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Review Article

Microbial Siderophores in Sustainable Agriculture: Molecular Insights, Smart Delivery Systems, and Biotechnological Applications

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Abstract: Microbial siderophores are low-molecular-weight compounds with a strong affinity for ferric (FSe^{3+}) ions. They play a pivotal role in plant-microbial interactions by enhancing iron bioavailability to plants, primarily through the chelation and mobilization of iron under iron-limited conditions. Their versatile and multifunctional nature has positioned them as promising agents for sustainable and eco-friendly agriculture. However, the practical application of siderophore-based systems is constrained by challenges related to stability, bioavailability, environmental degradation, and large-scale production. This review examines recent advancements in siderophore-mediated agricultural practices and applications, with a focus on formulation strategies and delivery systems, including seed coatings, foliar sprays, and nanoparticle-based encapsulation approaches. The review further highlights key technological innovations integrating nanotechnology, microbiology, and artificial intelligence (AI) for precision agriculture. Particular emphasis is placed on controlled-release systems, production scalability, and field-level applicability. Existing knowledge gaps, particularly in large-scale production and commercialization, are discussed alongside future prospects involving synthetic biology and engineered microbial systems. Siderophore-based technologies represent a transformative approach toward enhancing soil health, crop productivity, and sustainable bioeconomy development.

Keywords: Siderophores; Formulation development; Plant growth; Delivery systems; Iron chelation; Sustainable agriculture

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1. Introduction

Microorganisms, particularly fungi and bacteria, produce siderophores, which are specialized low-molecular-weight chelating agents, to acquire iron efficiently from their surrounding environment [1]. These compounds exhibit a high affinity for ferric ions (Fe^{3+}), enabling microorganisms to extract iron even in conditions where its bioavailability is extremely limited. Iron is abundantly present in soil in its oxidized (ferric) form, which makes it insoluble and unavailable to plants and other microbes [2]. Siderophores overcome this challenge by binding iron ions and forming soluble complexes that can be readily assimilated by plants and microbes [3]. These compounds play a crucial role in microbial survival and plant-microbe interactions by supporting plant nutrition [4]. In the pursuit of meeting the demands of contemporary medicine, agriculture, and environmental sustainability, siderophore-based products have emerged as a promising solution for challenges related to nutrient acquisition, pathogen control, and bioremediation [5, 6].

Siderophores have gained considerable importance in agriculture due to their ability to facilitate iron uptake in plants, particularly under iron-limited conditions [7]. Plants can absorb iron indirectly through siderophore-chelated complexes, which are released by the rhizospheric microorganisms. This enhanced iron availability supports essential physiological processes such as photosynthesis and chlorophyll biosynthesis, thereby promoting plant growth and improving crop yield [8]. Siderophore-producing microorganisms are also classified as plant growth-promoting rhizobacteria (PGPR), as they provide additional benefits, including enhanced nutrient uptake and suppression of soil-borne pathogens [9, 10].

Siderophore-based biofertilizers or microbial formulations have the potential to transform the agricultural industry by promoting plant health and improving crop productivity [11]. Iron scarcity in soils is a significant barrier to optimal plant development, and traditional iron supplements can be inefficient and environmentally damaging [12]. Siderophore-based systems, however, offer an eco-friendly alternative that naturally improves plant iron uptake, often resulting in improved resistance to soil pathogens and reduced dependence on chemical fertilizers [13]. Beyond biofertilization, siderophore-based products are also explored as biopesticides, disrupting pathogen iron acquisition in plant microbiomes, thus protecting crops without the adverse environmental impacts of synthetic pesticides [14]. Microbial siderophores provide protection against plant pathogens and improve iron nutrition. Many soil-borne pathogens rely on iron for their growth and virulence [15]. Siderophore-producing microbes outcompete these pathogens for iron, thereby inhibiting their propagation. This dual function of siderophores, improving plant iron uptake and suppressing pathogens, positions them as powerful tools for sustainable agriculture [16]. Figure 1 shows the iron acquisition and suppression of root pathogens via siderophores produced by fluorescent *pseudomonas*.

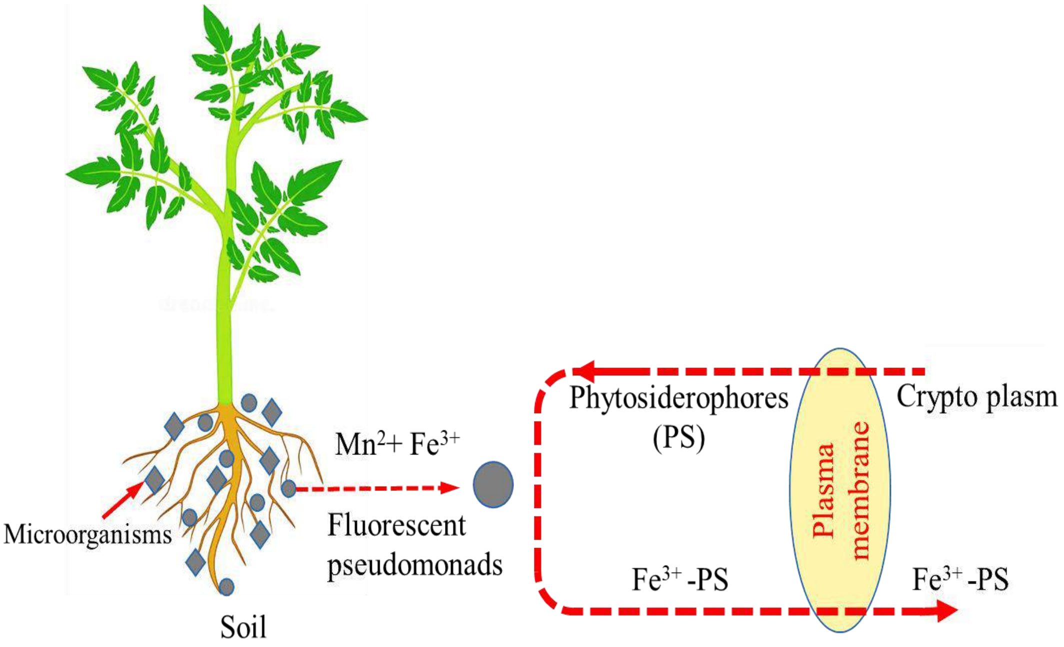


Figure 1. Iron Acquisition and Suppression of Root Pathogens via Siderophores Produced by Fluorescent *Pseudomonads.*

Moreover, microbial siderophores contribute to the health of the soil-plant-microbe ecosystem. By fostering beneficial microbial communities in the rhizosphere, they improve soil fertility and create a supportive environment for plant growth [17]. The integration of siderophore-producing microbes as biofertilizers and biocontrol agents has shown great potential in modern agriculture, reducing the reliance on synthetic fertilizers and pesticides while improving crop resilience and yield [18, 19]. Despite significant advancements in laboratory-scale research, the translation of siderophore- based technologies into field applications remains limited. The variability of soil composition, microbial adaptiveness, environmental degradation, and inconsistent practices across agro-climatic conditions continue to hinder their widespread usage and applications. Furthermore, most studies focus on controlled experimental systems, which lack large-scale and *on-site* field validations. Addressing these gaps requires an integrated approach combining microbial engineering, advanced formulation strategies, and field-applicable agricultural technologies.

One of the most promising areas for siderophore applications lies within healthcare, where these molecules are incorporated into novel antimicrobial strategies [20]. Pathogenic bacteria are highly dependent on iron, and the presence of siderophores can be used as a gateway for introducing antibiotics or antifungal agents directly into bacterial cells [21]. This approach, commonly referred to as a "Trojan horse" mechanism, harnesses bacteria's inherent need for iron while enabling precise drug targeting. Such methods not only enhance therapeutic efficacy but also offer a potential means to combat antibiotic resistance, as the delivery system specifically targets bacterial iron acquisition pathways without affecting human cells [22]. Consequently, these formulations represent a sophisticated, more selective option for combating resistant strains of bacteria [23].

In addition to enabling nutrient uptake, siderophores play an important role in plants' ability to survive stress. They enhance the plant resilience by providing nutrient uptake and minimizing oxidative damage caused by abiotic stressors such as drought, salinity, and heavy metal contamination [24]. Siderophores also contribute indirectly to plant defense responses, including modulation of reactive oxygen species (ROS) [25, 26]. Iron is often found in soils in its oxidized form, ferric iron (Fe^{3+}), which is tremendously insoluble in aerobic and neutral to alkaline environments despite being abundant in soils [27]. This low bioavailability of iron poses a challenge for plants, particularly in calcareous soils, where iron shortage is predominant. Iron-deficient plants show symptoms such as chlorosis (yellowing of leaves), stunted growth, and reduced yield, highlighting the need for effective mechanisms to acquire this nutrient [28]. In plants, microbial siderophores are important for reducing iron deficiency. In response to low iron availability, bacteria and fungi produce these specialized compounds, which bind ferric iron with high affinity and form soluble complexes [29]. These complexes can be taken up by plants either directly, through root exudates containing specific transporters, or indirectly, via microbial interactions in the rhizosphere. By enabling iron acquisition, siderophores improve chlorophyll synthesis, improve photosynthetic efficiency, and promote overall plant growth and productivity [30].

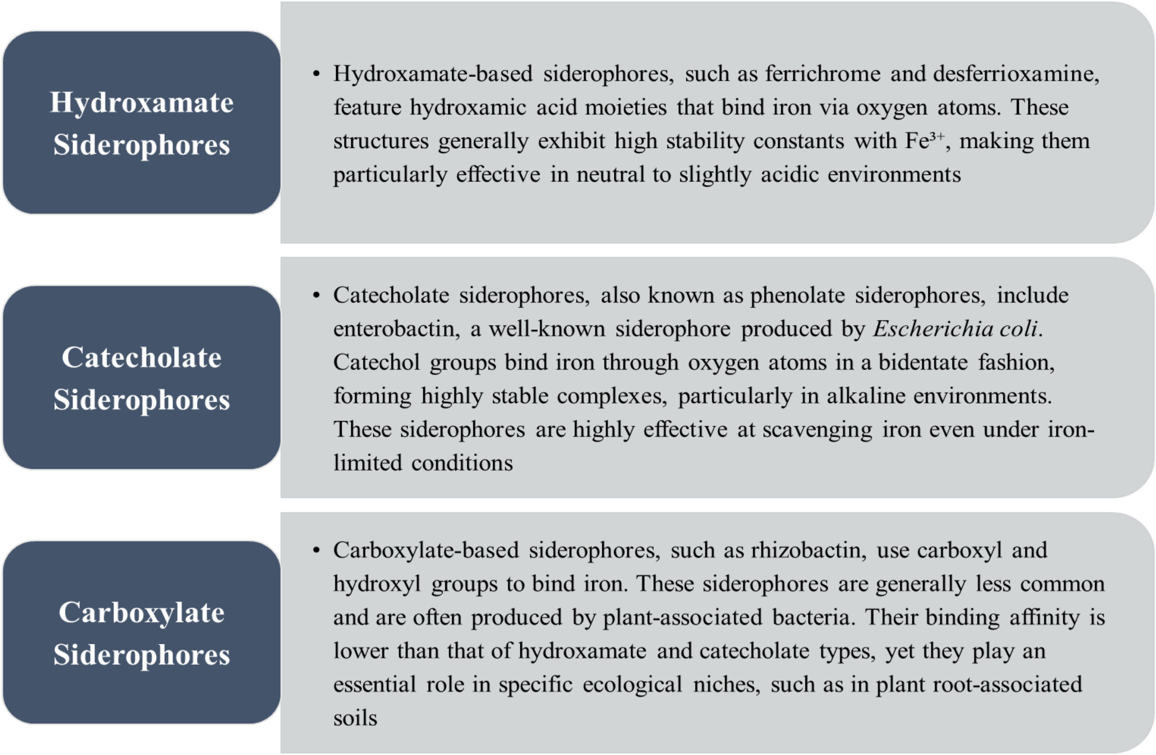
The complex delivery systems are crucial to ensure the stability, bioavailability, and active delivery of siderophore-based products from the position of formulation science [31]. To exploit the functionality of such products, encapsulation methods like liposomes, nanoformulations, and controlled-release hydrogels are significant [32]. Encapsulation not only protects the stability of siderophores under variable environmental conditions but also enables controlled release, enhancing efficacy and decreasing the potential for unintended interactions with non-target organisms [33]. Bioavailability and targeted action of siderophore-antibiotic conjugates are improved in clinical settings by Nanocarriers, while controlled-release systems in agriculture support the maintenance of ideal levels of bioavailable iron in the rhizosphere [34]. The multidisciplinary research of siderophore-based formulations establishes the convergence of microbiology, pharmacology, agronomy, and materials science, as these molecules are combined into highly personalized delivery systems [35]. As advancement in understanding siderophore chemistry and its interaction with host and environmental factors, the applications for these compounds are expected to expand, offering sustainable, targeted, and efficient solutions in health, agriculture, and environmental remediation [36, 37, 38].

2. Molecular Diversity and Chemistry of Siderophores

Siderophores play a significant role in iron acquisition, with different chemical structures that reflect their adaptability to ecological niches. Based on their iron-binding functionality, the classification reveals a complex relationship between their chemical characteristics and biological roles [39]. Their prime function is to bind and transport iron, a vital but often limited nutrient in many environments, particularly within host organisms. By chelating iron with high affinity, siderophores enable iron uptake, crucial for metabolic processes, enzyme function, and cellular growth [40]. Structurally varied, siderophores are categorized based on their chemical makeup and the exact coordination sites used to bind iron ions, which reflects both their complexation chemistry and ecological role.

2.1. Chemistry of Siderophores

At the core of siderophore chemistry is their iron-binding capacity, which is driven by functional groups capable of coordinating Fe^{3+} ions. Most siderophores exhibit a high affinity for ferric iron (Fe^{3+}), forming stable, hexadentate (six-coordinate) complexes. This strong binding is facilitated through specific functional groups that act as iron chelators, including hydroxamate, catecholate, and carboxylate groups. These ligands surround the ferric ion in an octahedral geometry, maximizing stability and solubility [41]. The three primary siderophore types (Figure 2), hydroxamate, catecholate, and carboxylate, are distinguished by these functional groups, each providing a unique set of coordination properties that suit different environmental niches and metabolic requirements (Table 1). The structural diversity of siderophores reflects their evolutionary adaptation to a wide range of ecological niches [42]. For example, catecholate siderophores exhibit exceptionally high iron-binding abilities, which confer a competitive advantage in iron-limited conditions; on the other hand, hydroxamate siderophores demonstrate greater stability across varying pH environments [43]. However, this adaptability may pose challenges in the development of universal delivery systems, as variations in chemical stability, transport mechanisms, and receptor specificity can significantly influence their effectiveness in agricultural applications.



Hydroxamate Siderophores

- Hydroxamate-based siderophores, such as ferrichrome and desferrioxamine, feature hydroxamic acid moieties that bind iron via oxygen atoms. These structures generally exhibit high stability constants with Fe^{3+}, making them particularly effective in neutral to slightly acidic environments

Catecholate Siderophores

- Catecholate siderophores, also known as phenolate siderophores, include enterobactin, a well-known siderophore produced by *Escherichia coli*. Catechol groups bind iron through oxygen atoms in a bidentate fashion, forming highly stable complexes, particularly in alkaline environments. These siderophores are highly effective at scavenging iron even under iron-limited conditions

Carboxylate Siderophores

- Carboxylate-based siderophores, such as rhizobactin, use carboxyl and hydroxyl groups to bind iron. These siderophores are generally less common and are often produced by plant-associated bacteria. Their binding affinity is lower than that of hydroxamate and catecholate types, yet they play an essential role in specific ecological niches, such as in plant root-associated soils

Figure 2. Types of primary siderophores: hydroxamate, catecholate, and carboxylate, with their distinct iron-chelating properties.

Table 1. Siderophore sources, application areas, and descriptions.

Siderophore	Source Organism	Application Area	Description	Reference
Desferrioxamine B	*Streptomyces pilosus*	Antibiotic Delivery	Aluminum and gallium conjugates show broad-spectrum antibacterial activity.	[44]
		Iron Chelation Therapy	Used to manage iron overload, oxidative stress, and hypoxic conditions.	
		Cancer Treatment	Induces apoptosis in breast cancer cells at high doses.	
		Medical Imaging	Facilitates radiolabeling for precise cancer cell imaging.	
Enterobactin	*Escherichia coli*	Antibiotic Delivery	Ciprofloxacin conjugates effectively target virulent strains of *E. coli*.	[45]
		Cancer Treatment	Demonstrates anti-cancer activity against specific tumor cell lines.	
		Vaccination Strategies	Conjugation with cholera toxin subunit B triggers protective immunity against *Salmonella*.	

Triacetylfusarinine C	*Aspergillus nidulans*	Iron Chelation Therapy Medical Imaging	Suppresses fungal pathogens by limiting iron availability. Enables detection of *Aspergillus* infections using PET scans.	[46]
Mycobactin	*Mycobacterium tuberculosis*	Cancer Treatment	Reduces the growth of cancer cells, including adherent and non-adherent types.	[47]
Aerobactin	*Escherichia coli*	Diagnostic Labeling	Functionalized aerobactin can label pathogenic bacterial strains for detection.	[48]
Preacinetobactin	*Acinetobacter baumannii*	Antibiotic Delivery	Targets multidrug-resistant *A. baumannii* by disrupting iron acquisition.	[49]

2.2. Classification of Siderophores on the basis of Metal-binding properties

The classification of siderophores is primarily based on their functional group chemistry and metal-binding mechanisms [50]. However, siderophores can also be classified by their structural forms and biosynthetic origins. Figure 3 shows the Classification of Siderophores on the basis of metal-binding properties.

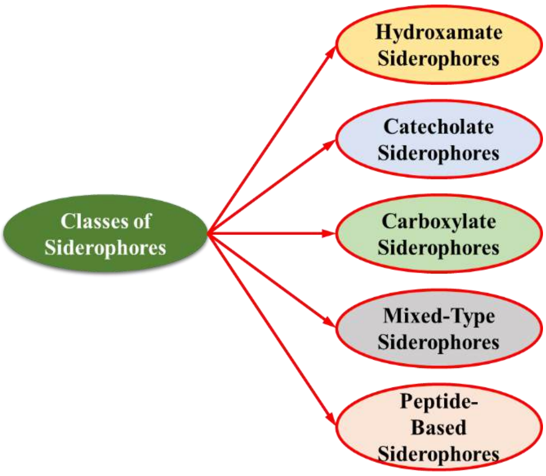


Figure 3. Classification of siderophores based on functional groups, including hydroxamate, catecholate, carboxylate, and mixed-type siderophores.

2.2.1. Hydroxamate and Catecholate Siderophores

Hydroxamate siderophores are synthesized from amino acids and hydroxylamine derivatives and are widely produced by both bacteria and fungi. Examples include ferrichrome and aerobactin, which are characterized by their high iron-binding constants [51]. Catecholate siderophores are predominantly produced by enteric bacteria. Enterobactin is one of the most potent iron-chelating molecules due to its tricatecholate binding sites, which confer exceptionally high affinity for ferric ions [52]**.** The presence of the catecholate functional group also enhances high specificity and binding strength for ferric ions, making these siderophores highly effective under competitive and iron-limited environments.

2.2.2. Carboxylate, Mixed-type, and Peptide-based Siderophores

Carboxylate siderophores are primarily produced by soil-dwelling bacteria, particularly those associated with plant-interacting systems. These siderophores, such as rhizobactin, utilize carboxylate and hydroxyl functional groups for iron coordination [53]. They are typically adapted to ecological niches that are less competitive compared to those dominated by hydroxymate and catecholate siderophores. Mixed-type siderophores contain a combination of functional groups, such as catecholate and hydroxamate moieties, enabling them to function effectively across diverse environmental conditions [54, 55]. This versatile composition and diversity in their surface functional group empower them with enhanced adaptability and iron-chelating efficiency. Peptide-based siderophores incorporate amino acids or peptide bonds within their structure [56]. Their complex molecular design contributes to distinctive iron-binding properties and also plays roles in microbial virulence and host-microbe interactions.

3. Biosynthesis of Siderophore

The complex biosynthetic pathways responsible for producing these compounds are highly sensitive to iron availability, leading to variations among the different types of siderophores produced [57]. The biosynthesis process includes many enzymatic reactions that combine to create iron-binding functional groups, resulting in a high affinity to iron [58]. Figure 4 indicates the key steps of siderophore biosynthesis. The biosynthesis of siderophores typically follows a modular approach, involving distinct biosynthetic enzymes that collaboratively produce the final siderophore molecule. This process can be divided into different steps as shown in Figure 5.

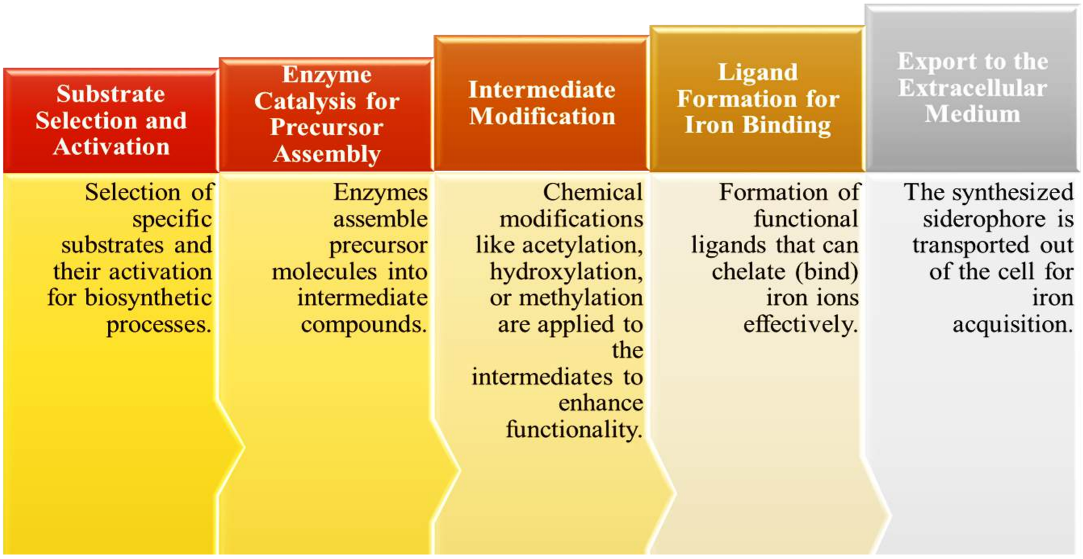
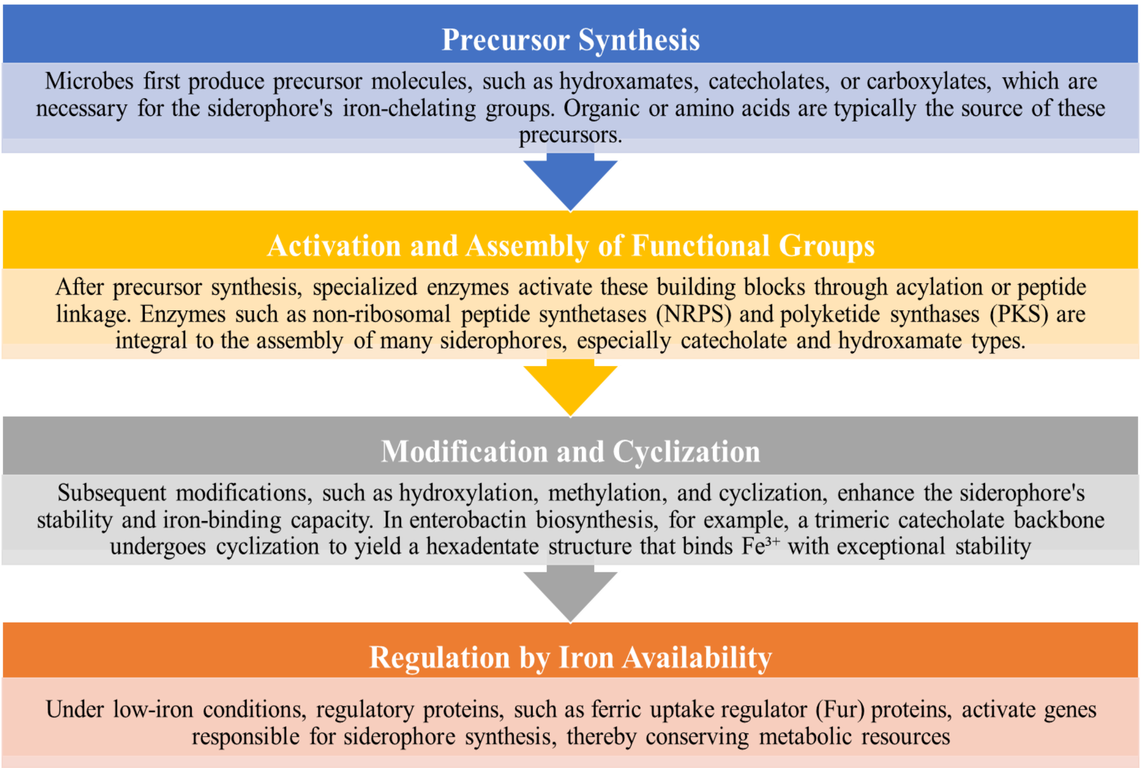


Figure 4. Illustration showing key steps in siderophore biosynthesis: substrate activation, enzymatic precursor assembly, intermediate modification, ligand formation, and extracellular export.



Precursor Synthesis

Microbes first produce precursor molecules, such as hydroxamates, catecholates, or carboxylates, which are necessary for the siderophore's iron-chelating groups. Organic or amino acids are typically the source of these precursors.

Activation and Assembly of Functional Groups

After precursor synthesis, specialized enzymes activate these building blocks through acylation or peptide linkage. Enzymes such as non-ribosomal peptide synthetases (NRPS) and polyketide synthases (PKS) are integral to the assembly of many siderophores, especially catecholate and hydroxamate types.

Modification and Cyclization

Subsequent modifications, such as hydroxylation, methylation, and cyclization, enhance the siderophore's stability and iron-binding capacity. In enterobactin biosynthesis, for example, a trimeric catecholate backbone undergoes cyclization to yield a hexadentate structure that binds Fe^{3+} with exceptional stability

Regulation by Iron Availability

Under low-iron conditions, regulatory proteins, such as ferric uptake regulator (Fur) proteins, activate genes responsible for siderophore synthesis, thereby conserving metabolic resources

Figure 5. Flow chart illustrating the major groups of siderophore biosynthesis, including NRPS-dependent and NRPS-independent (NIS) pathways.

3.1. Biosynthesis Pathway Variations among Siderophore Types

The differences in siderophore biosynthesis pathways are reflected in the diversity of siderophore structures [59]. While catecholate siderophores, like enterobactin, utilize NRPS pathways to link catechol moieties in a trimeric form, hydroxyamate siderophores, which are produced by bacteria such as *Pseudomonas aeruginosa*, rely on hydroxylation and peptide linkage [60]. Simpler processes involving the direct incorporation of organic acids are used by carboxylate siderophores [61], which are primarily produced by bacteria associated with plants.

Siderophores play a significant role in helping plants tolerate both biotic and abiotic stresses by improving nutrient uptake, mitigating toxic effects, and fostering a healthier rhizosphere [62]. Abiotic stresses such as drought, salinity, heavy metal toxicity, and nutrient deficiency severely affect plant growth and yield. Siderophores mitigate these stresses by enhancing the availability of essential nutrients, particularly iron, under challenging conditions. In saline soils, siderophore-producing microbes improve plant iron uptake, which is critical for maintaining photosynthetic efficiency and metabolic functions [63]. In heavy metal-contaminated soils, siderophores bind with toxic metals like cadmium or lead [64], reducing their bioavailability and protecting plants from metal-induced oxidative damage.

Additionally, by improving nutrient uptake, siderophores contribute to better root and shoot development, enhancing overall plant resilience to water scarcity and soil degradation. Biotic stresses caused by pathogens, such as fungi, bacteria, and nematodes, can devastate crops. Siderophores help suppress these pathogens by depriving them of iron, which is essential for their growth and virulence. Siderophore-producing beneficial microbes in the rhizosphere outcompete pathogens for iron, creating an environment that inhibits their proliferation [65]. This competitive exclusion reduces the incidence of diseases and promotes healthier plant growth. Additionally, some siderophores have direct antimicrobial properties, further enhancing their role as biocontrol agents.

3.2. Genetic Regulation and Engineering of Siderophore Biosynthesis

Siderophore biosynthesis is tightly regulated by intracellular iron levels through global regulatory systems such as the ferric uptake regulator. Under iron-replete conditions, Fur represses the expression of siderophore biosynthetic genes, whereas iron limitation triggers their activation. Key biosynthetic pathways include non-ribosomal peptide synthetase (NRPS)-dependent systems, responsible for producing complex siderophores such as enterobactin, and NRPS-independent pathways that generate simpler structures [65]. Advances in metabolic engineering have enabled the enhancement of siderophore production through genetic modifications. Strategies such as overexpression of biosynthetic gene clusters, deletion of competing metabolic pathways, and promoter engineering have significantly improved yields. Furthermore, synthetic biology approaches allow the design of novel siderophore analogs with improved stability and metal-binding efficiency. These developments are particularly relevant for large-scale applications, where optimized microbial strains can address current limitations related to low yield and production costs.

At the molecular level, siderophores act as high-affinity iron chelators, which significantly influence the iron availability in rhizospheric region of the soil. Iron is a necessary cofactor for enzymes involved in respiration, DNA synthesis and oxidative stress management, its' sequestration triggers the microbial responses for expression of iron acquisition systems and production of competing siderophores [65, 66]. On the other hand, plant beneficial microorganisms like plant growth-promoting rhizobacteria (PGPR) can also access siderophore-bound iron for increasing their metabolism and competitiveness. Siderophore-mediated regulation of gene expression is controlled by iron-dependent regulatory systems, the principal one being a DNA binding protein called the Ferric Uptake Regulator (Fur-protein) [62]. Low iron conditions trigger the microbes to regulate the genes responsible for siderophore production, transport proteins formation and other iron scavenging mechanisms. Furthermore, stress response, biofilm-forming, and antimicrobial-related genes could be regulated as well. Prolonged exposures may even result in adaptive genetic modifications, including mutations or horizontal gene transfer events, to improve iron acquisition ability [58, 62, 66].

4. Challenges in Siderophore Utilization

4.1. Secretion of Siderophores into the Environment

The secretion of siderophores into the environment is a critical microbial strategy to acquire iron, a necessary element that is often limited in bioavailability [66]. Bacteria secrete these small, high-affinity iron-chelating compounds, enabling them to scavenge iron from external sources, which is then transported into the cell [67]. Siderophore secretion offers distinct ecological and evolutionary advantages, allowing bacteria not only to access remote iron pools but also to establish interactions with neighboring cells, promoting cooperation or competition depending on the community structure and environmental conditions.

In environments where iron is unevenly distributed, the diffusible nature of siderophores is advantageous, as it enables iron solubilization at locations distant from the producing cell [68]. This mechanism is particularly beneficial when bacteria are attached to surfaces, such as in biofilms, where siderophores can chelate iron beyond the immediate vicinity, thereby making it accessible to the broader microbial community [69]. However, due to their diffusion, a substantial proportion of siderophores may be lost to the surrounding environment, especially in unstructured habitats. This limitation has driven some bacterial species to evolve membrane-bound iron uptake mechanisms as an alternative strategy [70]. The secretion of siderophores also influences bacterial social dynamics. Cooperative interactions may arise in dense populations where siderophores act as public goods, benefiting both producers and non-producers (cheaters) that possess compatible iron receptors [71]. These social interactions are particularly evident in biofilm-forming bacteria, where the communal benefit of siderophore production can outweigh the cost of individual secretion [72].

4.2. Environmental factors influencing the efficiency

The efficiency of siderophore-based products in agriculture is strongly influenced by environmental conditions or factors based on their physicochemical and biological composition. The environmental factors regulate both the microbial activity and the siderophore behavior in soil. A comprehensive understanding and analysis of these factors is essential for optimizing production, application, and performance of siderophore-based products [73]. For example, the pH of the soil significantly affects siderophore stability and iron-binding efficiency. Alkaline conditions generally enhance the functional efficacy of siderophores by increasing their iron-binding activity due to reduced iron solubility in soil [73, 74]. In contrast, under acidic conditions, iron is more soluble and readily available, which relatively diminishes the significance of siderophore activity. Therefore, siderophore-based products are more effective for alkaline soils where bioavailability of iron is the limiting factor.

Temperature affects both microbial growth and metabolic rates; moderate temperatures are generally suitable for optimal siderophore production, whereas extremes of temperature can inhibit microbial activity and enzymatic processes, which hinder siderophore production [74]. Another factor is the moisture level of the soil, which plays a crucial role by influencing microbial proliferation and nutrient diffusion. Higher moisture levels stimulate the siderophore production by supporting microbial metabolic activities, but in extreme watery conditions, siderophores may have a reduced activity due to increased dilution. Drought conditions can hinder microbial activity and decrease siderophore production [75]. The composition and diversity of the soil microbial community further modulate siderophore dynamics, as interactions such as competition, cooperation, and siderophore piracy can influence their availability and utilization [76]. Additionally, soil organic matter and nutrient status significantly impact siderophore production, as organic-rich soils promote microbial activity and metabolic diversity, while higher availability of accessible iron and other nutrients can downregulate siderophore synthesis due to reduced physiological demand [77].

4.3. Challenges in Scalability

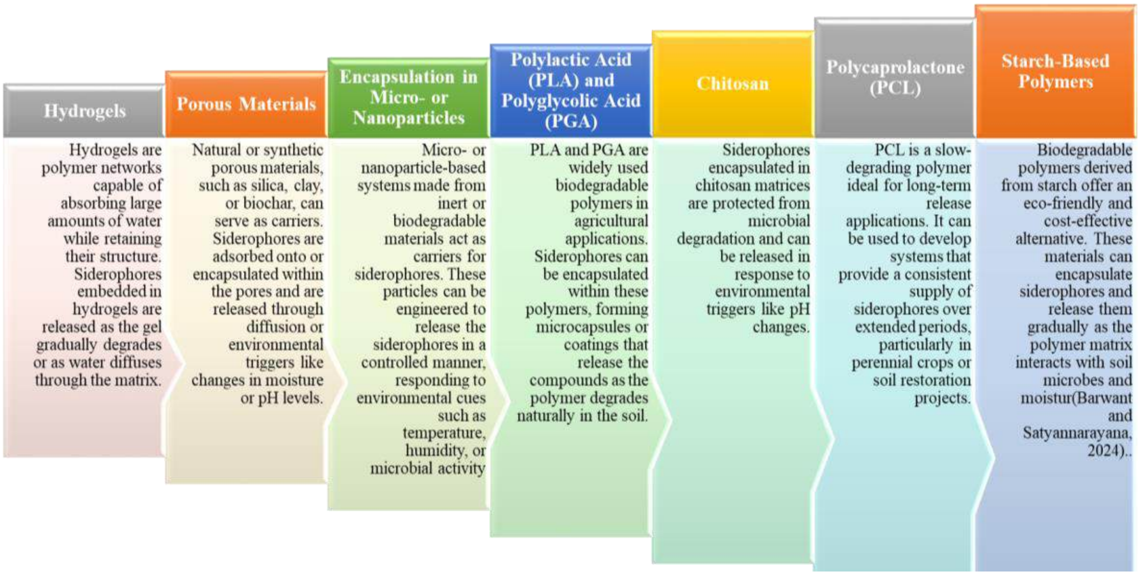
The large-scale deployment of siderophore-based products in agriculture is constrained by multiple technical and economic challenges associated with production, formulation, and regulatory compliance. The production of siderophores typically requires highly controlled fermentation conditions along with optimal nutrient composition, pH, and aeration; all these factors collectively complicate scale-up processing and increase operational costs. Downstream processing, particularly extraction and purification, further adds to the complexity and economic burden due to the need for high purity and stability [78]. In addition, siderophore production during fermentation is frequently constrained by low yields and reduced functional efficiency. They also vary significantly among microbial strains, necessitating the development of high-yielding and robust production systems for industrial feasibility. Furthermore, formulation also presents a critical challenge, as siderophore-based products must retain stability and functionality under diverse environmental conditions while remaining compatible with existing agricultural practices. However, advanced strategies such as encapsulation or controlled-release systems can substantially increase production costs and technical complexity [79, 80]. Furthermore, regulatory and quality assurance requirements impose additional constraints, as these products must demonstrate consistent efficacy, environmental safety, and non-toxicity, which can prolong approval timelines and elevate overall development costs [81].

The large-scale production and commercialization of siderophore-based products is constrained by many correlated challenges. The foremost limitation is the high production cost, which remains a significant barrier in commercialization, particularly in developing countries where economic feasibility is critical for adoption. In addition, limited awareness among farmers and stakeholders, coupled with concerns regarding compatibility with existing agricultural practices further restricts the market penetration. Supply chain related issues also play a major role including inconsistencies in raw material supply, difficulties in maintaining product stability during storage and transport. There can be challenges associated with efficient field-level delivery [78, 80]. Together, these factors limit the economic viability and scalability of siderophore-based formulations, thereby hindering their widespread adoption in modern agriculture systems. Moreover, the absence of standardized regulatory frameworks and limited industrial-scale validation further complicate commercialization efforts, emphasizing the need for coordinated research, industry-driven solutions and field-applicable practices.

5. Delivery Systems and Application Strategies for Siderophore-Based Products

5.1. Controlled Release Mechanisms

To maximize the efficacy of siderophore-based products, controlled release mechanisms are critical. These systems ensure a steady, prolonged supply of siderophores to plants, enhancing their stability, bioavailability, and efficiency while minimizing losses due to environmental degradation or microbial competition [82]. Among the promising approaches are matrix-based delivery systems and the use of biodegradable polymers. For controlled, sustained, and stimuli-responsive release, different types of substrate matrices including hydrogel-based, microbial-based, and nanoparticle-based products involve embedding siderophores within a carrier material that gradually releases active compounds over a period of time. These systems are designed to protect siderophores from degradation and ensure their availability in the rhizosphere or on plant surfaces [83]. Biodegradable polymers are an advanced and sustainable option for controlled release systems. These materials gradually break down in the soil into non-toxic byproducts, releasing siderophores in a predictable and sustained manner [84]. Figure 6 illustrates various advanced delivery systems for siderophores, highlighting innovative carriers and encapsulation methods designed to ensure controlled, sustained release and enhanced stability in diverse agricultural environments. Table 2 gives a critical analysis and comparison between the existing application methodologies traditional, current and next generation.



Hydrogels	Porous Materials	Encapsulation in Micro- or Nanoparticles	Polylactic Acid (PLA) and Polyglycolic Acid (PGA)	Chitosan	Polycaprolactone (PCL)	Starch-Based Polymers
Hydrogels are polymer networks capable of absorbing large amounts of water while retaining their structure. Siderophores embedded in hydrogels are released as the gel gradually degrades or as water diffuses through the matrix.	Natural or synthetic porous materials, such as silica, clay, or biochar, can serve as carriers. Siderophores are adsorbed onto or encapsulated within the pores and are released through diffusion or environmental triggers like changes in moisture or pH levels.	Micro- or nanoparticle-based systems made from inert or biodegradable materials act as carriers for siderophores. These particles can be engineered to release the siderophores in a controlled manner, responding to environmental cues such as temperature, humidity, or microbial activity	PLA and PGA are widely used biodegradable polymers in agricultural applications. Siderophores can be encapsulated within these polymers, forming microcapsules or coatings that release the compounds as the polymer degrades naturally in the soil.	Siderophores encapsulated in chitosan matrices are protected from microbial degradation and can be released in response to environmental triggers like pH changes.	PCL is a slow-degrading polymer ideal for long-term release applications. It can be used to develop systems that provide a consistent supply of siderophores over extended periods, particularly in perennial crops or soil restoration projects.	Biodegradable polymers derived from starch offer an eco-friendly and cost-effective alternative. These materials can encapsulate siderophores and release them gradually as the polymer matrix interacts with soil microbes and moistur(Barwant and Satyannarayana, 2024)..

Figure 6. Various advanced delivery systems for siderophores, including nanoparticle, polymer-based, liposomal, and targeted carrier platforms.

Table 2. Comparative analysis of siderophore delivery systems.

Delivery Strategy	Mechanism of Action	Key Advantages	Limitations	Emerging Improvements / Innovations	References
Seed Coating (Bio-priming)	Direct coating of seeds with siderophore-producing microbes or purified siderophores enabling early rhizosphere colonization.	Targeted delivery at germination stage; improved root establishment; reduced nutrient loss.	Limited persistence; dependency on soil conditions; microbial viability issues.	Use of polymeric binders, biochar-based coatings, and encapsulated microbial consortia to enhance survival and gradual release.	[85]
Foliar Application	Direct application onto plant surfaces allowing absorption through stomata and cuticle.	Rapid nutrient assimilation; bypasses soil-related limitations; suitable for micronutrient deficiency correction.	Short-lived effects; susceptibility to UV degradation and wash-off; requires repeated application.	Nano-enabled foliar sprays, surfactant-assisted penetration systems, and stimuli-responsive formulations to improve uptake and retention.	[86]
Soil Amendment (Bulk Application)	Introduction of siderophore-producing microbes or compounds into soil to enhance rhizosphere iron mobilization.	Sustained interaction with plant roots; improves soil microbial ecology; long-term soil health benefits.	Competition with native microbiota; dilution effects; environmental variability.	Microbiome engineering, co-inoculation with PGPR consortia, and use of carrier matrices (e.g., compost, biochar) to improve persistence.	[87]
Nano-encapsulation (Nanocarriers)	Encapsulation of siderophores within nanoparticles enabling controlled and targeted release.	Enhanced stability; protection from degradation; controlled release kinetics; improved bioavailability.	High production cost; regulatory challenges; potential ecotoxicity concerns.	Smart nanocarriers (pH-/temperature-responsive), biodegradable nanopolymers, and hybrid nano-bio systems for precision delivery.	[88]
Hydrogel-based Controlled Release Systems	Incorporation of siderophores into polymeric hydrogels for gradual release in soil.	Prolonged release; moisture retention; reduced leaching losses.	Limited field validation; potential cost constraints.	Biodegradable hydrogels, stimuli-responsive gels, and integration with microbial inoculants	[89]
Microbial Consortia-based Delivery	Use of multi-strain PGPR systems producing siderophores synergistically.	Enhanced functional diversity; improved stress tolerance; synergistic nutrient mobilization.	Complex formulation; stability and compatibility issues.	Synthetic microbial consortia, engineered microbiomes, and systems biology-driven strain selection.	[90]
Electrospun Nanofiber Delivery Systems (Emerging)	Immobilization of siderophores within nanofibers for slow diffusion and targeted release.	High surface area; tunable release profiles; enhanced stability.	Early-stage research; scalability challenges.	Functionalized nanofibers with biodegradable polymers and integrated sensors for precision agriculture.	[91]
AI-assisted Precision Delivery Systems (Next-gen)	Integration of real-time soil data with AI models to optimize siderophore application timing and dosage.	Reduced wastage; optimized nutrient delivery; site-specific management.	Requires infrastructure and data integration; high initial cost.	IoT-based sensing platforms, predictive modeling, and automated delivery systems.	[92]

5.2. Method of Nanoparticle Encapsulation

Nanoparticle encapsulation is a cutting-edge approach in the formulation of siderophore-based products [93]. This method involves incorporating siderophores into nanoscale carriers to enhance their stability, bioavailability, and targeted delivery as illustrated in Figure 7. The use of nanoparticles provides several advantages for agricultural applications, addressing challenges such as environmental degradation, microbial competition, and inefficient delivery [94]. Nanoparticle encapsulation offers a transformative approach to enhancing the performance of siderophore-based products. By leveraging the benefits of nano-formulations and employing advanced encapsulation techniques, agricultural applications can achieve improved efficiency, sustainability, and scalability [95].

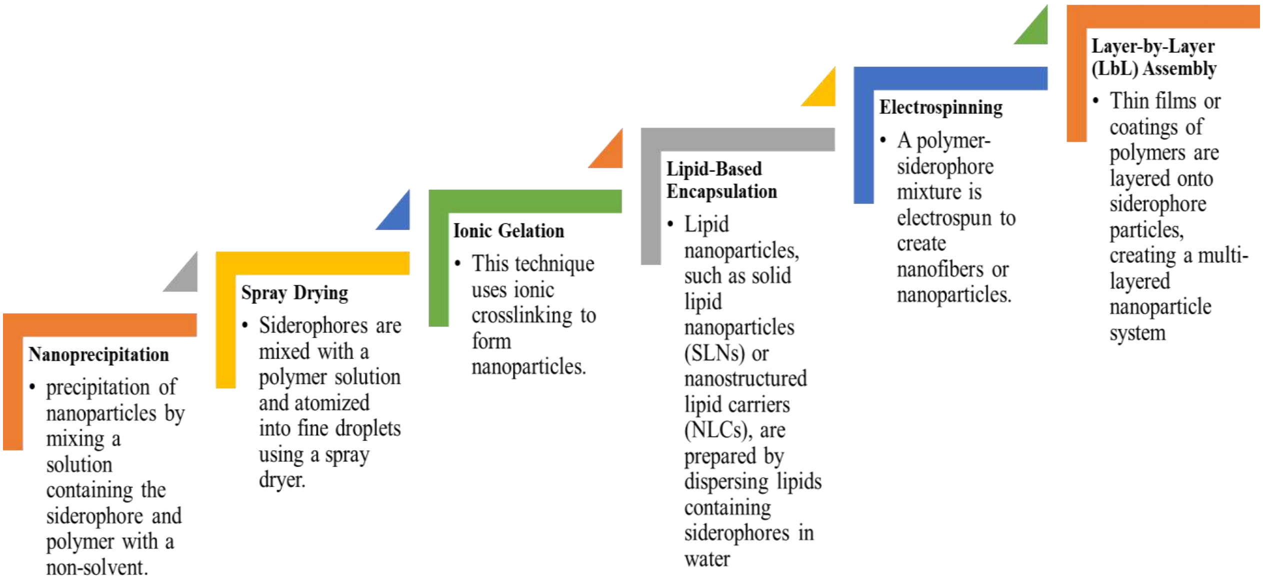


Figure 7. Nanoparticle-mediated encapsulation approach demonstrating controlled and targeted delivery via nano-sized carriers with improved stability and release.

5.3. Foliar Sprays

Foliar sprays represent a practical and efficient method for delivering siderophores directly to plants [96]. This approach involves applying a liquid formulation containing siderophores to the aerial parts of plants, such as leaves, stems, and flowers. Foliar application enables quick absorption of nutrients, bypassing potential challenges associated with soil application [97]. Foliar spray formulations are designed to ensure stability, absorption, and effectiveness [98]. The typical components are shown in Figure 8 and Figure 9 shows the application techniques.

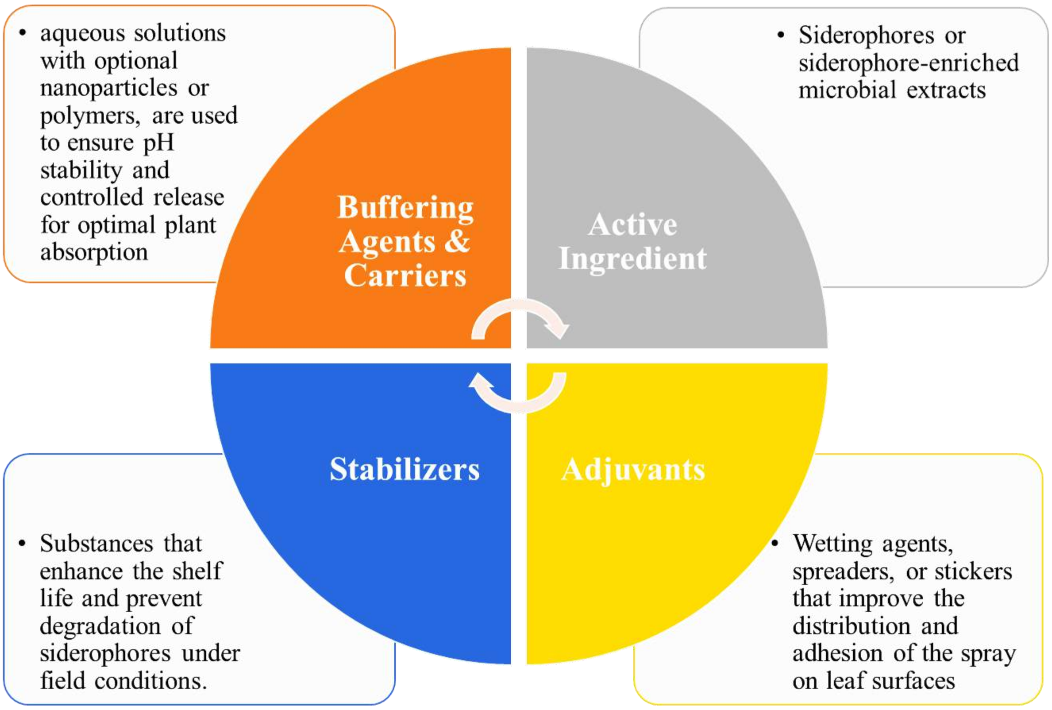


Figure 8. Formulation components of siderophore-based agricultural products depicting active ingredients, buffering agents and carriers for controlled release and pH stability, stabilizers for enhanced shelf life, and adjuvants for improved spray distribution and adhesion on plant surfaces.

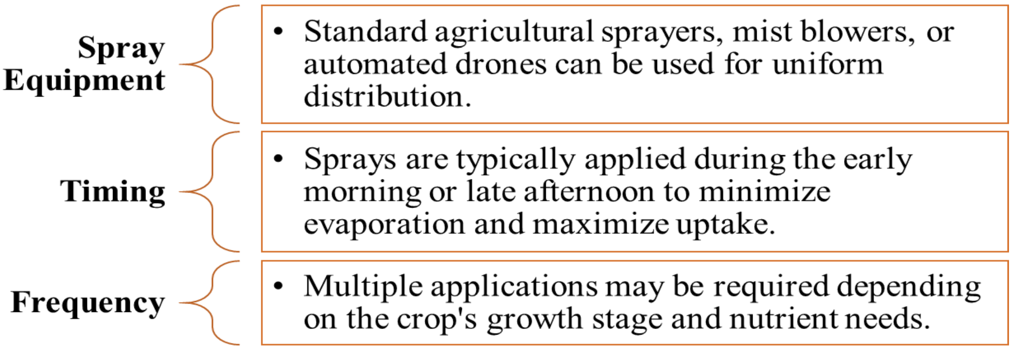


Figure 9. Guidelines for foliar application of siderophore based formulations highlighting uniform distribution using sprayers or drones, optimal timing to reduce evaporation, enhance uptake and need for repeated applications.

Foliar application is a viable method to get siderophores directly to plant leaves, ensuring rapid uptake and immediate benefits. This method enables efficient means of delivering siderophores directly to plants [99]. However, this method has certain drawbacks such as environmental sensitivity and the requirement for frequent application. With optimized composition and application strategies, foliar sprays can play a significant role in integrating siderophore-based products into modern agricultural practices [100]. Figure 10 shows the foliar applications. Foliar application of siderophores ensures rapid uptake, bypasses soil issues, and mitigates stresses, but is limited by low leaf absorption, environmental sensitivity, phytotoxicity risks, labor intensity, and short-term effects. The major pros and cons are shown in Figure 11.

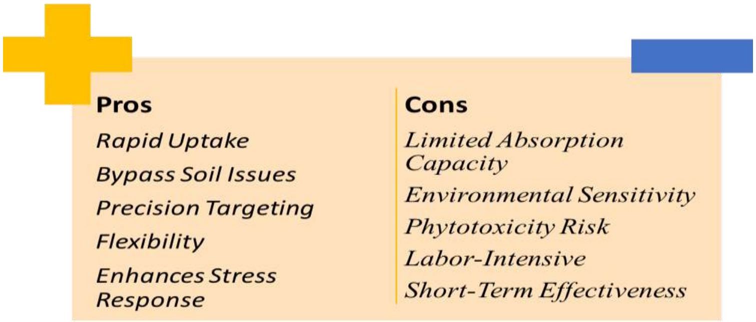
Spray Equipment: Employing precision sprayers or drones for uniform distribution across the canopy.

Droplet Size: Using nozzles that produce fine droplets to maximize coverage without runoff.

Formulation Improvements: Incorporating adjuvants and spreaders to enhance adhesion and reduce evaporation losses.

Timing: Applying sprays during cooler parts of the day to avoid rapid drying and ensure absorption. Such optimizations improve nutrient uptake efficiency and minimize wastage, making foliar application an effective delivery strategy.

Figure 10. Factors influencing foliar application efficiency for uniform canopy coverage, optimized droplet size for enhanced deposition, formulation improvements with adjuvants to reduce losses, and appropriate timing to maximize nutrient uptake and minimize evaporation.

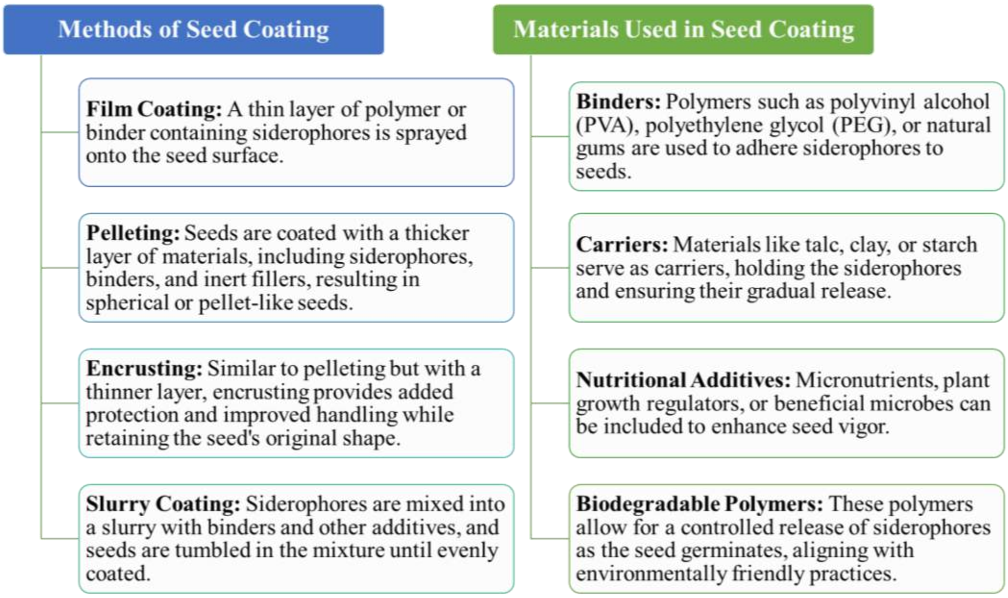


Pros	**Cons**
Rapid Uptake	*Limited Absorption Capacity*
Bypass Soil Issues	*Environmental Sensitivity*
Precision Targeting	*Phytotoxicity Risk*
Flexibility	*Labor-Intensive*
Enhances Stress Response	*Short-Term Effectiveness*

Figure 11. Tabulation figure including advantages and limitations of foliar application, highlighting benefits such as rapid uptake, precision targeting and stress mitigation, with constraints including limited absorption capacity, environmental sensitivity, phytotoxicity risk and short-term effectiveness.

5.4. Seed Coatings

An effective technique for siderophore delivery that provides a focused and effective means of improving plant growth and health is seed coating [101]. In order to guarantee that the bioactive compounds are present in the root zone during germination, where they can be most effective, a protective layer containing siderophores is applied to seeds [102]. Figure 12 shows the Methods and Materials Used for Coating. By improving nutrient accessibility, infection protection and controlling hydration siderophore-coated seeds enhance germination rate [103]. Impact of siderophore-coating on Seed Germination and Plant Health are explained through Figures 13 and 14.



Film Coating: A thin layer of polymer or binder containing siderophores is sprayed onto the seed surface.

Pelleting: Seeds are coated with a thicker layer of materials, including siderophores, binders, and inert fillers, resulting in spherical or pellet-like seeds.

Encrusting: Similar to pelleting but with a thinner layer, encrusting provides added protection and improved handling while retaining the seed's original shape.

Slurry Coating: Siderophores are mixed into a slurry with binders and other additives, and seeds are tumbled in the mixture until evenly coated.

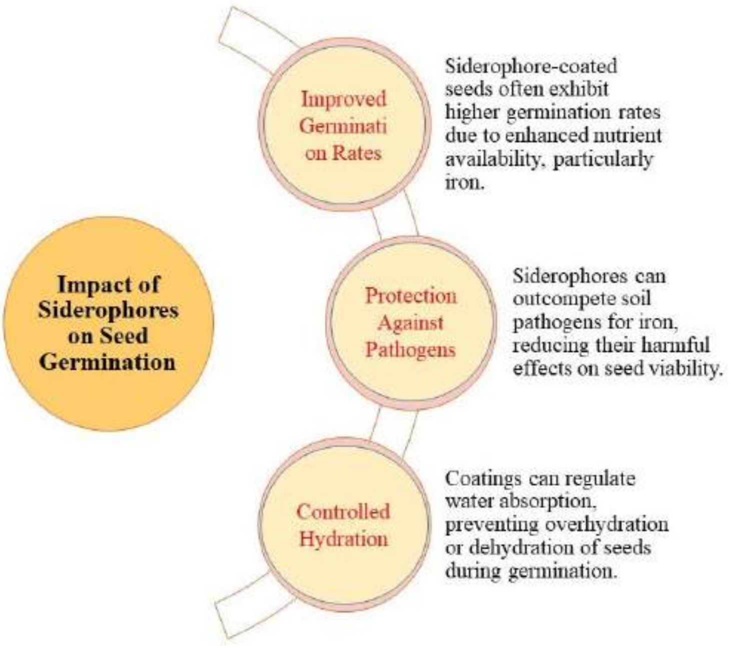
Binders: Polymers such as polyvinyl alcohol (PVA), polyethylene glycol (PEG), or natural gums are used to adhere siderophores to seeds.

Carriers: Materials like talc, clay, or starch serve as carriers, holding the siderophores and ensuring their gradual release.

Nutritional Additives: Micronutrients, plant growth regulators, or beneficial microbes can be included to enhance seed vigor.

Biodegradable Polymers: These polymers allow for a controlled release of siderophores as the seed germinates, aligning with environmentally friendly practices.

Figure 12. Flowchart showing methods and materials used in seed coating with techniques like film coating, pelleting, encrusting, and slurry coating, alongside key formulation components such as binders, carriers, nutritional additives, and biodegradable polymers for improved seed performance.



Siderophore-coated seeds often exhibit higher germination rates due to enhanced nutrient availability, particularly iron.

Siderophores can outcompete soil pathogens for iron, reducing their harmful effects on seed viability.

Coatings can regulate water absorption, preventing overhydration or dehydration of seeds during germination.

Figure 13. Impact of siderophore-based seed coating on seed germination, highlighting improved germination rates through enhanced iron availability, protection against soil-borne pathogens and regulation of seed hydration during early growth stages.

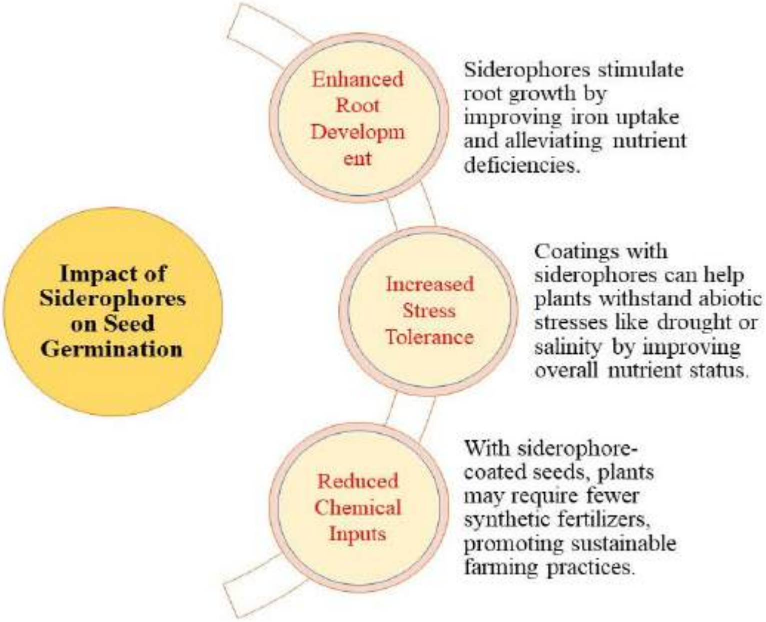


Figure 14. Impact of siderophore-based seed coating on plant health, stating improved root development, abiotic stress tolerance and reduced dependency on chemical fertilizers for sustainable crop production. y

5.5 Soil Amendment

In the controlled-conditions agriculture systems such as hydroponics and vertical farming, siderophores play a vital role by addressing nutrient shortages and promoting efficient nutrient uptake [104, 105], Figure 15 represent the soil amendment.

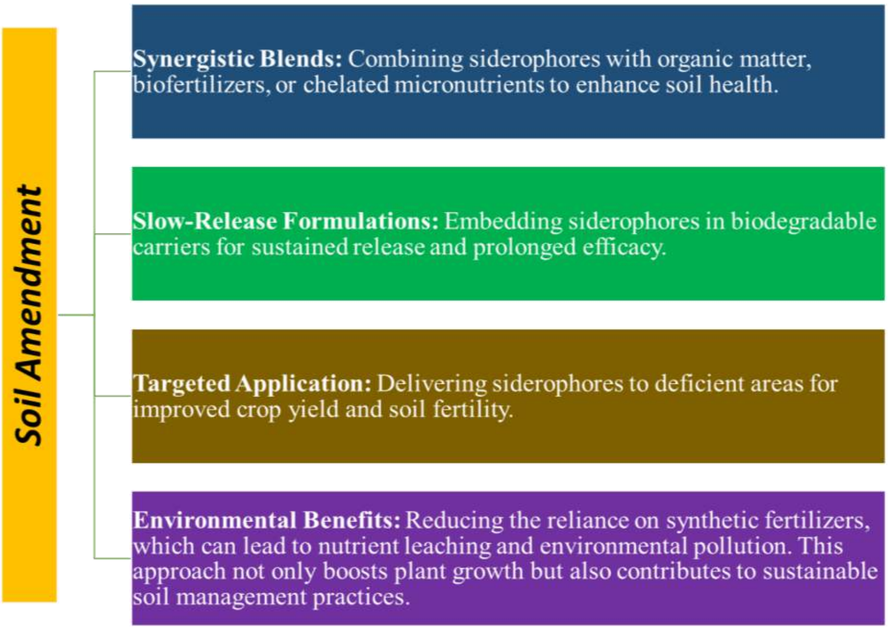
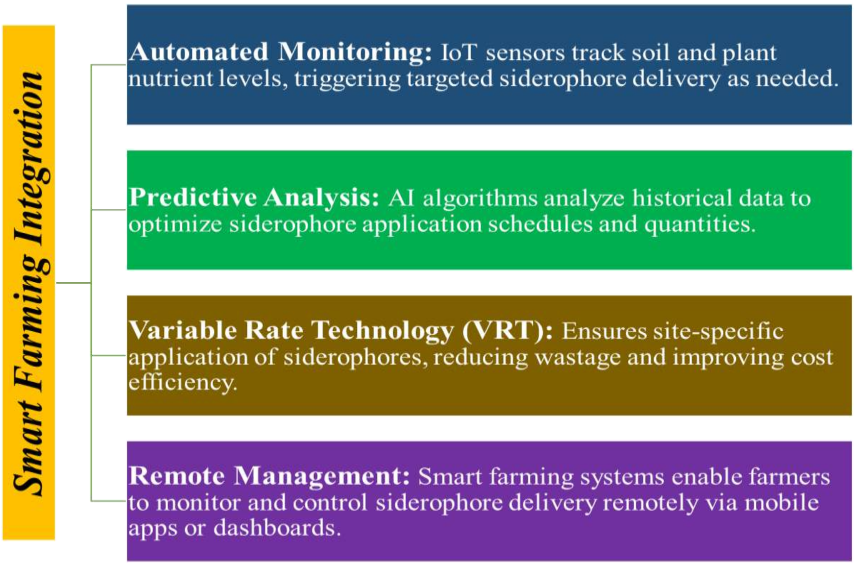


Figure 15. Siderophore-based soil amendment strategies: Synergistic blending with biofertilizers, slow-release formulations using biodegradable carriers, targeted application in nutrient-deficient zones, and environmental benefits through reduced reliance on synthetic fertilizers.

5.6 Smart Farming

The combination of IoT and AI technologies with siderophore-based products marks a leap toward precision agriculture [106]. Figure 16 represents the smart farming integration components.



Automated Monitoring: IoT sensors track soil and plant nutrient levels, triggering targeted siderophore delivery as needed.

Predictive Analysis: AI algorithms analyze historical data to optimize siderophore application schedules and quantities.

Variable Rate Technology (VRT): Ensures site-specific application of siderophores, reducing wastage and improving cost efficiency.

Remote Management: Smart farming systems enable farmers to monitor and control siderophore delivery remotely via mobile apps or dashboards.

Figure 16. Workflow of smart farming integration approaches for siderophore application, including IoT-based automated monitoring, AI-driven predictive analysis, variable rate technology for site-specific delivery and remote management through digital platforms.

6. Brief on applicaations of Siderphores other than agriculture

6.1. Diagnostic Applications

Zirconium-89-labeled desferrioxamine B is an example of a siderophore-based PET imaging agent [107]. These systems are applicable in diagnostic imaging of infections and cancer using positron emission tomography (PET). Iron receptors that are overexpressed in pathogens or target cells are bound by radiolabeled siderophores. Siderophore-fluorophore conjugates are example of fluorescent siderophore probes [108]. Use fluorescence imaging in vivo to recognize and monitor bacterial infections. Excellent pathogenic bacterial sensitivity and specificity are its advantages. Siderophores can also be encapsulated with nanomaterials like carbon dots for fluorescence based diagnostic applications in biosensors to detect nucleic acid, metals, drugs etc [109, 110].

6.2. Research and Development Products

Applications of Synthetic Siderophore Libraries: Metal chelators and the search for novel antibiotics. Mechanism: To improve target specificity, siderophores were designed with altered structures. Siderophore-carrying nanoparticles including carbon based nanocomplexes are used as drug delivery vehicles for antimicrobial and cancer treatments [111]. Nanoparticle-functionalized siderophores guarantee targeted delivery to cells that need a high iron uptake rate [112].

6.3. Application to Control Phytopathogens

Microorganisms produce siderophores, which are low-molecular-weight iron-chelating compounds that are essential for phytopathogen biocontrol [113]. These substances work as incredibly effective iron sequestration tools, preventing competing pathogenic organisms from accessing this vital micronutrient. Siderophores promote plant health by indirectly inhibiting the growth and virulence of phytopathogens by outcompeting them for iron. Phytopathogens, like other microorganisms, rely on iron for critical cellular processes, including respiration, DNA synthesis, and enzymatic functions. Siderophores produced by beneficial microbes, such as *Pseudomonas* spp. and *Bacillus* spp., have an exceptionally high affinity for ferric iron [114]. Once secreted into the rhizosphere, these molecules scavenge iron from the environment, forming strong siderophore-iron complexes. Beneficial microorganisms can uptake these complexes through specific receptors, whereas phytopathogens often lack the mechanisms to utilize non-native siderophores, leaving them iron-deficient. Siderophores in conjugation with nanomaterials and antimicrobials stand out to be a great advancement in combating the antimicrobial resistance even against the plant pathogens and not only in field of human health [115, 116].

7. Future Perspectives

Promising developments in biotechnology, AI, and synergistic compound development are expected in the future of siderophore-based formulations, offering significant potential for raising agricultural sustainability and productivity [118]. Bio-nanotechnology is foreseen to transform siderophore delivery systems by providing novel methods to improving controlled release, stability, and bioavailability. The nanocarriers such as liposomes and nanoparticles improve siderophore encapsulation, protecting them from degradation and ensuring prolonged efficacy. Smart release systems, triggered by environmental changes like pH or temperature, improve nutrient delivery, while nanoscale precision enables controlled, effective, and consistent application, reducing waste and improving plant uptake [119, 120].

Future perspectives in siderophore research strongly lie in the metabolic engineering of siderophore-producing microbes and the application of synthetic biology tools to design novel siderophores or enhance their production. Modern genetic engineering techniques such as CRISPR-Cas9-mediated genome editing can be used to modify key biosynthetic genes involved in siderophore production, enabling improved yield, structural diversity, and functional efficiency. Pathway engineering strategies, including overexpression of rate-limiting enzymes, deletion of competing metabolic pathways, and promoter optimization, can further enhance siderophore biosynthesis. Additionally, systems biology approaches, such as transcriptomics, proteomics, and metabolomics, can provide comprehensive insights into the regulatory networks governing siderophore production, facilitating rational strain design [66, 78, 121, 122]. Synthetic biology platforms can be utilized to construct artificial biosynthetic pathways or hybrid siderophores with tailored properties, enhanced stability, and targeted metal-chelating capabilities. Furthermore, adaptive laboratory evolution and high-throughput screening methods can be utilized to develop microbial strains with enhanced siderophore secretion under diverse environmental conditions. Collectively, these advanced biotechnological approaches hold great potential for scalable, sustainable, and efficient production of siderophore-based formulations for agricultural and biomedical applications.

Recent research demonstrates a strong convergence of AI, machine learning, and siderophore biology in agriculture and biotechnology, which give a bright perspective for future of this field. Multi-omics and AI-driven approaches to analyze siderophore biosynthetic gene clusters and optimize their production for climate-resilient crops, highlighting the role of predictive modeling and smart delivery systems in sustainable agriculture are already coming up with positive outcomes. Similarly, the recently developed sidero-mining strategy employs large language models (LLMs) to systematically extract and analyse siderophore biosynthetic data from thousands of studies, which represents a major innovation in AI-assisted genome mining and data-driven metabolic engineering. In the context of smart farming, researches demonstrates how AI integrated with multi-omics and microbiome studies can enhance crop resilience and nutrient acquisition, directing a great support to precision agriculture systems. Furthermore, emphasis on the use of AI, imaging, and data analytics to decode rhizosphere processes, including microbial interactions such as siderophore production, for field-scale agricultural applications are yet to be thoroughly investigated. Detailed characterization of novel siderophores forming the biochemical foundation for integrating such molecules into AI-guided agricultural and biotechnological systems with government-based schemes will add up a sharp progress in siderophore based product applications. Collectively, a shift toward AI-enabled discovery, prediction, and deployment of siderophore-based solutions, bridging molecular microbiology with smart and precision agriculture is now an advancing field but requires more scientific and community-based attention.

8. Conclusion

Siderophore-based formulations are emerging as a sustainable and innovative approach in modern agriculture, offering an eco-friendly alternative to synthetic fertilizers and pesticides. By enhancing nutrient uptake, particularly iron availability in plants, these formulations significantly contribute to improved plant growth, resilience, and productivity. Their ability to mitigate biotic and abiotic stresses makes them valuable in addressing agricultural challenges, including climate change and soil degradation. The integration of advanced delivery systems, such as seed coatings, foliar sprays, and nanoparticle encapsulation, has further improved the efficiency of siderophore applications. Additionally, cutting-edge technologies like bio-nanotechnology and AI-driven solutions hold significant potential for optimizing these formulations, enhancing their stability, bioavailability, and large-scale applicability. While challenges remain in terms of scalability, cost-effectiveness, and field adaptability, ongoing research and industry-driven innovations continue to address these limitations. Available studies indicate that siderophore-based products have the potential to revolutionize sustainable agriculture. Moving forward, interdisciplinary research efforts should focus on optimizing formulation strategies, exploring synergistic combinations with biostimulants, and leveraging precision agriculture techniques to maximize the impact of siderophores. With continued innovation and adoption, these formulations can play a crucial role in improving global food security while preserving environmental sustainability.

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