Iron Biofortification in Maize: A Review of Recent Progress and Future Prospects

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Article Info

P-ISSN: 3051-3448
E-ISSN: 3051-3456
Volume: 07
Issue: 02
Received: 05-05-2026
Accepted: 04-06-2026
Published: 03-07-2026
Page No: 31-40

Abstract
Iron Deficiency (ID) continues to be one of the main hidden hunger issues in the world today, impacting billions of people and becoming a major hurdle for human food security and health. Maize (*Zea mays* L.) is one of the widely cultivated and consumed cereal crops and thus has the potential to be an important target for iron biofortification to improve dietary iron intake, especially in cereal-centric diets. During the last decade efforts have been undertaken to understand the physiological, agronomic, genetic and molecular aspects associated to Fe uptake, transport, accumulation and bioavailability in maize. The recent progress in biofortification of maize with iron is reviewed, with a focus on soil Fe, strategy II Fe acquisition, Fe transport and Fe homeostasis and their effects on the accumulation of Fe in grain. Modern breeding technologies including conventional breeding, quantitative trait locus (QTL) mapping, genome wide association studies (GWAS), genomic selection, transgenic technologies and CRISPR/Cas mediated genome editing are discussed critically along with the recent advances of agronomic biofortification including soil and foliar fertilization, seed priming, nano-fertilizers and organic amendments. The review also focusses on the new functions of plant growth-promoting rhizobacteria (PGPR), microorganisms producing siderophores and arbuscular mycorrhizal fungi in the improvement of the iron availability and uptake in a sustainable biological way. Moreover, recent advances in multi-nutrient biofortification, precision agriculture, omics, artificial intelligence and genome-assisted breeding are explored as tools to facilitate the acceleration of the development of biofortified maize cultivars rich in iron. However, a number of challenges still exist, such as the bioavailability of iron, genotype × environment interaction, soil limitations, climate change, and regulation and farmer adaptation. It is concluded that the combination of molecular breeding, microbial-assisted technologies, precision agriculture and agronomic management are most likely to lead to the development of nutritionally improved maize varieties which will reduce the prevalence of ID and help to achieve sustainable FSNSS. Finally, future research priorities are seen which will assist in the efficient development and scale-up of iron-biofortified maize.

DOI: https://doi.org/10.54660/JSFR.2026.7.2.31-40

Keywords: Biofortification, Iron transport, *Zea mays* L.

1. Introduction

The micronutrient malnutrition that so many people refer to as "hidden hunger" still remains one of the most urgent challenges facing the world in terms of nutrition with over two billion people suffering from the problem despite significant gains in the agricultural productivity and the availability of food (Oluwole *et al*, 2023) [53]. Hidden hunger differs from protein-energy malnutrition in that it is a consequence of either insufficient consumption of micronutrients and/or limited bioavailability of micronutrients and is associated with significant health impacts even when energy needs are fulfilled (Weffort *et al*, 2024) [69]

(Elegbeleye *et al*, 2025) [14]. Iron deficiency is the most common micronutrient deficiency worldwide (Han *et al*, 2022) [23], which plays a significant role in anaemia, cognitive dysfunction, a decrease in work productivity, maternal and child health, and immune function (Bela *et al*, 2025) [7]. This burden is especially high in low and middle-income countries, where cereal diets are common, and diets are lacking in nutrient-rich foods. Thus increasing the dietary iron intake has become a major concern of global nutrition programmes and sustainable food security programmes.

Conventional strategies such as dietary diversification, pharmaceutical supplementation and fortification of mass foods by industry have proven successful in various parts of the world in the struggle against iron deficiency. But they often prove to be expensive to implement, do not have the necessary infrastructure, are subject to inconsistent public health programmes, are difficult to access in rural areas (Bell *et al*, 2024; Ashraf, 2025) [8, 5]. All these challenges have turned the scientific interest to biofortification, a food-based strategy which increases the nutritional value of staple food crops during crop cultivation through plant breeding, biotechnology and integrated crop improvement. Biofortification offers a long-term, sustainable and cost-effective option for the populations relying heavily on staple foodstuffs, as compared to post harvest fortification (Jha *et al*, 2022; Kumar *et al*, 2023; Azeem *et al*, 2025; Tessema *et al*, 2026) [28, 39, 6, 65].

Maize (*Zea mays* L.) is considered one of the most important cereal crops, at the heart of worldwide agricultural and human nutrition. Production is carried out in a wide variety of agro-ecological regions and it is one of the most important cereals of the world in terms of production, consumption and economic value (Erenstein *et al*, 2022) [16]. Maize is also a key raw material for industry, as well as a significant source of feed for livestock, and has become a major staple food crop for over a billion people, especially in Sub-Saharan Africa, Latin America, and parts of Asia, where it is a significant part of the daily food intake (Mudadirwa *et al*, 2023; Dass *et al*, 2025) [50, 12].

Conventional maize grain, however, typically contains low levels of bioavailable iron and the maize grain is also loaded with antinutritional compounds, like phytic acid which hinders the uptake of iron in the human gastrointestinal tract (Nsabimana *et al*, 2024) [51]. This means that those populations that are mainly fed on maize based diets are particularly at risk of iron deficiency and resulting health problems. Because of these nutritional constraints, maize is one of the key target crops for the research on biofortification of staple food crops with iron (Galani *et al*, 2022; López-Moreno *et al*, 2025) [17, 44].

Iron is an essential element for not only humans, but normal plant growth and development. In maize, it serves as a cofactor for many enzymes of photosynthesis, respiration, of chlorophyll biosynthesis, of the nitrogen assimilation and of the antioxidant defense. However, ferrous forms of iron that are available to plants are very small in the most of crop lands mainly because it easily forms inaccessible or non-soluble form of iron, especially in alkaline and calcareous soils (Khan *et al*, 2023; Günther, 2023; Chen *et al*, 2024) [34, 21, 11]. This difference between the total amount of Fe in the soils and the amount of Fe available to the plant is one of the major factors which restrict both plant growth and nutritional quality of the grain. Therefore, a better acquisition, transport, and accumulation of Fe in maize have been a key goal in the field of plant nutrition and crop improvement in recent years. The total concentration of iron in a grain does not guarantee that nutrition will inevitably be improved, as the bioavailability of iron in a grain will greatly depend on the grain's composition, antinutritional factors, and the method of food processing and on how the grain is part of the diet. Moreover, the stability of the accumulation of iron in various production systems is often influenced by genotype × environment interactions, variability of soil properties, climate changes and regulation of iron homeostasis (Roy *et al*, 2022; Kermeur *et al*, 2023; Kumar *et al*, 2025) [56, 32, 38].

Besides these are additional constraints associated with the adoption by farmers, the regulatory aspects, acceptance by consumers of crops derived from biotechnology and economic viability of the advanced biofortification technologies that need careful consideration to reach large scale implementation. Solutions to these challenges require a interdisciplinary effort among plant breeders, molecular scientists, agronomists, soil scientists, microbiologists, nutritionists and policy makers to obtain an integrated solution that can enhance crop productivity and human nutrition. New technologies like multi-omics approaches, Artificial Intelligence, machine learning, high throughput phenotyping, digital agriculture, precision farming and microbiome engineering will be helping to boost the identification of better genotypes and nutrient management optimization in different environments.

Furthermore, the increasing focus on multi-nutrient biofortification aims to develop crops that address several micronutrient deficiencies all in one, such as iron, zinc, provitamin A or other micronutrients. The developments refer to the shift that occurred from single discipline research to integrated, systems-based research, which combines knowledge from plant sciences, agriculture, nutrition and biotechnology to secure food and nutrition security in sustainable ways. This review aims to comprehensively synthesize the existing knowledge on biofortification of maize for iron and discuss recent scientific advances and research opportunities in light of these new developments.

2. Iron Nutrition in Humans and Plants

2.1. Role of Iron in Human Health

Iron is an essential micronutrient which is necessary for many physiological and biochemical processes to promote human health. About 2/3 of the iron is embedded in haemoglobin for oxygen transport from the lungs to the body tissues and the rest is contained in the iron enzymes, which are related to cellular respiration, DNA synthesis, energy metabolism, immune function and neurological development. Iron is also a cofactor of enzymes of electron transport, oxidative metabolism and antioxidant defence including cytochromes, catalases and peroxidases and is essential for normal growth and function of cells (Jomova *et al*, 2025) [30].

There is no active mechanism for iron excretion and the intestinal absorption, recycling from senescent erythrocytes and the storage in ferritin and haemosiderin are the main mechanisms by which iron homeostasis occurs. Thus, low intakes, decreased absorption or greater needs can quickly lead to low iron stores and ultimately iron deficiency anaemia (IDA). IDA is the most common micronutrient deficiency globally and is linked to fatigue, poorer cognitive function, decreased immune function, and lower levels of work productivity and adverse outcomes of pregnancy. For children, chronic IDAs have negative effects on cognition

and psychomotor ability, while in pregnant women, IDAs increase the risk of maternal complications, pre-term delivery and low birth weight infants (Ray *et al*, 2025) [55].

The bioavailability of Fe is also a key factor besides the amount of Fe ingested with the diet. There are two types of iron in the diet: haem iron (from animal to animal origin) and non-haem iron (from plant to plant origin) such as cereals, legumes, fruits and vegetables. Haem iron is easily absorbed and the absorption of non-haem iron much depends upon the foods present in the diet. Phytates, polyphenols and dietary fibre inhibit the availability of iron by forming insoluble complexes with it, whereas vitamin C or other organic acids help the absorption of iron by converting the more insoluble ferric Fe^{3+} to more soluble ferrous form Fe^{2+}. Since maize is a major food crop consumed by millions of people in locations where Fe deficiency is prevalent, biofortification combining Fe grain concentration with bioavailability is a sustainable solution to help address hidden hunger, along with traditional methods like supplementation and industrial food fortification (Chaudhary *et al*, 2025) [10].

2.2. Importance of Iron in Maize Growth and Biofortification

Although iron is a micronutrient for plant growth it is essential. It can switch between ferrous (Fe2+) and ferric (Fe3+) forms which help it to be involved in oxidation–reduction reactions to support the processes of photosynthesis, respiration, assimilation of N, biosynthesis of chlorophyll and many enzymatic activities (Kovalova *et al*, 2026) [37]. Iron-containing proteins including cytochromes, ferredoxins, and iron-sulphur proteins are intrinsic to the photosynthetic electron transport chain with a direct impact on energy generation, biomass accumulation and crop productivity in maize.

Iron deficiency causes abnormal development of the chlorophyll and chloroplasts and gives rise to the typical symptoms such as interveinal chlorosis of young leaves, decreased photosynthetic activity, growth retardation, delayed maturity and considerable yield losses. These deficiencies are often found in calcareous and alkaline soils although iron is abundant in the soil (Sharma *et al*, 2025; Tubana *et al*, 2026) [59, 66]. Hence it is necessary to keep plants in good iron nutrition to assure plant growth and grain production.

In addition to vegetative growth, iron is also important during reproductive growth and grain filling. The uptake of Fe at the root needs to be efficient and pass through the vascular tissue efficiently to the developing kernels where remobilization occurs. However, very little absorbed iron is deposited in maize grains and most of them are bound to phytate complexes that are poorly bioavailable for human use. These physiological constraints are important barriers to biofortification of iron, and highlight the importance of enhancing iron uptake, transport, storage and remobilization.

Table 1. Role of Iron in Maize Growth and Physiology

3. Soil iron dynamics and influencing factors of iron availability

3.1. Soil Iron Chemistry and availability

Although iron is the fourth-most abundant element in the earth's crust it is not always readily available to plants because it is mostly in very insoluble forms within the mineral structure. In well aerated soil, the majority of iron can be found as ferric (Fe3+) oxides, hydroxides and silicates which are extremely insoluble and only a small portion of the total iron is available to plant uptake (Mansha *et al*, 2025; Hassan *et al*, 2025) [47, 24]. Thus, the amount of soluble iron in the rhizosphere is more important to the growth of the plant than total iron present in the soil.

The dynamic processes of soil chemistry and biology are related to soil redox conditions, mineral composition, and soil moisture and microbial activities. Soluble ferrous iron (Fe2+) will be quickly oxidized to insoluble ferric compounds in aerobic environments, decreasing the plant's ability to access the iron (Gulcin and Alwasel, 2025) [20]. On the other hand, under waterlogged or anaerobic condition, Fe^{3+} can be reduced to Fe 2+, temporarily increasing the iron solubility (Zhang *et al*, 2025; Olifir *et al*, 2025) [77, 52]. These transformations are the reason of the frequent occurrence of iron deficiency, despite the availability of iron in the soils.

The most limiting soil types for maize production are calcareous soils with high levels of calcium carbonate and alkaline soils with high levels of bicarbonate which greatly affect the iron solubility. Maize plants, therefore, frequently show interveinal chlorosis, a decrease in the formation of chlorophyll, photosynthesis and grain production under circumstances of adequate total soil iron. Hence, the need is to seek ways of increasing iron availability, and not just soil iron content, in order to improve iron nutrition.

Rhizosphere is important in the regulation of iron acquisition. Root exudates such as organic acids, amino acids, phenolic compounds and phytosiderophores influence the chemical environment around the root that enhances the solubility of Fe and also aids in its absorption. The beneficial soil microorganisms additionally improve the mobilization process of iron by the secretion of organic acids, weathering of minerals and production of siderophores (Malik *et al*, 2026; Khalid *et al*, 2026) [46, 33]. Thus, it is now known that the availability of Fe is the result of a complicated interplay between soil chemistry, plant physiology and microbial activity, and not only from chemical reactions. Knowledge of these interactions can help underpin agronomic, genetic and microbial strategies to enhance Fe uptake and biofortification in maize.

3.2. Factors Influencing Iron Availability and Recent Advances in Soil Management

Several soil, environmental and biological factors affect the availability of iron Fe to maize, with the most important factor being the soil pH. In alkaline and calcareous soils, ferric iron (Fe3+) quickly precipitates as insoluble hydroxides and oxides in which it becomes unavailable to plants (Hussain *et al*, 2026) [25]. Thus, one often sees iron deficiency chlorosis in maize grow on such soils even with a large amount of iron in total soil. It is therefore necessary to ensure favorable soil conditions so as to improve the ability to acquire iron and the productivity of the crop.

The soil organic matter contributes to the availability of iron by releasing humic substances, fulvic acids and low molecular weight organic acids during the process of decomposition (Wang *et al*, 2025; Li *et al*, 2025) [68, 43]. These compounds sequester Fe, keeping it soluble so that it can be readily taken up by the plant roots.

The organic matter will also increase microbial activity, which will aid in the cycling of nutrients and the generation of microbial metabolites to help mobilize iron.

Hence, soil agronomic practices like use of compost/manure,

use of green manure and incorporation of crop residues helps in ensuring sustainable iron nutrition as well as enhances soil health.

The interactions between mineral nutrients also affect iron uptake. Iron may be made unavailable by excessive phosphorus fertilization, due to the formation of iron-phosphate complexes and is insoluble, or by imbalances of zinc, manganese, calcium or copper fertilization, as a result of competitive uptake mechanisms. Thus, integrated nutrient management is crucial to maximize the use efficiency of micronutrients and improve agronomic biofortification.

Recent developments in soil management are directed towards enhanced use efficiency of Fe such as precision agriculture, use of controlled release fertilisers, chelated iron, nanofertilizers and site-specific nutrient management. Furthermore, rhizosphere engineering which involves the use of beneficial microorganisms, biochar, and organic amendments has been seen as a promising sustainable method to increase the iron solubilization and uptake and consequently to decrease the consumption of synthetic fertilizers. The integrated approaches established good foundations for boosting the bioavailability of the iron and thus for the success of maize biofortification programmes.

Table 1: Iron nutrition, soil Fe dynamics, and their relevance to maize biofortification

Major aspect	Key factor/process	Mechanism	Significance for Fe biofortification in maize	References
Fe nutrition	Oxygen transport	Fe forms the functional core of hemoglobin and myoglobin.	Fe-enriched maize may improve dietary Fe intake in maize-dependent populations	Jackson *et al*., 2025
Fe nutrition	Cellular metabolism	Fe–S proteins and cytochromes mediate electron transfer and energy production.	Adequate dietary Fe supports normal metabolic and physiological functions	Enko *et al*., 2025
Fe deficiency	Low intake/bioavailability	Reduces Fe storage and impaired hemoglobin synthesis	Provides the major nutritional rationale for maize Fe biofortification	Yan *et al*., 2023
Dietary bioavailability	Phytate–Fe interaction	Phytate chelates Fe and reduces its intestinal absorption	Biofortification should improve bioavailable Fe, not merely total grain Fe	Anwar *et al*., 2022
Maize Fe nutrition	Photosynthesis	Fe participates in cytochromes, ferredoxin and Fe–S proteins of the photosynthetic electron-transfer system	Adequate Fe supports photosynthesis, biomass production and grain development	Yousaf *et al*., 2024
Maize Fe nutrition	Fe deficiency	Fe deficiency disrupts chlorophyll formation	Causes interveinal chlorosis, reduced growth and potentially lower yield	Sun *et al*., 2022
Soil Fe chemistry	Fe speciation	Aerobic soils favor poorly soluble Fe(III) oxides/hydroxides; reducing conditions increase soluble Fe(II)	Soil may contain abundant total Fe but insufficient plant-available Fe	Masalha *et al*., 2000
Soil pH	Fe solubility	pH > Fe hydrolysis	Alkaline/calcareous soils strongly restrict Fe acquisition by maize	Ji *et al*., 2025
Soil redox status	Fe(III) ↔ Fe(II) transformation	Low redox potential promotes Fe(III) reduction and Fe(II) solubilization	Controls Fe mobility and availability in the rhizosphere	Yang *et al*., 2025
Organic matter & microbes	Fe complexation/mobilization	Organic ligands and microbial siderophores complex and solubilize Fe	Rhizosphere management can improve Fe availability to maize	Sterckeman *et al*., 2025
Soil management	Fe fertilizers/chelates	Fe fertilizers increase supply, while chelates maintain Fe in soluble forms	Soil/foliar Fe and chelated fertilizers provide agronomic routes to biofortification	Szerement *et al*., 2022

4. Iron Uptake, Transport and Accumulation in Maize

4.1. Iron Uptake Mechanisms

Iron is ubiquitous in most agricultural soils but because of its low solubility, plants have evolved special strategies to acquire it. Maize belongs to the graminaceous species and, like them, adopts Strategy II iron uptake (synthesis and excretion of phytosiderophores) as the mechanism of uptake. Maize roots under Fe deficiency excrete mugineic acid family phytosiderophores (MAs) into rhizosphere which bind to aqueous Fe^{3+} to create complexes of soluble Fe^{3+} with MA that are taken up by specific membrane transporters (Kobayashi and Nishizawa, 2025; Abdellatef *et al*, 2025) [36, 1].

How efficient it is depends upon coordinated physiological responses that are triggered when plants suffer from iron deficiency. These three changes (increased phytosiderophore secretion, increased expression of iron transporter genes and changes in root architecture) are all helping to increase iron acquisition under low iron. The uptake process is under a very close regulation to maintain iron homeostasis as well as to avoid iron toxicity due to excessive accumulation. The effectiveness of Strategy II uptake is highly dependent upon soil properties. A high soil pH, high bicarbonate levels, an imbalance in the nutrients and drought all dampen the activity of phytosiderophores, and limit iron availability (Yousaf *et al*, 2025; Hussain *et al*, 2026) [74, 25].

In contrast, rhizosphere microorganisms that promote the growth of plants and/or increase nutrient solubilization can enhance the acquisition of iron by the production of siderophores (Praženicová *et al*, 2026; Zhu *et al*, 2026) [54, 78]. Such interactions between plants and microbe are now a key aspect of sustainable nutrient management. Recent molecular work led to the identification of several genes which are involved in the biosynthesis, secretion and the transport activity of phytosiderophores in maize, which led to valuable insights into the regulation of iron uptake. Insight into these physiological and genetic processes has rendered new possibilities for enhancing the ability of plants to acquire iron via plant breeding, agronomic management and molecular biotechnology. The most important and initial stage to gain a better concentration of iron into the grain and achieve successful biofortification, is to increase the efficiency of the iron uptake.

4.2. Iron Transport, Distribution and Grain Accumulation

Once absorbed by the roots, Fe is carried to aerial parts of the plant in the Xylem as Fecitrate. After being transported to developing organs and the leaves, Fe is re-mobilized in the phloem, for the purpose of supporting photosynthetic, respiratory and reproductive development (Yu *et al*, 2025; Duan *et al*, 2025; Hadj *et al*, 2025) [76, 13, 22]. During the grain filling, the demand for iron rises significantly and efficient long distance transport and remobilisation is essential.

In plant tissues, the iron is stored either in ferritin proteins or bound to a number of iron containing enzymes in order to prevent oxidative damages and be available for metabolic activities (Ru *et al*, 2025) [57]. The stored iron gets remobilized from vegetative tissues to the developing kernels through coordinated action of transporters and vascular transport pathway during reproductive growth. Only a small fraction of the iron absorbed, however, ends up in maize grains, thus posing serious challenges to biofortification. An additional significant constraint is that a significant amount of the grain iron is found in the embryo and aleurone layer as phytate. After human consumption, phytate is able to bind to iron and form stable complexes, which significantly lowers the bioavailability of iron. Thus, a simple increase in total iron content of the grain is not enough unless the bioavailability of iron in the grain is also increased.

4.3. Molecular Regulation and Recent Advances

In maize, iron homeostasis is regulated by a complex network, which is coordinated to allow iron uptake, transport, storage and utilization depending on the nutritional state of the plant (Yang *et al*., 2025; Li *et al*., 2026). The activation of numerous genes involved in phytosiderophore biosynthesis, membrane transport and internal redistribution is the result of iron deficiency and sufficient iron in the plant suppresses these activities to ensure that iron is not overly excessive and causes oxidative stress. This coordinated regulation acts as a sufficient supply of iron for the metabolic activities without causing toxicity (Bishnoi *et al*., 2026; Sharma *et al*., 2026).

Recent progress in molecular genetics and functional genomics research have greatly increased the knowledge of the maize genes that are involved in iron metabolism. Using high throughput sequencing, transcriptomics, proteomics and metabolomics, potential genes and regulation pathways for iron uptake, translocation, and grain loading have been identified. Breeding for high efficiency in iron use is now gradually beginning to be carried out using molecular markers.

These new opportunities for gene manipulation of genes involved in iron homeostasis have been afforded by genome editing technologies such as the CRISPR-Cas systems. The prospect for better accumulation of Fe without negative impact on plant growth seems to exist via targeted modification of the genes coding for transporter proteins, transcription factors, and iron storage genes.

5. Microbial-Assisted Iron Biofortification

5.1. Plant Growth-Promoting Rhizobacteria (PGPR) and Siderophore-Producing Microorganisms

Beneath the surface of the soil beneficial microorganisms are present that are important in the processes of improving iron availability and plant nutrition. Plant growth promoting rhizobacteria (PGPR) are able to help with the acquisition of iron by releasing siderophores, which chelate the insoluble ferric iron and make it more accessible for plants (Praženicová *et al*., 2026; Garg *et al*., 2026). Additionally many PGPR induce root growth; generate phytohormones; solubilize nutrients; and increase plant resistance to abiotic stress, contributing overall to increased nutrient use efficiency (Yang *et al*., 2026; Kumari *et al*., 2026).

Several other beneficial microorganisms, such as species of the genera Bacillus, Pseudomonas, and Azospirillum are able to increase rhizosphere activity and to contribute towards sustainable nutrient management (Sun *et al*., 2025; Majhi *et al*., 2025). They have been proven to positively impact maize growth, grain iron levels and soil health when combined with organic amendments and balanced fertilization. Thus, microbial inoculants are now starting to be appreciated as eco-friendly alternative to over fertilization.

5.2. Mycorrhizal Fungi, Rhizosphere Engineering and Future Prospects

In addition, the presence of arbuscular mycorrhizal fungi (AMF) may also involve in improving Fe nutrition, by increasing the effective root surface area and nutrient acquisition under nutrient deficient soil. Through their symbiotic relationship they enhance the development of plant roots, soil aggregation and stress tolerance, as well as the ability to take up iron in the rhizosphere. It has been observed that the use of AMF and PGPR can give synergistic effects on plant growth and micronutrient accumulation (Ahmed *et al*., 2025; Mohammadnia *et al*., 2025; Joshi *et al*., 2026; Shah *et al*., 2026).

Recent progress in rhizosphere engineering is to tweak plant, soil and microbe interaction to rebalance nutrients and make them more readily available in a natural way. Microbial inoculants, biochar, compost, cover crop and precision nutrient management are promising approaches for sustainable biofortification of Fe (Gautam *et al*., 2025; Jalal *et al*., 2025). Future research should focus on the understanding of the dynamics of the community of microorganisms, improving the performance of inoculants in the field, and combining microbial technologies with breeding and agronomic strategies. These multi-disciplinary approaches are likely to be important in developing resilient cropping systems that can produce nutritionally rich maize, and minimize the environmental impact.

Table 2: Microbial-Assisted Strategies for Iron Biofortification in Maize (PGPR, Siderophore-Producers and AMF)

Microbial Agent / Mechanism	Key Contribution to Fe Biofortification	Author(s) & Year
PGPR	PGPR release siderophores that chelate insoluble ferric iron, improving its availability to plant roots.	Praženicová *et al.* (2026)
PGPR	PGPR inoculation enhanced Zn and Fe biofortification of millets.	Garg *et al.* (2026)
PGPR	PGPR support root growth, phytohormone production and nutrient-use efficiency under abiotic stress.	Yang *et al.* (2026)
PGPR	PGPR improved nitrogen-use efficiency and stress tolerance in pearl millet, relevant to combined nutrient management.	Kumari *et al.* (2026)
PGPR / Siderophore-producers	Azospirillum strains increased rhizosphere activity, productivity and stress resilience.	Sun *et al.* (2025)
PGPR / Rhizosphere microbes	Beneficial rhizospheric microbes (e.g., Bacillus, Pseudomonas) support sustainable nutrient management in stressed crops.	Majhi *et al.* (2025)
AMF	AMF enhance nutrient uptake, stress tolerance and soil health via molecular and hormonal mechanisms.	Ahmed *et al.* (2025)
AMF	Mycorrhizal inoculation combined with Fe-amino chelate improved growth and physiology of seedlings across soil pH levels.	Mohammadnia *et al.* (2025)
AMF / Rhizosphere	Soil health shapes root-associated nutrient uptake, linking soil biology to nutritional security.	Joshi *et al.* (2026)
AMF	AMF mediate N, P and C acquisition, supporting synergistic nutrient benefits alongside Fe uptake.	Shah *et al.* (2026)
Rhizosphere engineering	Microbial inoculants, biochar, compost and precision nutrient management support sustainable Fe biofortification.	Gautam *et al.* (2025)
PGPR / Cropping systems	Interaction of mineral nutrients with PGPR improves biofortification across different cropping systems.	Jalal *et al.* (2025)
Root exudates / Rhizosphere	Root exudate composition and dynamics underpin microbial recruitment and nutrient mobilization in the rhizosphere.	Malik *et al.* (2026)
AMF / Siderophore-producers	AMF recruit siderophore-producing, phosphate-solubilizing bacteria, illustrating AMF-PGPR synergy for nutrient mobilization.	Zhu *et al.* (2026)

Discussion

The best way to conceptualize iron biofortification of maize is as a multifactorial issue that affects both humans and soil, plants, and food. Although maize it contributes significantly to iron deficiency, a variety of factors also play a role, such as anemia, which is brought on by dietary insufficiency, infection/inflammation, genetic haemoglobin disorders, and reproductive health issues. In this regard, the use of biofortification of staple crops is attractive because, in addition to supplementation and industrial fortification, which may be restricted by access and adherence, it can consistently raise micronutrient intakes through regular consumption of staple crop products (WHO 2023). Due to its significance as a primary energy source in many regions, maize is a strategic target from the crop side; yet, the grain iron content of the current maize population and management is comparatively low and inconsistent. Interestingly, a global synthesis of maize grain mineral data shows that stacking several levers, such as genetics, agronomy, and bioavailability-oriented processing, is typically necessary to achieve nutritionally substantial benefits at scale (Kihara *et al*, 2024) [35]. After eliminating high outliers, the median grain iron concentration was roughly 22 mg kg^{-1}, and the likelihood of surpassing a 60 mg kg^{-1} nutrient criterion was low across all data. Fe is abundant in most soils but becomes poorly soluble under aerobic, neutral to alkaline conditions where Fe (III) precipitates to sparingly soluble oxides/hydroxides. Bicarbonate-rich calcareous soils
frequently cause Fe chlorosis due to both chemical and physiological limitations, so soil Fe dynamics continue to be the first major constraint (Kermeur *et al*, 2023) [32]. The success of biofortification is largely dependent on soil pH and rhizosphere processes, according to a recent synthesis of plant strategies in alkaline soil. It notes that the primary limiting factor is the extremely low Fe (III) activity at high pH and that additional rhizosphere acting strategies (acidification, reduction, and ligand release) are needed to mobilize Fe from the surface of oxides (Vélez-Bermúdez *et al*, 2023) [67].

Therefore, rather than raising Fe salts, contemporary developments in soil/field management have more to do with improving the rhizosphere's efficacy and the delivery chemistry of Fe salts. While agronomic meta-analysis evidence in maize indicates that mineral outcomes are highly sensitive to background fertility management, application technique, and soil attributes and are better suited to integrated packages rather than single input solutions, the use of "bio chelates" and "bio stimulant-like complexes" is gradually replacing the use of conventional synthetic chelators as potentially more sustainable means of Fe nutrition. Alternatives of the mugineic-acid family, like proline-2′-deoxymugineic acid (PDMA), have been shown to be more effective than conventional chelators for improving Fe nutrition in maize, indicating a pathway in which Fe fertilizers are tailored to cereal uptake chemistry (Zuluaga *et al*, 2023) [79]. This is a noteworthy development in parallel with the grass Fe biology. If iron deficiency is common in alkaline environments, a biofortification strategy that focuses on Strategy II iron acquisition (Phyto siderophore synthesis and release, Fe (III) chelation, uptake of Fe (III)–Phyto siderophore complexes) is biologically appropriate at the plant level and should be taken into consideration. The interaction between ZmFIT and ZmIRO2 has been shown to be crucial for the regulation of iron homeostasis and links upstream iron sensing/regulation to the downstream expression of Fe-deficiency response components in maize. Recent molecular advances are also revealing regulatory control points that can be exploited by breeding or genome editing.

This mechanistic resolution shifts the research from a descriptive concept of "Fe-efficient genotypes" to a more targeted approach to altering uptake and homeostasis

modules with more precise predictions of trade-offs (Li *et al*, 2024) [42]. But just being absorbed is not enough; iron must be internalized, divided, and deposited in the tissues in a form that is both accessible and resistant to digestion. An important finding in this regard is the identification of ZmNAC78 as a regulator of Fe content in the kernel. It shows that the transporters use content regulation to control the loading of Fe into growing kernels, which makes the loading into the grain a manageable goal rather than a mystery. The use of multi-locus breeding strategies in conjunction with major regulatory loci is highlighted by biofortification genetics syntheses of maize, which confirm that Fe-related traits are polygenetic and that transport and chelator pathways (including YS/YSL and TOM associated functions) have been repeatedly identified as mapping targets (Yan *et al*, 2023) [70]. Finally, as phytate and grain fractionation/processing can greatly alter the bioavailability of Fe, the term "biofortification" should be used to refer to the amount of Fe available in the grain rather than merely its content. Recent studies have demonstrated that fermentation, especially when combined with soaking and germination, significantly reduces the food's phytate content (up to ~85.6% in one study) and increases the phytate molar ratios. However, depending on the total Fe content, the genotype of maize and processing-related factors, such as degemination, can affect Fe bioavailability in an unpredictable way. In order to guarantee that agronomic and genetic improvements have an impact on diet, future biofortification pipelines must co-optimize kernel Fe loading, phytate-reducing tactics, and locally feasible processing techniques. (Nsabimana *et al*, 2024) [51].

A new and developing "third pillar" connecting soil Fe chemistry to plant uptake biology is microbial assisted approaches: Fe/Zn producing microorganisms can mobilize Fe by high affinity chelators (siderophores) and modify the rhizosphere by PGPR; studies based on maize have documented Fe/Zn biofortification responses to Bacillus/Paenibacillus inoculation. Siderophore biology is being shed light on at the mechanistic frontier in influential microbiology research papers and experimental studies that describe the mitigation of Fe-deficiency chlorosis using metabolites from Priestia megaterium, increasing the viability of developing microbial solutions for the Fe-limited soils. Significantly, field translation is shifting toward "rhizosphere engineering" methods, which include host genotype selection, microbiome function, and soil amendment. Field data show that the nutrition of maize depends on the interaction between host genotype and the micro biome, indicating that matching genotype with microbiome and soil context will be necessary for consistent biofortification results rather than "one size fits all" inoculation. Additionally, biochar is being promoted as a useful carrier technology to aid in the delivery and survival of inoculants. Future maize Fe biofortification initiatives may incorporate biofortification products and management packages (Ahmad *et al*, 2023) [2].

Conclusion

Maize remains a key food and nutrition security challenge in global areas to the extent of where it is a major dietary staple, because of iron deficiency. In the race against the problem, iron biofortification has become a sustainable and economic solution to increase the nutritional value of maize using complementary agronomic, genetic, molecular and microbial methods. In the past, however, considerable advances have been made in understanding iron physiology, soil nutrient dynamics, plant–microbe interactions, molecular breeding and genome-editing technologies that have greatly improved prospects for the development of maize cultivars with improved grain iron concentration and nutritional value. While significant advances have been made, several key issues still exist in relation to iron bioavailability, variability in the environment, resilience to climate change, farmer adaptation, and regulatory approval. Dealing with these constraints will necessitate integrated research approaches that integrate conventional breeding and modern genomic technologies, precision agriculture, microbial biotechnology, and digital decision-support systems. Going forward, biofortification efforts would need to be increasingly geared towards multi-nutrient improvement as well as sustainable resource management and climate-smart farming in order to maximize the gains on both the agricultural production and human health fronts. Hence, biofortification of maize with iron is one of the most promising interventions to address hidden hunger and increase global nutrition security. Further scientific creativity, collaboration among disciplines and enabling policies for agriculture will be crucial to transfer the latest research results into actual solutions for farmers, which can provide nutritionally superior maize cultivars to the populations most impacted by iron-deficiency.

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How to Cite This Article

Ashfaq M, Iqbal MA, Khan AM, Bukhari SFH, Aslam N. Iron biofortification in maize: a review of recent progress and future prospects. J Soil Future Res. 2026;7(2):31-40. doi:10.54660/JSFR.2026.7.2.31-40.

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