reported from fungi include dimerum acid, fusigen, coprogen, and ferricrocin from *Trichoderma* spp. [25]; ferrirubin from *Paecilomyces variotii* [26]; ferrichrome from *Ustilago sphaerogena* [27]; and fusarinine C from *Fusarium roseum* [27]. Other metallophores include staphylopine, which uptakes a broad spectrum of metals [28], pseudopaline, specific for nickel and zinc [29], and yersiniabactin, which chelates iron and nickel [30]. Recent research has also begun to explore metallophores such as chalkophores (copper metallophores), molybdophores, vanadophores, and zincophores, although these remain less studied [31–33]. Additionally, metallophores specific to cobalt, gold, and lanthanides have been reported [34–36].

Microbial metallophores play a crucial role in microbe–microbe and plant–microbe interactions, directly and indirectly contributing to plant-growth-promoting mechanisms. Consequently, these molecules hold great potential for sustainable agriculture. Despite extensive studies on microbial siderophores involved in Fe^{3+} chelation, relatively little is known about the role of metallophores in chelating additional micronutrients or heavy metals [37–39]. To explore the full potential of metallophores in sustainable agricultural practices, further research is needed to investigate their diversity, mechanisms of action, and practical applications. This review provides a comprehensive overview of metallophore types, their roles in plant–microbe interactions, and their potential contributions to sustainable agriculture.

2. Biosynthesis and Transcription of Metallophores

Under conditions of metal scarcity, metallophore production is upregulated to facilitate the scavenging of essential metal ions; but environmental factors such as pH, temperature, oxygen availability, and the presence of competing ligands can influence metallophore synthesis. These factors regulate transcription factors, which bind to specific DNA sequences to activate metallophore biosynthesis genes. Complex regulatory networks involving transcription factors, small RNAs, and signaling molecules further fine-tune metallophore production in response to cellular needs. For instance, siderophore production is often controlled by the ferric uptake regulator (*Fur*), which represses iron acquisition genes in iron-replete conditions [40,41]. Several well-characterized gene clusters are involved in metallophore biosynthesis. For example, the *ent* genes in *Escherichia coli* encode enzymes

for enterobactin production [42], while the *pvd* genes are responsible for pyoverdine biosynthesis [43]. Similarly, the *dhb* genes are involved in bacillibactin production [44]. These gene clusters contain conserved domains, such as 2,3-dihydro-2,3-dihydroxybenzoate dehydrogenase and the TonB-dependent siderophore receptor domain. Moreover, in fungi, the siderophore operon includes *sidA*, *sidC*, *sidD*, *sidG*, *sidF*, and *sidL* gene, but the locations of these genes are different on the fungal chromosomes [45].

Metallophores are synthesized by an intricate enzymatic machinery, primarily involving nonribosomal peptide synthetases (NRPSs) and polyketide synthases (PKSs). Siderophores synthesized via NRPS/PKS include enterobactin [46], and vibriobactin [47]. Additionally, some siderophores are assembled from dicarboxylic acid subunits and dinucleophile linkers by the action of a conserved family of adenylation/condensation enzymes distinct from NRPS and PKS [48–50]. These NRPS-independent synthases (NISs) catalyze the biosynthesis of achromobactin [51,52], and staphyloferrin A and B [53,54]. All these modular enzymes catalyze a series of reactions, including substrate activation, peptide bond formation, and side-chain modification, to assemble amino acids and other building blocks into diverse metallophore structures. Non-standard amino acids and post-translational modifications, such as methylation, hydroxylation, and cyclization, further diversify the metallophore chemistry. Additionally, even though chalkophore biosynthesis has been linked to several NRPS gene clusters [55,56], methanobactins are produced as ribosomally synthesized and post-translationally modified peptides (RiPPs) [32,57].

Metallophore biosynthetic pathways have evolved through a gradual and complex process [58]. These systems are thought to have originated from pre-existing enzymes involved in peptide and polyketide synthesis, and gene duplication, followed by mutations and recombination events, has facilitated the diversification of these pathways and the emergence of metallophore synthesis. Horizontal gene transfer has also contributed significantly to the evolution of metallophores [58–60].

3. Mechanisms of Excretion, Action, and Transport of Microbial Metallophores

Microorganisms employ a variety of strategies to transport metallophores out of the cell (Figure 1). These compounds can be actively effluxed across the cell membrane via ATP-binding cassette (ABC) transporters or secreted through specialized secretion systems such as the T1SS, T2SS, T3SS, and T4SS [61,62]. Alternatively, metallophores may be passively released through porins or channels; some microorganisms package metallophores into membrane-bound vesicles to facilitate targeted release and protect them from degradation, while others release them through cell lysis [63]. Recently, a multidrug and toxic compound extrusion (MATE) transporter, MbnM, has been associated to be in charge of the excretion of some methanobactins [64].

Once secreted, metallophores bind tightly to metal ions in the environment, forming highly stable complexes that significantly enhance the solubility and bioavailability of the metal ion [65]. This chelation process is mediated by various functional groups, including hydroxamates, catecholates, carboxylates, amines, imidazoles, thiols, phosphonates, and others [66,67]. Metal–metallophore complexes, in combination with dissolved organic matter, contribute to a ligand-sphere that enriches the local environment with accessible metal complexes, promoting microbial growth and ecological functions [68,69]. After the metal–metallophore complex is formed, it is transported back into the cell (Figure 1).

The metal–metallophore complex can enter the cell through various mechanisms. The complex can directly cross the cell membrane via specialized transporters, such as those in the major facilitator superfamily (MFS) or the ATP-binding cassette (ABC) transporter family [61,67]. Moreover, the metal–metallophore complex may bind to specific receptors

on the cell surface, triggering endocytosis [45]. Other systems, including those from the Resistance–Nodulation–Division (RND) superfamily and the Tripartite ATP-Independent Periplasmic (TRAP) transporter family, may also facilitate the uptake of metal–metallophore complexes, depending on the microorganism and the metal ion being transported [61,70,71]. Once inside the cell, the metal ion is released from the metallophore and becomes available for essential cellular processes, including enzymatic catalysis, electron transfer, and biosynthesis (Figure 1).

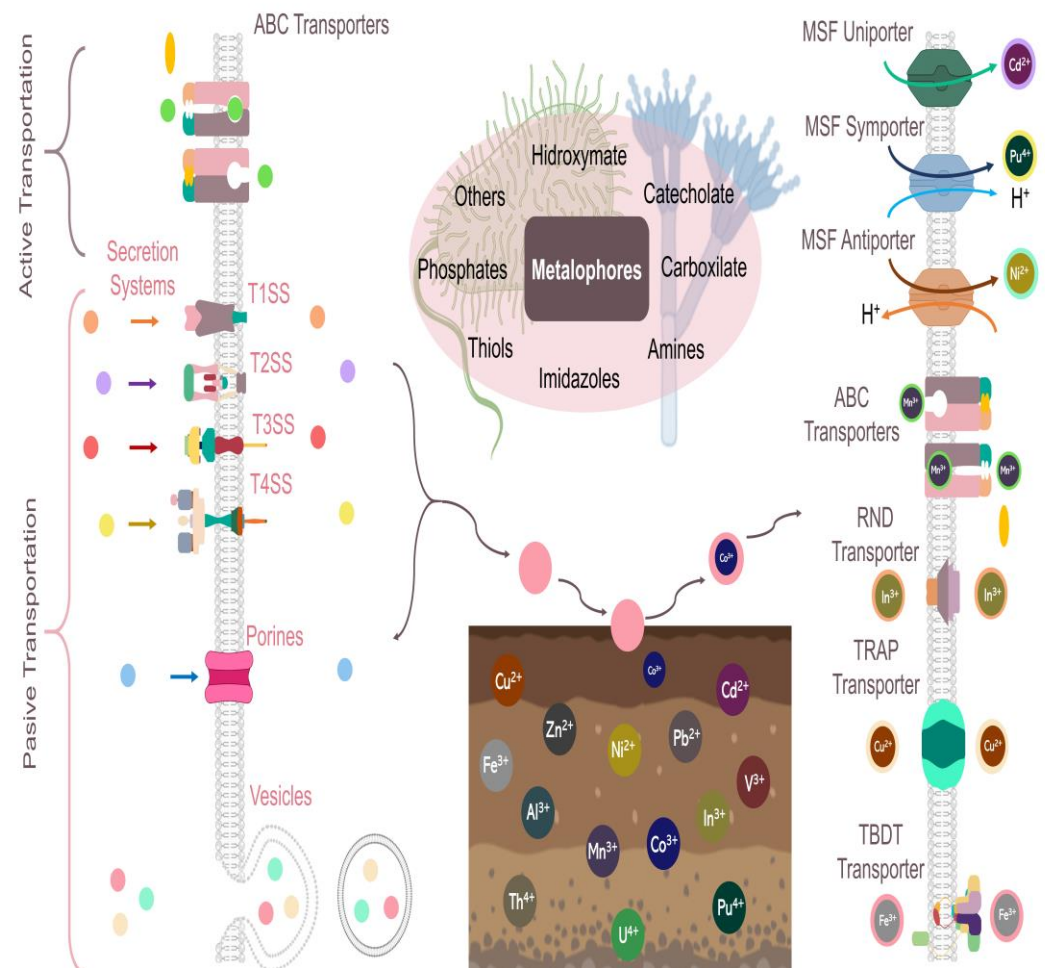


Figure 1. Metallophore excretion and uptake transport systems. ABC: ATP-Binding Cassette Transporters; TnSS: Type n Secretion System; MSF: Major Facilitator Superfamily Transporters; RND: Resistance–Nodulation–Division Transporters; TRAP: Tripartite ATP-Independent Periplasmic Transporters; TBDT: TonB- or TonR-Dependent Transporters.

Siderophores exemplify the sophisticated strategies microorganisms use to acquire essential metals. They are typically secreted by efflux pumps of the major facilitator superfamily (MFS), the resistance, nodulation, and cell division (RND) superfamily, and the ATP-binding cassette (ABC) superfamily [70,72]. Siderophores contain functional groups such as hydroxamates, phenol-catecholates, carboxylates, and mixed groups, which form high-affinity complexes with ferric iron (Fe^{3+}). The coordination of iron to these functional groups varies based on the siderophore structure: hydroxamates generally form hexadentate complexes, while catecholates often form octahedral complexes [73]. This structural diversity allows siderophores to bind iron effectively under a range of environmental conditions.

Once formed, the siderophore–iron complex is recognized by specific receptors on the bacterial outer membrane and internalized via active transport systems. These mechanisms involve proteins like TonB- or TonB-dependent transporters (TBDT), periplasmic siderophore-binding proteins (SBP), ABC transporters, or siderophore-mediated endocytosis [74]. While the specific genes *fepA*, *fepB*, *fepC*, *fepD*, and *fepG* are primarily found in *Escherichia coli*, other bacterial genera like *Pseudomonas*, *Yersinia*, *Salmonella*, and *Klebsiella* possess analogous genes that encode for proteins involved in the uptake of siderophores [75–77]. In addition, in Gram-positive bacteria, siderophore-dependent ferrichelatases have been recently proposed to act as iron shuttles [78]. Within the cell, the iron is released from the siderophore and utilized for various metabolic processes, while the siderophore may either be destroyed or recycled [79,80]. Although iron is the primary target of siderophores, they can also chelate other metal ions, including divalent cations (e.g., Zn^{2+} , Ni^{2+} , Cd^{2+} , Cu^{2+} , and Pb^{2+}), trivalent cations (e.g., Al^{3+} , In^{3+} , Mn^{3+} , V^{3+} , and Co^{3+}), actinides (e.g., Th^{4+} , U^{4+} , and Pu^{4+}) [74]. This broad chelation capacity highlights the versatility of siderophores in adapting to diverse environmental metal availability [81–83], or maybe they correspond to metallophores that have been misidentified and named. In the case of fungi, they produce hydroxamate-type siderophores that are grouped into the families: rhodotorulic acid, fusarinines, coprogens, and ferrichromes [20]. Little is known about the mechanism of fungal siderophore secretion [37]; however, some mechanisms proposed for the iron-loaded siderophore uptake depend on the specific recognition of various siderophores, and Fe^{3+} reduction occurs at the membrane and Fe^{2+} is then absorbed into the cell [84]. For example, in fungi such as *Rhodotorula* spp., Fe^{3+} transfer across the membrane from the siderophore rhodotorulic acid to intracellular ligands occurs without the entry of rhodotorulic acid into the cell [85]. Meanwhile, in *Ustilago sphaerogena*, the iron-loaded siderophore ferrichrome A is not transported into the cell; instead, Fe^{3+} reduction occurs at the membrane, and Fe^{2+} is then absorbed into the cell [84].

4. Metallophore Detection, Extraction, Purification, and Quantification

Metallophore detection is crucial for understanding their biological roles in agriculture, mainly in complex matrices such as soil. Chromogenic assays, such as the CAS assay, apply the ability of metallophores to form colored complexes with specific metal ions, providing a direct method for their detection. The CAS assay has undergone various modifications, including changes to the metal ion, surfactant, and dye, as well as the addition of adsorbent resins to facilitate the growth of fungi and yeast [86–89]. Additionally, the assay has been adapted to use a concentrated CAS reagent and different growth media for broader applications [90,91]. Furthermore, the technique has been implemented in microplates to enable both a qualitative and quantitative estimation of siderophore production [92,93]. Other colorimetric methods can be used to detect different types of siderophores, such as the Arnow's and FeCl_3 tests for catecholates; the ferric perchlorate assay, and tetrazolium Csaky's tests for hydroxamates, and the Vogel's chemical test for carboxylates [82], whereas fluorescent siderophores, like pyoverdines, can be detected using fluorescence-based methods [94]. Complementary to these assays, spectroscopic techniques like ultraviolet–visible spectroscopy (UV–Vis) and nuclear magnetic resonance (NMR) offer detailed structural information about metallophores. Moreover, bioassays using mutant strains that are deficient in metal uptake are used to identify the function, biosynthesis, and regulation of metallophores [93]; for instance, the mutant strains ΔpvdA and ΔpvdE of *P. fluorescens* PF08 indicated the participation of pyoverdine in biofilm formation and motility, and in the regulation of flagellum and stress resistance of the strains [95].

The in-depth characterization of metallophores and metallophore–metal complexes requires their isolation and purification. For example, siderophore extraction into organic solvents, such as ethyl acetate for the catechol type or either benzyl alcohol or chloro-

form:phenol (1:1) for the hydroxamate types, have been used as an effective purification step for many types of siderophores since both salts and macromolecules are removed effectively [96]. Solid-phase extraction (SPE) offers a more selective approach, using solid sorbents to retain metallophores. Polystyrene resins like XAD-2 or Amberlite XAD-7 can be used to adsorb metallophores from complex mixtures. For instance, the resin amberlite XAD has been widely used for the purification of the neutral, ferrichrome type of siderophores and polyamide resin for the chromatographic separation of the catechol type [97]. Siderophore-rich cell-free concentrated broth from *Alcaligenes faecalis* BCCM ID 2374 was purified on the Amberlite XAD-4 column; it resulted in the separation of two fractions having absorption maxima at 264 and 224 nm, that belonged to the hydroxamate and catecholate type of siderophores, respectively [96]. With the cultivation of *Gordonia rubripertincta* CWB2 on succinate and extraction using an adsorbing mixture of XAD4 and XAD16 resins, 28 desferrioxamine-like compounds were purified; five of these were identified as desferrioxamines B, E, and G1, and bisucaberin and bisucaberin B, and the siderophore function of the remaining compounds remains to be elucidated [98]. Moreover, Fourier-transform infrared analysis (FT-IR) has been used to determine the functional groups in a siderophore and the functional groups involved in the interaction of the siderophore with the metal [99]; for instance, by the FT-IR spectra, Mazari et al. [100] characterized the pyoverdine of the PGPR strains *Pseudomonas atacamensis* PO22, *Pseudomonas lactis* R2P30, and *Pseudomonas* sp. PS11, isolated from roots of grapevine. Recently, ionization and analytical techniques, such as electrospray ionization mass spectrometry, matrix-assisted laser desorption/ionization mass spectrometry, inductively coupled plasma mass spectrometry, and mass spectrometry imaging have been used to identify and characterize siderophores [82].

Subsequent purification steps, such as high-performance liquid chromatography (HPLC), electrophoresis, and mass spectrometry and associated technologies such as liquid chromatography–mass spectrometry and gas chromatography–mass spectrometry, further separate and characterize metallophores based on their physicochemical properties. A reversed-phase HPLC method can screen for siderophore-producing strains, and can be used to control their purification and immobilization, as demonstrated in *Gordonia rubripertincta* CWB2, which produces desferrioxamine-like siderophores [101]. Moreover, crystallization yields pure crystals suitable for X-ray crystallography, providing a high-resolution structure of the metallophore. The zincophores isoavenaciol and 7-hydroxy-isoavenaciol produced by the root-endophyte *Pezizicula ericae* w12-25 of the zinc-accumulating plant *Aucuba japonica* were determined to be (3aS,4S,6aR)-3ahydroxy-3-methylene-4-octyldihydrofuro[3,4-b]furan-2,6(3H,4H)-dione and (3S,3aS,4S,6aR)-3a-hydroxy-3-(hydroxymethyl)-4-octyldihydrofuro[3,4-b]furan-2,6(3H,4H)-dione using HRMS, ¹H and ¹³C NMR, and 2D NMR spectroscopic methods and X-ray crystallography [102]. Recently, immobilized metal affinity chromatography, metal oxide affinity chromatography, and titanium dioxide affinity chromatography are new and improved methodologies that have been used for the purification of siderophores [82]. Additionally, ultra-high-performance liquid chromatography coupled to a time-of-flight mass spectrometer (UHPLC-ToF-MS) has been developed to quantify and monitor the production of metallophores. Using this methodology, Deicke et al. [103] reported that, under a low Mo concentration, *Azotobacter vinelandii* OP produces peaks of Mo-protocelin concentration in the middle lag phase, and the Fe-protocelin concentration rises twice, at the beginning of the exponential phase and during the stationary phase, indicating that, in *A. vinelandii* OP, the production of metallophores is highly dynamic throughout growth [103].

Recent advancements in high-throughput sequencing and bioinformatic tools, such as sequence homology searches, domain architecture analyses, and comparative genomics,

have significantly accelerated the discovery and prediction of metallophore biosynthesis gene clusters, and revealed that some of them are conserved across diverse microbial taxa, suggesting a widespread role of metallophores in diverse environments. For instance, the *dhbACEBF* cluster has been predicted in *Bacillus subtilis* EA-CB0575 to encode the enzymes responsible for bacillibactin production [44]; this siderophore was first reported in *B. subtilis* ATCC 21332 [104]. Moreover, genome mining focusing on the core operon *Mbn* has revealed the presence of methanobactins in a broader spectrum of bacteria beyond methanotrophs; bacterial groups such as Proteobacteria (e.g., *Pseudomonas*, *Burkholderia*, *Gluconacetobacter*, and *Azospirillum*), Actinobacteria (e.g., *Streptomyces*), and Firmicutes (e.g., *Bacillus*) have been identified as producers of these chalkophores [105,106]. Furthermore, Calderón-Celis et al. [107] developed an approach to detect metallophores using a two-dimensional solid-phase extraction–liquid chromatography–mass spectrometry (SPE-LC-MS) coupled with the taxonomic profiling of the prokaryotic community and mining of the antiSMASH database to link metallophores with potential producers; this approach enables the direct detection and identification of metallophores in native environments, including agricultural settings. Additionally, molecular modeling techniques, including homology modeling, molecular docking, and molecular dynamics simulations, could provide atomic-level insights into metallophore structure and function [108]. For instance, docking and molecular dynamics simulations reveal that, in rice, the two yellow stripe-like (YSL) transporters responsible for carrying siderophore–Fe³⁺ complexes into roots show a higher binding affinity for the bacterial siderophore bacillibactin–Fe³⁺ complex compared to the plant siderophore 2'-deoxymugineic acid (DMA)–Fe³⁺ complex. This suggests that the use of siderophores produced by PGPR can enhance the iron uptake in rice, as this crop possesses receptors that also bind for bacterial siderophores [109].

5. Microbial Metallophores in Microbial Communities

Microbiomes form intricate interactions within their habitats that contribute to ecosystem balance. In this way, microbial diversity is essential for maintaining ecosystem equilibrium [110,111]. These microbial interactions are largely governed by secondary metabolites, including metallophores, which mediate cooperation, exploitation, and competition among microbial populations and communities. For example, siderophores can be acquired by cells of the same or different species possessing the matching receptors, and distributing the costs and benefits of siderophore production among individuals. However, siderophores can also induce iron starvation in cells lacking specific receptors [39,112,113]. Thus, in microbial communities, siderophores can be shared cooperatively or exploited by non-producing “cheater” cells [114,115]. The production of multiple siderophores with different binding affinities can limit the success of cheaters, leading to the stable coexistence of producers and non-producers. When metal availability is limited, the production of metallophores by microorganisms can shape the microbial community structure by promoting both cooperative and competitive interactions [107,116]. For example, the majority of fungi possess the ability to take up iron carried by xenosiderophores (siderophores synthesized by other microbial communities), and *Aspergillus nidulans* exhibits affinity for ferrirubin released from *Aspergillus ochraceus* [117] and for bacterially synthesized enterobactin [118]; and *Saccharomyces cerevisiae* also depends on siderophores produced by other species [119]. Furthermore, siderophores influence quorum sensing, nutrient availability, and stress responses within and between species [18,120]. For example, siderophores participate in sporulation stimulation, the induction of siderophore production in other species, protection against reactive oxygen species and heavy metals, and the promotion of growth in cohabitating organisms [18,120]. Microorganisms are social organisms that employ quorum sensing to coordinate their behavior [121]. In this context, they can produce redundant met-

allophores for different metal ions, such as zinc, molybdenum, and vanadium, depending on the environmental conditions [62,68]. Moreover, metallophores can contribute to biofilm formation by facilitating cell adhesion and promoting intercellular communication. In the strains *P. fluorescens* PF08, pyoverdine is involved in the production of exopolysaccharides, formation of biofilm and motility, and regulation of the transcription levels of *htpX*, *phoA*, *flip*, *flgA*, and *rpoS*, influencing the strain's flagellar biosynthesis and resistance to stress [95].

The phyllosphere, rhizosphere, and plant-endosphere are environments shaped by complex interactions between plants and microorganisms. The structural and functional diversity of microbial communities significantly impacts plant health and ecosystem sustainability [122–125]. The rhizosphere and root-endosphere maintain a dynamic, nutrient-rich environment around and inside roots, sustaining specific bacterial populations involved in activities that ensure the stability and productivity of agroecosystems, where metallophores must play a fundamental role in the microbiome and plant–microbiome interactions [126–130]. Some of these microorganisms are known as PGPB and PGPF, that, due to their effective properties in promoting plant growth, specifically, increasing yield and controlling pests and diseases in agricultural crops, have been selected for the development of bioproducts. These bioproducts are considered suitable methods for introducing probiotics to agricultural soil or increasing soil microbial biodiversity by breaking the dormancy of soil microbial seed banks' dormancy and reinforcing the biodiversity–ecosystem functioning relationship [131–133].

6. The Role of Microbial Metallophores in Promoting Plant Growth

Metallophores play a crucial role in the cycling of essential metals in the environment; several of these metal ions are indispensable for plant growth and development. For instance, iron is critical for chlorophyll synthesis and maintaining chloroplast structure and function [134]. Manganese plays a key role in plant metabolism and development, participating in various enzymatic processes [135]. Molybdenum is a vital component of proteins involved in nitrogen assimilation, sulfur metabolism, phytohormone biosynthesis, and stress responses [136]. Nickel is an essential component of plant ureases, which protect against phytopathogens [137]. Zinc plays an important role in seed development and chloroplast function, with numerous zinc-dependent enzymes performing essential tasks [138]. Copper is essential for photosynthesis, carbon and nitrogen metabolism, oxidative stress protection, and cell wall synthesis [139]. Recent studies have demonstrated a hormetic effect of lanthanides in plants; they stimulate chlorophyll synthesis, enhance photochemical reactions in thylakoids, and improve stress tolerance; but the precise mechanisms underlying these hormetic effects remain largely unknown, and gaps in this area will be filled in future studies [140]. In environments with limited metal ion availability or under stress conditions, metallophores become crucial for bacterial communities to acquire and supply essential metals to plants [18]. For instance, siderophore-producing strains such as *Pseudomonas* sp. GRP3A and PRS have been shown to increase germination rates and promote plant growth in maize [141]. Similarly, the siderophore-producing strain *Pseudomonas aeruginosa* RSP5 enhances iron transport to maize plants, leading to increased shoot and root length, larger cobs, higher grain yields, and a greater iron content in plant tissues [142]. Siderophores also influence plant hormone levels, with siderophore-producing strains like *Trichoderma asperellum* Q1 supporting optimal root system development in *Arabidopsis thaliana* by increasing auxin concentrations [143]. Siderophores of *Streptomyces* sp. CoT10, an endophyte of *Camellia oleifera*, directly mediate Fe–P mobilization; this enhances P and Fe acquisition in *C. oleifera* and improves microbial interactions within the plant rhizosphere [144] (Figure 2). It has been proposed that plants acquire xenometallophores

produced by PGPR through the transporters employed for the acquisition of phytometallophores; for example, bacillibactin produced by the PGPR *Bacillus subtilis* is possibly transported by the YSL15 transporter and siderophore import proteins in *Oryza sativa* plants, and YSL15 transports PS-Fe³⁺ complexes from the rhizosphere to the root and from the root to flowering regions [145].

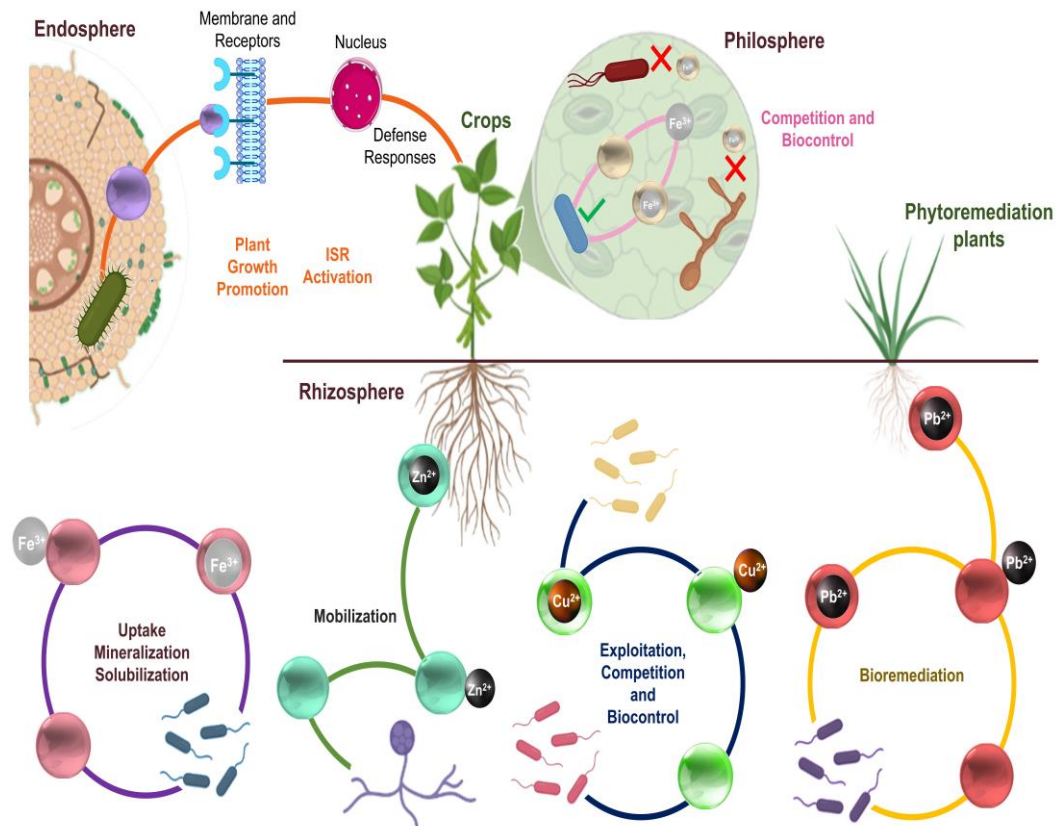


Figure 2. Role of metallophores in microbial and plant interactions. Metallophores are molecules that enable microorganisms to interact with their environment, other microorganisms, and plants. In the soil, they contribute to mineralization and solubilization, facilitating the uptake of essential ions. In the rhizosphere, they mobilize nutrients for plant bioavailability and participate in competition and biocontrol, as some microorganisms sequester metallophore-bound nutrients produced by others, depriving the original producers of access to these essential elements. They also play a role in bioremediation through interactions with specific plants. In the phyllosphere, metallophores produced by beneficial microorganisms are generally inaccessible to phytopathogens, contributing to competition and biological control, with some exhibiting antimicrobial activity. In the endosphere, they act as elicitors of systemic resistance and function as plant growth promoters.

Furthermore, bacterial siderophores can significantly impact plant gene expression. In *A. thaliana*, the apo-pyoverdine produced by *Pseudomonas fluorescens* C7R12 upregulates genes related to development and iron acquisition while downregulating defense-related genes [79]. Siderophores also play a crucial role in the fitness of phyllospheric bacteria, as demonstrated by their role in promoting the population growth of biocontrol agents like *Pseudomonas syringae* pv. *syringae* 22d/93 against the plant pathogen *Pseudomonas syringae* pv. *glycinea* [146]. Additionally, lanthanophores produced by the bacterial community of crop phyllosphere can enhance growth, crop yields, and drought resistance [34]. For instance, genes involved in metallophore–metal uptake support an increased AMF colonization of the arbuscular mycorrhizal fungi *Rhizophagus irregularis* [147]. Furthermore, as bacterial communities provide nitrogen to plants, they have high nutritional requirements for molybdenum, iron, and vanadium [19,148]. The free-living diazotroph *Azotobacter*

vinelandii, a well-studied nitrogen-fixing bacteria, produces metallophores like protochelin, azotochelin, azotobactin, aminochelin, and vibrioferrin efficiently to the three metal ions under low-concentration conditions [31,148–152]. Additionally, siderophores produced by the fungi *Aspergillus niger*, *Penicillium citrinum*, and *Trichoderma harzianum* increase the shoot and root lengths of chickpeas [153]; and ectomycorrhizal fungi, such as *Aspergillus niger*, *Penicillium citrinum*, and *Trichoderma harzianum*, supply iron to the host roots of plants [154].

Microbial metallophores also play a critical role in suppressing plant diseases. In the rhizosphere, microbial communities compete with plant pathogens for space and access to metal ion pools. Moreover, siderophores contribute to disease suppression through various mechanisms, including the production of antibiotic compounds, the synthesis of fungal cell wall-lytic enzymes, and the induction of systemic acquired resistance [18,155–160]. For example, the siderophore enantio-pyochelin produced by *Pseudomonas protegens* CS1 exhibits antagonistic activity against *Xanthomonas citri* subsp. *citri* by generating reactive oxygen species (ROS) from pyochelin. Similarly, the enantio-pyochelin produced by *Pseudomonas fluorescens* CHA0 provides protection against Tobacco necrosis virus infection in tobacco, and the pseudobactin produced by *P. fluorescens* WCS374 provides resistance to Fusarium wilt in radish [161,162]. Pyoverdine and enantio-pyochelin produced by *P. protegens* are also responsible for its resistance to fusaric acid [163]. Siderophore-producing strains, such as *Bacillus subtilis* MF497, *Pseudomonas koreensis* MG20938, and *Pseudomonas taiwanensis* MTCC11631, positively affect maize (*Zea mays* L.) and anthurium (*Anthurium andreanum* L.) by inducing a priming effect. They activate plant defense enzymes, such as polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), and peroxidases (POX), which are associated with lignification processes that strengthen cell walls and reduce the incidence and severity of diseases caused by *Cephalosporium maydis* and *Xanthomonas axonopodis* pv. *dieffenbachiae*, respectively [164,165].

Furthermore, certain siderophore-producing strains improve plant growth and development while also playing a crucial role in biological control. For example, *Pseudomonas aeruginosa* P4 promotes the growth, nutrition, and health of peanut plants (*Arachis hypogaea* L.) through siderophore production, organic acid secretion, iron and phosphate supply, and the production of secondary metabolites [166]. The siderophores of *Rhizobium meliloti* function as biocontrol agents against *Macrophomina phaseolina* in *Mucuna pruriens* while simultaneously increasing the seedling biomass and fresh nodule formation [167]. Additionally, siderophores produced by *Streptomyces* sp. AzR-051 and *Bacillus velezensis* NKG-2 promote plant growth and antagonizes major fungal pathogens in tomato plants (*Solanum lycopersicum* L.) [168,169]. Additionally, the plant-growth-promoting fungus *Aureobasidium pullulans* L1 produces siderophores to improve the iron availability in soils with a low iron content and acts as an antagonist to the soil-borne pathogen *Rhizoctonia solani* through iron competition [170].

Additionally, phytometallophores are also involved in the uptake of Fe, Zn, Cu, Mn, Ni, Cd, and Co. Specifically, phytosiderophores, including 2'-deoxymugineic acid (DMA) and eight different compounds from the mugineic acid (MA) family, are secreted by the root cells of cereals via MA transporters. This constitutes the chelation strategy (Strategy II) for Fe uptake in gramineous plants [171–173].

7. Applications of Microbial Metallophores in Agroecosystems

In the context of agriculture, microbial metallophores play a crucial role in promoting plant health and productivity (Figure 2). Several biofertilizers, biostimulants, and soil inoculants incorporate metallophore-producing microbial strains that improve crop yields. Microbial metallophores enhance the availability of essential nutrients to plants; these molecules reduce the need for synthetic fertilizers and improve nutrient availability. At the same time, microbial metallophores stimulate the growth of beneficial soil microorganisms

that improve soil structure and fertility, and contribute to enhanced soil health. The use of metallophores in nutrient cycling can develop targeted fertilization strategies, reduce fertilizer inputs, and minimize environmental impacts. For instance, siderophore-producing strains show promise as auxiliaries in specific production systems where iron availability is limited, such as hydroponics. For example, in hydroponically grown strawberry (*Fragaria ananassa* cv. Pajaro), a significant increase in root area, plant growth, and iron content in its tissues was observed. This effect was greater in plants inoculated with the hydroximate-siderophore-producing *Glauconoacetobacter diazotrophicus* PAL5 than in those inoculated with the catechol-siderophore-producing *Azospirillum brasilense* REC3, likely due to the hydrophilic nature of hydroximate siderophore [174]. Moreover, nocardicin A has the ability to improve nitrogen fixation in legumes like alfalfa by increasing the availability of cobalt for nitrogen-fixing bacteria [175]. In this way, metallophores enhance metal homeostasis mechanisms, making metal ions available to plants and favoring their growth [107,176].

Microbial metallophores also offer a sustainable and environmentally friendly approach to mitigating heavy metal contamination in agricultural soils (Figure 3). For instance, the production of siderophores with diverse chemical properties enables microorganisms to sequester iron under different environmental conditions or perform complementary functions, making them ideal for ecosystem bioremediation; moreover, by reducing metal stress, metallophores indirectly protect crops from both biotic and abiotic stresses [82,177–179]. Thus, metallophores contribute to bioremediation efforts by cleaning up contaminated soils and waterways, and enhancing phytoremediation processes. Microbial metallophores are effective because, generally, they are stable in soil environments and resistant to degradation; they form stable complexes with heavy metal ions that remain in the soil, or bind to the cell surfaces of microorganisms or plant roots [73]. In this way, microbial metallophores immobilize heavy metals and prevent their uptake, protecting plants from oxidative stress, growth inhibition, and other harmful effects [67]. The mechanisms through which metallophores mitigate metal toxicity induce chelation (forming stable metal–metallophore complexes), biosorption (binding to cell surfaces), and bioaccumulation (intracellular accumulation of metal–metallophore complexes) [82]. For instance, siderophores produced from *Pseudomonas putida* KNP9 in the presence of Cd increase the biomass of *Phaseolus vulgaris* without any toxicity symptoms [180]. Moreover, siderophore-containing culture filtrate from *Streptomyces acidiscabies* E13 supplied cowpea plants with Fe in the presence of high levels of Al, Cu, Mn, Ni, and U, metals that inhibit Fe acquisition; this led to an increased chlorophyll content and reduced the formation of free radicals, thereby protecting microbial auxins from degradation and enabling them to enhance plant growth [181]. As well, piochelin remediate soils contaminated with copper and nickel, demonstrating a reduction in the bioaccumulation of these metals in plants such as mustard [73], and acinetoferrin enhance the tolerance of crops like rice to copper toxicity in saline soils [182].

Additionally, microbial metallophores produced by the microbial community associated with hyperaccumulator plants enable those plants to tolerate higher concentrations of metals in their tissues. For example, zincophores produced by *Pseudomonas monteilii*, *Microbacterium saperdae*, and *Enterobacter cancerogenes* enhanced four-fold the accumulation of Zn in the Zn-hyperaccumulate plant *Thlaspi caerulescens* [183]. However, chalkophores such as methanobactins can negatively impact agricultural production by affecting denitrification, specifically at the step of nitrous oxide (N₂O) reduction and possibly also at nitrite reduction [184,185]. The enzyme N₂O reductase (NosZ) is copper-dependent [186], and, in soil, methanobactin-producing bacteria can inhibit *nosZ* expression in the denitrifying microbial community [187,188], leading to increased N₂O emissions, as reported in rice paddies and forest soils. This process can intensify the impacts of climate change on

agriculture, contribute to nitrogen loss from the soil, and promote the use of nitrogen fertilizers [189]. Furthermore, the use of siderophore-producing microbial strains can reduce Fe deficiency and plant stress under saline soil conditions. For instance, *Bacillus aryabhattai* MS3 showed the maximum siderophore production at 200 mM NaCl, due to the activation of the *entD* gene (gene in charge of siderophore biosynthesis) by salinity [190]; and the strain *Streptomyces* sp. C increased siderophore production at the high concentration of 300 mM of NaCl, increasing the iron content in the shoot of wheat plants grown in saline soil [191].

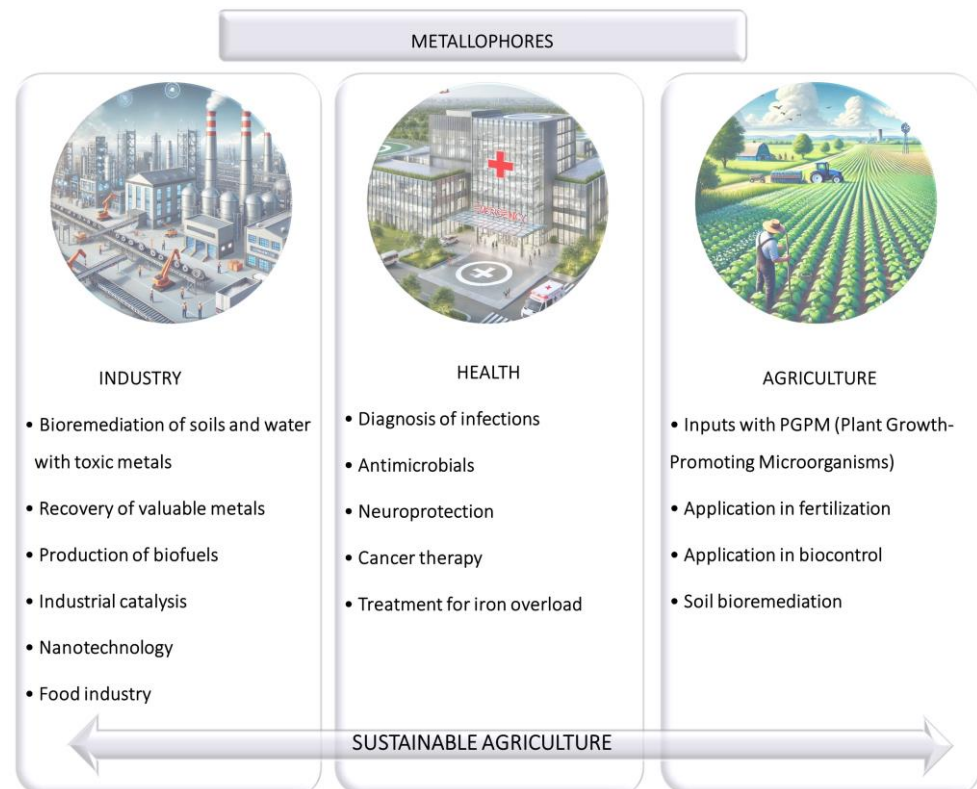


Figure 3. Current and potential applications of metallophores in the industrial, medical, and agricultural sectors.

In addition to the rise in the use of microbial strains that produce metallophores in agricultural production, the potential use of metallophores in the industry, medicine, and environmental field should be reflected in the agroecosystem stability (Figure 3). For example, in the medical sector, siderophores have been used as a “Trojan horse” to simplify the management of multi-resistant strains, prevent the emergence of new antibiotic resistance, and reduce ecological and environmental impacts [192–194]. The Trojan horse strategy consists of metalloantibiotics, metal complexes with antimicrobial activity that depend on deceiving the target bacteria into actively internalizing a metallophore–antibiotic conjugate, but more advanced antibiotics synthesis methods based in the use of metallophores are needed; these methods could involve transporting the metallophore outside the cell, capturing and blocking the free metallophore or the metallophore–metal complex outside the bacterial cell, or taking up metal ions loaded onto metallophores [195]. In the industrial sector, advancements in metallophore research can significantly impact agricultural practices. Bioremediation, utilizing metallophores to remove heavy metals from industrial waste and contaminated sites, is crucial for agriculture as it prevents the contamination of agricultural lands and water sources, ensuring the long-term health and productivity of agricultural ecosystems [73]. The chelation efficacy of *Pseudomonas lactis* and *Pseudomonas*

atacamensis pyoverdine is comparable to that of EDTA and citric acid, emphasizing its viability as an eco-friendly alternative for the remediation of metal-contaminated soils, which can be used in environmentally sustainable soil decontamination strategies [100]. In the removal of harmful heavy metals from water or wastewater, metallophores can be used as an alternative treatment technique; polymeric adsorption resins can be modified with chemically or naturally synthesized metallophores such as staphylopine, pseudopaline, acinetobactin, or yersiniabactin to remove iron, copper, nickel, or a broader range of different metal ions [196]. Furthermore, resource recovery processes facilitated by metallophores can efficiently extract valuable metals from industrial waste streams. This reduces the need for mining and minimizes the environmental impact associated with resource extraction, thereby promoting sustainable agricultural practices [67]. Additionally, siderophores from fungi such as *Gleophyllum trabeum* and *Coriolus versicolor* have been used during the bleaching process in paper and pulp industries as biobleaching agents to depolymerize the cellulose, lignocellulose, and hemicellulose in wood pulp [197]. In this way, industrial applications of metallophore research can significantly contribute to the stability and long-term sustainability of agroecosystems.

8. The Future of Metallophores

The interest in finding molecules capable of processing metals for use in various scientific and technological areas is not recent; the first siderophores were described in the 1950s [198]. Currently, research directed toward the study of metallophores is focused mainly on the medical, environmental, and industrial fields [199–201]; even so, the use of siderophores in human health is limited to few cases, such as desferrioxamine B (Desferal) applied in the treatment of chronic iron overload [202] and the antibiotic cefiderocol [203]. In agriculture, it is necessary that we encourage the evaluation of plant-growth-promoting microbial strains on their ability to produce metallophores, not only of iron, but also of metallophores of the different metals important for plants, as well as include in labels or the promotion of microbial strains their ability to produce these different metallophores.

Several challenges need to be addressed to enable the widespread application of microbial metallophores (Figure 3). Advanced omics techniques, such as genomics, transcriptomics, and proteomics, can be used to identify novel metallophores and elucidate their regulatory mechanisms. These efforts include finding metallophores with a high specificity for target metals, and scaling up their production to meet agricultural demands. Furthermore, the characterization of the membrane receptors involved in metal ion uptake opens a wide opportunity to improve current applications and develop new ones. Examples of emergent areas include their use as biosensors, diagnostic molecules, and vaccines, and in the production of safer and healthier food, thus contributing to a more just and sustainable society [204].

9. Conclusions

Metallophores represent a promising class of molecules with significant potential for addressing global challenges in agriculture sustainability. Their ability to chelate metals and influence microbial interactions offers a wide range of applications, including nutrient management, plant disease control, and soil remediation. Future research should focus on searching new metallophores, and elucidating the molecular mechanisms underlying metallophore biosynthesis, transport, and regulation, expanding our knowledge of their diversity and distribution in microbial communities; as well as developing novel biotechnological applications to support a more sustainable and resilient agricultural systems, while mitigating the negative impacts of environmental pollution.

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