Review

Exploring the Roles of Arbuscular Mycorrhizal Fungi in Plant–Iron Homeostasis

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Abstract: Arbuscular mycorrhizal fungi (AMF) form a vital symbiotic relationship with plants. Through their extensive hyphal networks, AMF extend the absorptive capacity of plant roots, thereby allowing plants to reach otherwise inaccessible micronutrient sources. Iron, a critical micronutrient involved in photosynthesis and other metabolic processes, often becomes inaccessible owing to its tendency to form insoluble complexes in soil. AMF symbiosis significantly ameliorates this challenge by enhancing iron uptake and homeostasis in plants, altering root architecture, and producing root exudates that improve iron solubility. Moreover, the interaction with diverse soil bacteria, particularly plant growth-promoting rhizobacteria, can potentiate the benefits of AMF symbiosis. Siderophores are low-molecular-weight chelators with iron-binding capacities produced by various microorganisms and plant roots. They play pivotal roles in regulating intracellular iron and have been identified in different mycorrhizal associations, including AMF. While molecular mechanisms behind AMF-mediated iron uptake have been partially explored, the intricate networks involving AMF, plants, siderophores, and other soil microbiota are largely unknown. This review focuses on the multifaceted roles of AMF in plant–iron homeostasis, interactions with soil bacteria, and the potential of siderophores in these processes, emphasizing the possibilities for harnessing these relationships for sustainable agriculture and enhancing plant productivity.

Keywords: metal homeostasis; siderophores; symbiosis; plant–microbe interactions; soil bacteria

1. Introduction

Arbuscular mycorrhizal fungi (AMF) are soil-dwelling fungi that have been in a mutual symbiotic relationship with plants for millions of years. Approximately 85% of plant species in all terrestrial ecosystems have interdependent associations with AMF [1]. AMF belong to the phylum Glomeromycota and form arbuscules, vesicles, and hyphal coils within root cells during symbiotic development. They use their extensive hyphal network to acquire nutrients, such as phosphorus, nitrogen, potassium, and micronutrients, from the soil, deliver them to the host plant, and take up carbohydrates in return [1,2]. The complex network of fungal hyphae augments the absorptive area of roots, extending beyond the depletion zone around the root and effectively improving the accessibility of soil nutrients for plants. AMF can markedly enhance the uptake of micronutrients, including Cu, Zn, and Fe, which are often limited in bioavailability owing to their tendency to form insoluble complexes or their spatial distribution in soil [3,4]. Furthermore, AMF can mobilize and solubilize micronutrients by excreting organic acids and enzymes, thereby transforming these elements into more plant-accessible forms [5]. By regulating micronutrient concentrations in plant tissues, these fungi offer a buffering mechanism that mitigates the risks of deficiency or toxicity [6]. Consequently, AMF play a pivotal role in enhancing nutrient absorption by plants, transforming less accessible micronutrients into bioavailable forms, and safeguarding against nutrient imbalances.

Iron is a vital micronutrient, fundamental to several metabolic processes, including photosynthesis, respiration, and nitrogen fixation [7]. Even though the total amount of iron is abundant in soil, most iron is present mainly in the Fe^{3+} form, which is less soluble than Fe^{2+}. The solubility of Fe^{3+} is largely dependent on pH and redox conditions [8]. Owing to the lower solubility of iron under high pH levels, iron becomes deficient for living organisms, posing a challenge to plant nutrition. In this context, AMF symbiosis significantly enhances iron uptake and homeostasis in plants. The association of plants with AMF alters root architecture, promoting the proliferation and elongation of roots and consequently increasing the root surface area [9,10]. This increase in root size and branching allows for a high contact area with soil, thereby facilitating excellent nutrient acquisition. Additionally, AMF can stimulate the production of root exudates that can chelate and solubilize iron, increasing its bioavailability for plant uptake [11]. The role of AMF extends beyond iron acquisition to encompass a broad role in plant stress tolerance. For instance, under iron-deficient conditions, plants in a symbiotic relationship with AMF exhibit enhanced stress tolerance mediated by improved nutrient homeostasis and triggering of stress-associated signaling pathways [12–14]. A noteworthy aspect of this symbiotic relationship is its association with the diversity of other soil bacteria. Bacterial communities in the rhizosphere and mycorrhizosphere can influence AMF–plant symbiosis and consequently affect iron uptake and homeostasis [15]. Certain bacteria, known as plant growth-promoting rhizobacteria, can enhance the efficiency of AMF symbiosis, potentially leading to improved iron acquisition and homeostasis.

Several pieces of evidence have provided insights into the molecular mechanism by which AMF positively alleviate iron deficiency in host plants; however, intricate networks of interactions involving AMF, plant, and other soil bacteria involved in iron homeostasis are still unknown. In particular, siderophores, which play the most important role in iron competition or cooperation in the environment, are important in regulating these networks. Siderophores are low-molecular-weight chelators produced by various microorganisms and plant roots and can produce high-affinity complexes with Fe^{3+} [16]. Siderophores facilitate iron acquisition and play a vital role in regulating intracellular iron levels by coordinating iron uptake, storage, and utilization [17,18]. Mycorrhizal fungi, representing the ericoid, orchidaceous, and ectomycorrhizal symbioses, release hydroxamate-type siderophores. Arbuscular mycorrhiza, which establishes a nutrient-exchange symbiosis, is identified by the presence of siderophores typical for the phylum Zygomycota. This distinction is made by detecting the rhizoferrin signature in arbuscular mycorrhizal plant tissue [19]. Understanding the role of siderophores in the intricate network of interactions involving AMF, plant, and other soil microbiota for iron homeostasis can open avenues for harnessing these symbiotic relationships for sustainable and resilient agriculture. In this review, we introduce the role of AMF in these interactions, their implications for plant–iron homeostasis, and potential ways to manipulate these interactions to improve plant health and productivity.

2. Do AMF Thrive in the Presence of Iron?

AMF do not thrive specifically in the presence of iron, but iron availability in soil plays a crucial role in the interaction between AMF and plants. Iron deficiency may reduce arbuscule formation and function, hindering the symbiotic relationship and overall nutrient uptake for both the fungi and host plant [20]. Moreover, iron is essential for the growth and development of fungal hyphae, promoting them to form robust hyphal networks and facilitating root colonization [2]. These behaviors indicate that iron availability in soil is vital for optimal AMF–plant interactions [21,22].

The efficient uptake of iron and its transfer to plants are major features of symbiosis. To acquire iron, all plant species must confront the challenges of iron insolubility and toxicity and evolve different mechanisms for iron acquisition [23]. Each fungus utilizes at least two of the four iron uptake mechanisms that are dependent on metalloreductases and involve Fe^{3+}/Fe^{2+}. These involve direct Fe^{2+} permeation, coupled ferroxidase/permease

uptake, heme/hemin uptake, and siderophore-mediated iron uptake [24] (Figure 1). Fe^{2+} can be transported directly into fungal cells via divalent ion transporters such as Fet4p, which has been characterized in *S. cerevisiae*. The most abundant membrane reductase in fungi is Fre1p [25]. Initially, Fe^{3+} is reduced to Fe^{2+} by Fre1p, and reduced Fe^{2+} is then specifically taken up by a high-affinity transporter complex, i.e., Fet3p and Ftr1p. Some opportunistic pathogenic fungi, including *Candida albicans* and *Histoplasma capsulatum*, express a heme receptor *Rbt5* gene required for virulence in organisms, which depends on this heme-iron uptake pathway [26,27]. Regardless of their ability to produce siderophores, fungi generally possess the siderophore transporters that enable them to uptake different types of siderophores such as bacterial coprogen or enterobactin [28]. The siderophore–iron complex is taken up by specific transporters, such as Sit1p, in the fungal cell membrane that is stored in hyphae for inclusion into spores, potentially affecting sporulation [29,30].
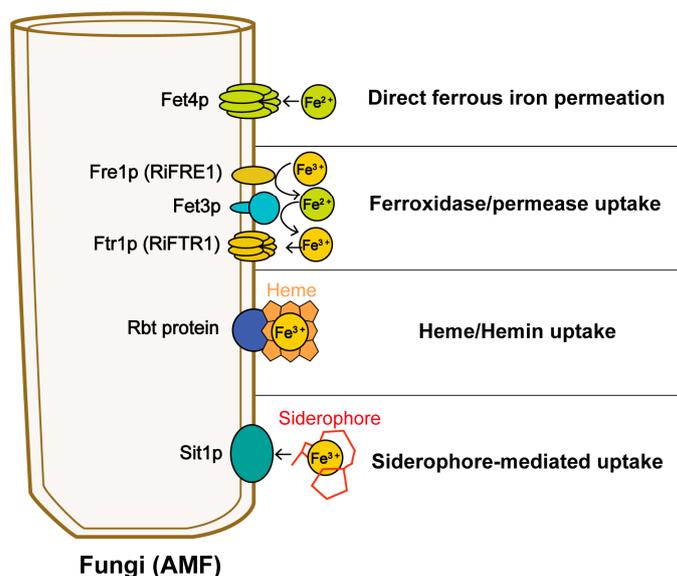

Figure 1. The four major iron uptake mechanisms in fungi. (i) Direct Fe^{2+} permeation, (ii) coupled ferroxidase/permease uptake, (iii) heme/hemin uptake, and (iv) siderophore-mediated iron uptake. In AMF, a putative ferrireductase RiFRE1 and iron permease RiFTR1 have been discovered recently. Other mechanisms are still not clear in AMF.

An in silico genome-wide analysis of Cu, Fe, and Zn transporters has identified 30 open reading frames in the whole genome of *Rhizophagus irregularis*, which potentially encode metal transporters [31]. It has been reported that *R. irregularis* contains a putative ferrireductase, RiFRE1, which encodes approximately 541 amino acids [32]. Ferroxidase pathways are then mediated by iron permease, namely RiFTR1 and RiFTR2 (two putative orthologs), which are, respectively, responsible for iron acquisition and iron homeostasis during iron deficiency. These iron permeases are expressed in germinated spores and mycorrhizal roots. Apart from this, *R. irregularis* consists of another ferroxidase pathway containing a single transmembrane domain and an extracellular multicopper oxidase (MCO) domain, which is responsible for the uptake of reduced Fe^{2+} via oxidation through a copper- and oxygen-dependent reaction. Recently, Tamayo et al. [33] observed nine genes that encode MCOs (RiMCO1–9), among which RiMCO1 and RiMCO3 might have possible roles in reductive and high-affinity iron uptake. Although the detailed mechanism of siderophore-mediated iron uptake by AMF remains to be elucidated, genome analysis has shown that AMF, including *Gigaspora rosea*, *R. irregularis*, *Glomus cerebriforme*, and *Diversispora epigea*, possess a non-ribosomal peptide synthetase-independent siderophore synthase [34].

3. Plant–AMF Interaction

In plants, iron serves as an indispensable cofactor for various enzymes involved in vital metabolic processes, and iron deficiency leads to diminished chlorophyll synthesis and photosynthesis, causing chlorosis and significant growth impairments [35]. To cope with iron deficiency, two main approaches are adopted by plants. The reduction strategy (strategy I) is mainly found in monocots and dicots [36]. Soil pH is decreased as a result of H^+ extrusion by epidermal proton H^+-ATPases on roots, thereby increasing the solubility of Fe^{3+}. Solubilized Fe^{3+} is reduced to Fe^{2+} by a ferric reduction oxidase and transported to the root by iron-regulated transporters. In contrast, the chelation strategy (strategy II) is found in all monocots [37]. It relies on the excretion of mugineic acids that belong to the phytosiderophores family. Being complexed with phytosiderophores, iron is introduced into the plant by Yellow Stripe-like transporters that are structurally related to metal–nicotinamine complexes and play a critical role in iron homeostasis in plants [38].

Mycorrhizal symbioses provide a high amount of essential nutrients to host plants compared to those of non-mycorrhizal plants [39] (Figure 2). Kabir et al. [40] observed that AMF significantly increase the dry mass, width, and chlorophyll synthesis and photosynthesis parameters of sunflower cultivated under iron-deficient conditions, suggesting that AMF restore iron balance in sunflower plants. The improved nutrient uptake by mycorrhizal symbiosis through the wide hyphal network increases the accessible soil volume of plants [41]. The symbiotic association between plants and AMF stimulates the production of strigolactones, which are important for rhizosphere signaling and play a key role in stimulating hyphal branching [42]. In return, AMF makes distant resources available for plants.
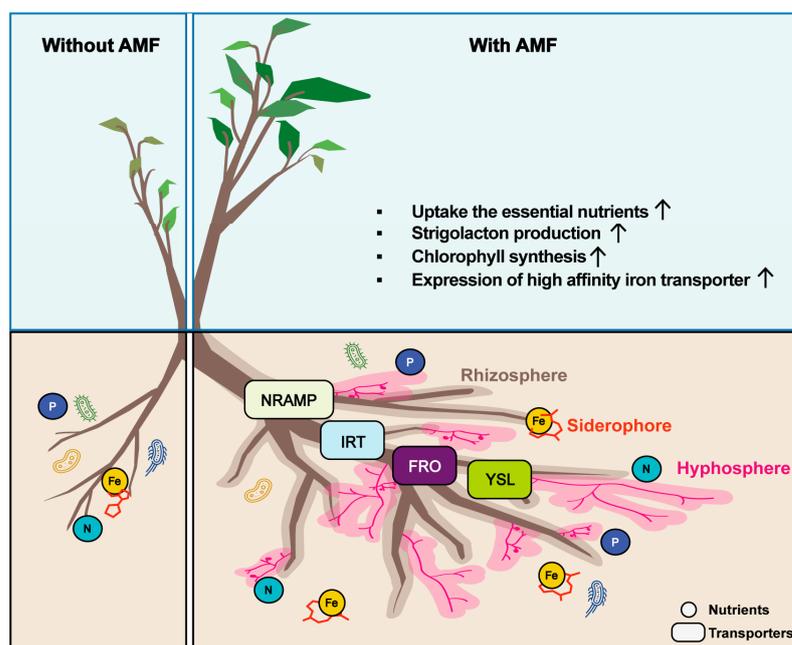

Figure 2. Importance of symbiotic relationship of arbuscular mycorrhizal fungi in plant growth. Arbuscular mycorrhizal fungi regulate plant metabolism in the rhizosphere to enhance iron uptake, and in the hyphosphere to make distant iron available for plants. Brown and pink zone represent rhizosphere and hyphosphere, respectively.

In addition to spatial expansion, AMF can enhance iron uptake in plants through various mechanisms. One such mechanism is the release of low-molecular-weight organic compounds, such as oxalic acid and citric acid, which can solubilize insoluble forms of iron in soil [5]. Rahman et al. [14] found that acidification in the rhizosphere is a common response in plants adopting the reduction strategy, and the presence of AMF aggravates the decrease in pH.

AMF can enhance the expression of high-affinity iron transporters in plant roots, facilitating iron uptake from soil [33]. Jung et al. [43] demonstrated that AMF colonization upregulates the expression of iron-regulated transporter 1 *(IRT1)* and ferric reductase oxidase 2 (*FRO2*) genes, which are responsible for iron uptake from soil. Kabir et al. [40] also found that AMF upregulate another ferric reductase gene, *HaFRO1*, alongside the expression of transport genes *HaNramp1* and *HaIRT1*. Moreover, in the context of iron homeostasis, natural resistance-associated macrophage protein transporters also play a key role, and members, such as *RiSMF1*, *RiSMF2*, *RiSMF3.1*, and *RiSMF3.2*, have been identified in *R. irregularis* [20,44].

AMF contribute to iron homeostasis by increasing the production of iron-chelating compounds, such as phytosiderophores, in plant roots. Li et al. [45] observed that two iron-phytosiderophore transporters are upregulated during AMF symbiosis in wheat roots, indicating a more substantial release of siderophores in wheat during symbiosis with AMF. The release of phytosiderophores increases in the presence of AMF cultured with Sorghum roots along with the expression of iron uptake-related genes *SbDMAS2*, *SbNAS2*, and *SbYS1* [46]. Chorianopoulou et al. [47] observed that the enzyme family of nicotinamine-synthases, *ZmNAS1* and *ZmYS1*, are severely overexpressed in non-mycorrhizal plants, while mycorrhizal plants do not intend to enhance the chelation strategy. AMF can even improve iron translocation within plants [48]. They enhance the expression of genes encoding transporters, such as iron-regulated transporter 3, involved in intracellular iron trafficking. This ensures that iron is properly distributed and utilized in various physiological processes in plant tissues to organs [16].

4. Bacteria–AMF Interaction

The interaction between bacteria and AMF in the endosphere and hyphosphere has gained significant attention in recent years. The hyphosphere refers to a more specific zone surrounding fungal hyphae. These interactions are mediated by a combination of physical associations, signaling pathways, and nutrient exchange, which in turn benefits plants by improving iron uptake and translocation within plants [49]. The bacteria–fungi interaction in the hyphosphere is influenced by various factors, including plant genotypes, environmental conditions, and a dynamic network of interactions within the plant biome [50]. Bacterial and fungal communities can differ depending on the developmental stages of plants, indicating a tight interaction with host physiology. Certain ectomycorrhizal fungi, such as *Paxillus involutus* and *Suillus bovinus*, have demonstrated the capability to host diverse bacterial communities, underscoring the presence of distinct niches within their mycorrhizospheres that exhibit high dependence on specific fungal species rather than host plants [51].

Bacteria–fungi interactions within the internal microenvironment of plants emerge as crucial modulators of iron dynamics. AMF play a pivotal role in the iron nutrition of plants, particularly in soils with low bioavailable iron. Both mycorrhizal and saprophytic fungi, along with bacteria, contribute to mineral weathering in the rhizosphere by inducing acidification [52]. Moreover, bacteria can produce siderophores and engage in synergistic relationships with fungi, which enhances this process. Bacterial strains derived from the hyphosphere of the ectomycorrhizal fungus *Scleroderma citrinum* exhibit a heightened capacity for mineral weathering compared to those sourced from the bulk soil [53]. Siderophores, which are essential for iron acquirement by soil microorganisms, have been identified as important factors in bacteria–fungi interactions. Bacteria can produce siderophores that are iron-chelating compounds and enhance iron availability and uptake by both bacteria and fungi [54]. Siderophores can influence the solubility and dissolution kinetics of iron oxides, leading to increased iron availability in the surrounding environment. Bacteria–fungi interactions can also influence the production of antifungal antibiotics by bacteria [55]. These antibiotics can inhibit the growth and activity of pathogenic fungi, thereby protecting the host plant from fungal infections [56]. The production of antifungal antibiotics by bacteria can contribute to iron homeostasis by preventing iron sequestration by pathogenic

fungi and promoting iron availability for plants and beneficial microorganisms. Furthermore, bacteria–fungi interactions can be influenced by the regulation of iron uptake and homeostasis in both bacteria and fungi. Bacterial receptors, such as outer membrane TonB-dependent receptors, play a role in iron uptake from siderophores produced by other microorganisms [57]. Iron uptake in bacteria is tightly regulated, and the expression of iron acquisition systems is hierarchically controlled. Therefore, the regulation of iron uptake and homeostasis in both bacteria and fungi is crucial for maintaining iron balance and ensuring efficient iron utilization.

The hyphosphere is basically characterized by distinctive biotic and abiotic factors compared to those of the surrounding bulk soil, and it is an area of intense microbial activity and interactions [58]. AMF release hyphal compounds (e.g., organic acids and sugars) into soil to orchestrate the hyphosphere colonized by diverse microbes [59]. Plants also quickly channel recent photosynthetic products through ectomycorrhizal hyphae, facilitating direct interactions with bacteria in soil areas distant from roots [60]. Recent advances in molecular biology and metagenomics have started unraveling the mechanistic details of these interactions involving several bacterial genera (e.g., *Microbacterium*, *Streptomyces*, *Bacillus*, *Enterobacter*, and *Rhizobium*) that colonize hyphae. These bacteria are able to produce indole-3-acetic acid (IAAs) and siderophores, which can be beneficial to plants [61]. *Sphingobacterium*, which is commonly found in commercial AMF inoculants, exhibits resilience in herbicide-contaminated soils and shows plant growth-promoting traits such as solubilization of inorganic phosphates, surfactant production, and synthesis of IAAs [62]. In contrast, some studies indicate that soil bacteria affect plant growth by affecting the structure or elongation of hyphae [63]. When combined with AMF, *Flavobacterium*, *Brevundimonas*, *Stenotrophomonas*, and *Devosia* can enhance plant growth during periods of drought or salinity stress and facilitate spore germination of AMF [64]. Mycorrhiza helper bacteria can facilitate or enhance the colonization of AMF on plant roots by suppressing soil-borne pathogens or producing growth factors that stimulate spore germination or hyphal branching of AMF [65]. *Paenibacillus validus* has shown the potential to stimulate in vitro growth and spore formation in *Rhizophagus irregularis* [66]. Therefore, enhanced fungal growth may be beneficial in developing mycorrhizal association with plants. Some bacteria, in turn, can solubilize soil-bound nutrients or fix atmospheric nitrogen, which becomes accessible to plants via the mycorrhizal network [67]. This collaborative nutrient exchange benefits both plants and bacteria. Understanding the interactions between AMF, plants, and soil bacteria is crucial for appreciating the intricate dynamics of soil ecosystems.

Recent studies have underscored the role of soil bacteria in chelating iron, making it available to plants, specifically through the intricate network of fungal hyphae. Caris et al. [68] have noticed that iron can be transferred via fungal hyphae in soil to peanut and sorghum plants (Figure 2). Patel et al. [69] observed that iron uptake increases in plants connected to siderophore-producing bacteria through fungal hyphal networks. Furthermore, Verma et al. [70] reported that these bacteria–fungi associations can significantly improve plant growth under iron-limited conditions. Interestingly, Złoch et al. [71] noted that some plants can signal bacteria to produce more siderophores when experiencing iron deficiency. A comprehensive review by Liu et al. [20] highlighted the complex interplay between bacteria, fungi, and plants in the process of iron acquisition, shedding light on the potential for harnessing these interactions in sustainable agriculture. Chelation of iron by soil bacteria and its transfer via hyphae to plants are integral components of soil–plant–microbe interactions.

5. Siderophores, Iron Uptake, and Its Role in AMF Symbiosis

Understanding the interactions between AMF, plants, and soil bacteria is crucial for appreciating the intricate dynamics of soil ecosystems. Microorganisms require elevated concentrations of iron (approximately 10^{-6} M) for sustenance, triggering the onset of siderophore production when they perceive levels beneath this threshold [72]. Siderophore production can reshape interactions within the environmental microbial community, fos-

tering cooperative or competitive mechanisms [73]. Notably, various types of fungal siderophores have been discovered in soil, mostly hydroxamate-type compounds with several complexities, spanning monomers, dimers, trimers, and cyclic forms that are categorized into three structural families, namely fusarinines, coprogens, and ferrichromes [74]. The ferrichromes also benefit other microorganisms, such as *Pantoea*, *Enterobacter*, *Erwinia*, and *Yersinia*, which contain receptors to uptake these siderophores [75].

Furthermore, bacterial siderophores are taken up by fungi such as *Saccharomyces* and *Aspergillus* [76]. Enterobactin, the principal siderophore generated by enterobacteria, can also be utilized by *Saccharomyces*, a microorganism that does not produce siderophores [75]. Battini et al. [77] identified bacterial strains from *Rhizophagus intraradices* spores that are capable of solubilizing phosphorus from organic (phytate) and inorganic sources and producing siderophores. The endobacterial symbiont *Candidatus Glomeribacter gigasporarum* [78,79], a Gram-negative bacteria affiliated with *Burkholderiaceae*, is found in the hyphae and spores of *Gigaspora margarita*, an AMF species [80]. Notably, the siderophore-producing genus *Ralstonia* also belongs to *Burkholderiaceae*, prompting speculation about the potential involvement of bacterial genomes in synthesizing carboxylate-type siderophores by *G. margarita* [34]. The filamentous structure of fungal mycelium, comprising extensive hyphal networks, traverses vast expanses of soil, reaching microenvironments often inaccessible to plant roots. This vast network, acting in tandem with siderophores, boosts the capacity of fungi to solubilize and acquire iron from distant sources.

Apart from this, the biosynthesis of phytosiderophores (produced by plants), as mentioned in Section 3, and fungal siderophores exhibit their respective pathway wherein phytosideropores, such as 2-deoxymugineic acid (DMA), are synthesized in vitro from both L-methionine and nicotianamine [81]. Ma et al. [82] and Sun et al. [83] demonstrated that DMA biosynthesis is associated with the methionine recycling pathway. As fungal siderophores are mostly hydroxamates, except for rhizoferrin (a carboxylate), they form a strong iron bidentate and require acylation with acetyl or anhydromevalonyl [84,85]. Plattner and Diekmann [86] have also explained the biosynthetic pathway of fungal siderophores by stating that hydroxamate siderophores are derived from L-ornithine and share N^5-acyl-N^5-hydroxyornithine, which has been repeatedly mentioned in studies about the involvement of genes in secondary metabolism [87].

The iron acquisition pathways in fungi, including AMF, involve common mechanisms; however, they exhibit a few differences. Fungi, including AMF, possess specific membrane transporters that recognize and transport iron–siderophore complexes into fungal cells [56]. Fungal transporters facilitate the internalization of iron-loaded siderophores; however, siderophore-mediated iron uptake in AMF is largely unexplored. Glomuferrin (bisimidorhizoferrin), a carboxylate-type siderophore produced by *Glomeromycotina*, has been observed in the root tissue of *Tagetes patula nana* [88]. Despite using a reductive pathway for iron uptake, *R. irregularis* lacks a Fet3p-type ferroxidase homolog in its genome, in contrast to the genomes of all phylogenetically investigated non-glomeromycotina fungi. In various fungal species, including *Saccharomyces pombe*, *Phanerochaete chrysosporium*, and *Laccaria bicolor*, a minimum of one *Fet3* homolog is arranged in the genome with an *Ftr1* homologue that regulates iron metabolism, which is lacking in AMF [89,90]. Previously, Caris et al. [68] and Kobae et al. [91] observed a radioactive signal in the shoots of peanut, sorghum, and maize host plants when ^{59}Fe was supplied to the hyphae. However, the reductive pathway for iron uptake evolved by AMF is more similar to the reduction strategy of plants than that of other fungi. Furthermore, compared to non-mycorrhizal roots, mycorrhizal roots show increases in transcript levels of oligopeptide transporter genes such as *ZmOPT8a* and *ZmOPT8b* [91]. Major iron uptake analogs during iron uptake by AMF and plants are shown in Figure 3.
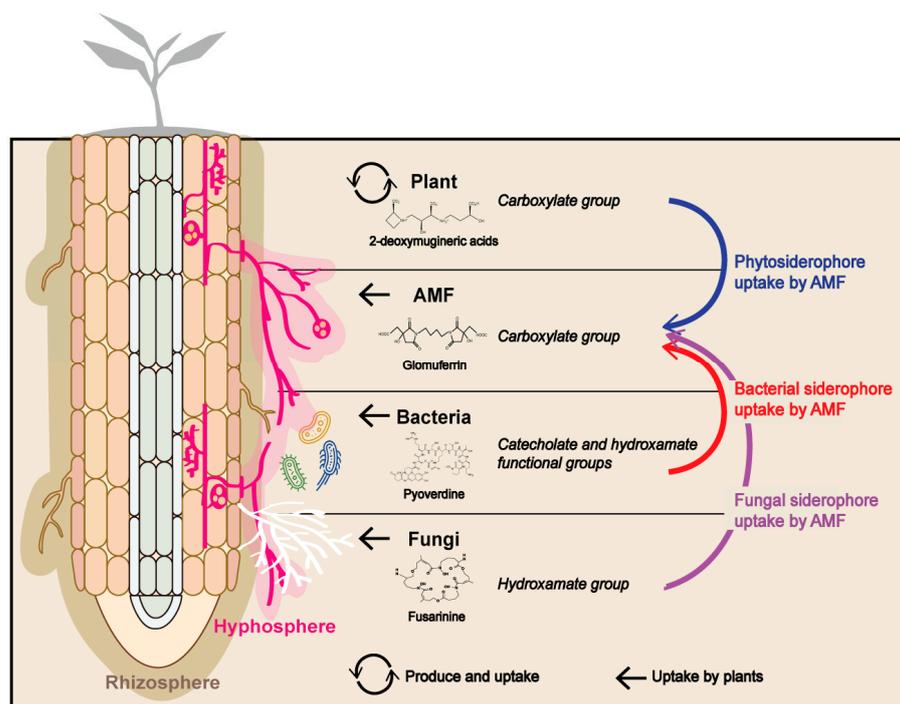
Figure 3. Production of siderophores by host plants and soil microorganisms. Arbuscular mycorrhizal fungi play an important role in maximizing iron uptake efficiency using phytosiderophores and in the uptake or transfer of iron chelated with siderophores produced by other soil microorganisms including bacteria, fungi, and arbuscular mycorrhizal fungi. Brown and pink zone represent rhizosphere and hyphosphere, respectively.

6. Future Perspectives and Challenges

As the significance of the bacteria–fungi–plant association in iron homeostasis comes to the fore, particularly regarding the role of siderophores, two main avenues emerge as being crucial in bridging current knowledge gaps. First, the intricate relationship between soil bacteria and AMF remains a topic of extensive interest. Siderophores produced by soil bacteria are instrumental in iron solubilization; however, how these molecules interface with AMF for subsequent iron uptake, transport, and translocation in plants is still elusive. Advanced molecular techniques, such as transcriptomic profiling of AMF in the presence of bacterial siderophores and isotopic labeling to track the movement of iron, may shed light on these mechanisms. Additionally, high-resolution imaging and computational modeling could provide invaluable insights into the spatio-temporal dynamics of siderophore-mediated interactions.

On a practical front, the next frontier lies in harnessing these molecular insights to devise effective strategies for optimizing iron uptake and homeostasis in plants. This necessitates a systems biology approach that integrates knowledge of siderophore production by bacteria, its uptake by AMF, and eventual assimilation by plants. Genetic engineering of both bacteria and AMF to potentially enhance siderophore production and uptake, respectively, may offer a promising avenue. However, field trials must be conducted to evaluate the feasibility and efficacy of these strategies, ensuring that laboratory successes translate to tangible agricultural benefits. Moreover, these endeavors must be underpinned by considerations of ecosystem balance, ensuring that any introduced change does not inadvertently destabilize existing microbial communities or plant health.

7. Conclusions

In conclusion, the interaction between plants and AMF plays a crucial role in iron homeostasis. AMF symbiosis enhances the expression of high-affinity iron transporters in plant roots, facilitating iron uptake from soil. Additionally, AMF can enhance the

production of iron-chelating compounds, such as phytosiderophores, in plant roots. These mechanisms contribute to improved iron uptake and translocation within plants, leading to enhanced growth and nutrient acquisition. Interactions between bacteria and AMF in endophytes and the hyphosphere play crucial roles in iron dynamics. Bacteria can produce siderophores, thereby enhancing iron availability and uptake by both bacteria and fungi. The presence of siderophores in endophytes can influence the solubility and dissolution kinetics of iron oxides, leading to increased iron availability in plants. Bacteria–fungi interactions in the hyphosphere can help transport iron to plants from usually unreachable, distant places for plant roots. The regulation of iron uptake and homeostasis in both bacteria and fungi is crucial for maintaining iron balance and ensuring efficient iron utilization by plants.

Overall, understanding the intricate interactions among plants, AMF, and bacteria is essential for optimizing iron uptake and homeostasis in plants. Future studies should focus on unraveling the molecular mechanisms underlying these interactions and developing strategies to manipulate them for sustainable agriculture. Plant health and productivity can be improved by harnessing the potential of these interactions, thereby contributing to resilient and sustainable agricultural systems.

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