

Iron nutrition management in calcisol soils as a tool to mitigate chlorosis and promote crop quality – An overview

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ABSTRACT

Iron (Fe) is an essential nutrient for plant growth and development and for human nutrition. However, its deficiency constitutes a serious problem in the agricultural sector and the food of populations worldwide. This nutrient can be present in different oxidation states, which condition its bioavailability. In calcisols (calcareous soils), it can precipitate and present low availability, causing iron deficiency chlorosis (IDC) in plants – a condition that reduces crop quality. Although plants naturally access soil Fe through acidification–chelation or chelation mechanisms, Fe nutrition management strategies have been proposed for alkaline soils to maximize or enhance these mechanisms. In this review, we have summarized the main research on ferric nutrition in calcisols, highlighting advances in the use of grafting systems, intercropping systems, ferric fertilizers, new chelates, nanotechnology, and bioengineering, and the underlying mechanisms. The use of fertilizers, chelates, and nanotechnology allows the stabilization of Fe, promoting a constant, continuous, and bioavailable supply in the soil–plant system. Practices such as grafting, intercropping, and organic complexes promote microbiological and enzymatic activity, inducing favorable environments that improve Fe availability and absorption. Moreover, knowledge of the mechanisms of Fe absorption, transport, and assimilation has allowed the selection and manipulation of genetic resources robust enough to cope with calcisol soil environments. Iron deficiency has been addressed elsewhere; our review was focused on calcisol soil conditions, bringing together new knowledge from the different tools used to alleviate IDC and promote growth and crop production. This review demonstrates how efficient and sustainable the use of Fe can be in calcisol soils, and it provides an overview of several unresolved or unaddressed issues with the expectation of attracting interest in the development of a research program to seek to mitigate IDC and ultimately promote crop quality in calcareous soils.

ARTICLE HIGHLIGHTS

- Grafting, intercropping, and resistant materials reduce the incidence of iron deficiency.
- New chelate molecules or fertilizers stabilize iron in calcisols.
- Organic complexes stimulate the soil microbiome by promoting iron bioavailability.
- Nanotechnology provides iron in a constant and continuous way in the soil–plant system.
- The use of iron nutrition strategies reduces iron deficiency and produces better-quality food.

1. INTRODUCTION

Iron (Fe) is an essential micronutrient for plants that can occur as Fe²⁺ or Fe³⁺. Its function is to act as an enzymatic cofactor and participate

in cellular respiration and photosynthetic processes, chlorophyll biosynthesis, electron transport, and cell division and expansion. It is also useful in the process of the source-sink translocation of photoassimilates [1,2].

Iron is abundant in the earth's crust. However, a large proportion of Fe is precipitated in the soil in forms that are not very available to plants, such as insoluble ferric (Fe[III]) hydroxide (Fe[OH]₃) – a very common form in calcisols. These soils are of great economic relevance because they cover approximately 25–30% of the world's agricultural area and are characterized by high pH, calcium carbonate (CaCO₃) and bicarbonate (HCO₃⁻) contents, and oxidative redox potentials, and low organic matter (OM) content [3,4]. These conditions cause low Fe availability in the soil and lead to Fe immobilization–precipitation in the apoplast [5,6], resulting in iron deficiency chlorosis (IDC). Iron deficiency chlorosis is characterized by the interveinal chlorosis of young leaves, chlorophyll loss, whitish-yellow discoloration, growth reduction, the deformation of young leaves, yield reduction, senescence, and tissue death [4] [Figure 1]. Likewise, this condition modifies nitric oxide homeostasis, reduces antioxidant system activity, and induces the accumulation of reactive oxygen species (ROS), all of which

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Figure 1: Iron deficiency symptoms in tomato plants grown in calcisol soil (picture by Fabián Pérez-Labrada).

affect the photosynthetic system [1,7]. In addition, light perception and signaling processes in the coordination of Fe homeostasis alter the morphophysiology of plants, and because calcisols are associated with semiarid and arid areas (with high solar radiation rates), the incidence and level of Fe deficiency can be exacerbated [8].

The low availability of Fe in calcisols leads to inadequate plant development. To improve crop growth in these soils, several alternatives in the management of Fe nutrition have been implemented and studied, from the use of tolerant plant varieties/hybrids, fertilizers, and chelates to the application of nanotechnology, new molecules, and genetic engineering tools [9,10]. This review represents an effort to show the main characteristics and potential of common strategies for the management of Fe nutrition in calcisols, demonstrate the efficient and sustainable use of Fe under calcisol conditions, and establish a critical perspective from which to approach unresolved or unaddressed aspects that should lead to the development of future research into mitigating IDC and producing better-quality crops.

2. IRON IN CALCISOL SOILS

Iron is abundant in soils (≈ 30 mg/kg) and can occur as water-soluble Fe, adsorbed Fe, Fe strongly adsorbed on carbonate, metal-organic complex Fe, Fe bound to manganese oxide, organically bound Fe, and residual Fe, although the most abundant form commonly found is Fe oxide, in the form of its main species – $\text{Fe}(\text{OH})_2^+$, $\text{Fe}(\text{OH})_3^0$, and $\text{Fe}(\text{OH})_4^-$ [11]. However, in the case of calcisols containing more than 15% CaCO_3 , this compound may be deposited in hard and impermeable layers, or it may accumulate in the pores of soil particles when dissolved in the soil CaCO_3 , resulting in alkaline conditions due to the increase in HCO_3^- ($\text{CaCO}_3 + \text{H}_2\text{O} \leftrightarrow \text{Ca}^{2+} + \text{HCO}_3^- + \text{OH}^-$), buffering the pH to between 7.5 and 8.5. This condition generates a saturation of Ca^{2+} and magnesium (Mg^{2+}) bases in the cation exchange sites, leading to Fe adsorption and precipitation reactions [12]. Calcisols may have adequate Fe contents, but this is in a form unavailable to transfer to plants [Figure 2].

These soils have a low soluble and exchangeable Fe content, are insoluble, and have difficulties with absorption and translocation [1,13] because the high pH causes the precipitation of Fe in the form of ferric hydroxides [mainly $\text{Fe}(\text{OH})_3^0$ – a chemical form that is not available to plants]. Similarly, soil redox conditions significantly affect Fe dynamics because, as the soil moisture content increases, “reduction

microsites” are created in the vicinity of the soil particles – a condition that reduces the redox potential by the release of electrons and protons from the microbiome – causing an increase in Fe solubility. Drought conditions (low soil moisture content) increase the redox potential, generating an environment, in which Fe again precipitates as $\text{Fe}(\text{OH})_3^0$ (insoluble and unavailable to plants) [12,14]. Similarly, waterlogged conditions increase Fe^{2+} levels due to microbial metabolism, which uses Fe^{3+} as an electron acceptor [15], and likewise, CaCO_3 dissociates into Ca^{2+} and CO_3^{2-} , raising the pH of the soil solution, and this environment causes the oxidation of Fe^{2+} to Fe^{3+} [12,16,17].

3. ABSORPTION AND TRANSPORT

On average, plants contain up to 50–150 mg/kg dry weight of Fe in their leaf tissue, and a certain percentage is mobilized for seed accumulation during senescence [18]. These concentrations vary according to the carbon (C)-fixation pathway; for example, species with the Hatch-Slack pathway require more Fe than species using the Calvin–Benson–Bassham cycle [19]. To reach these requirements, plants present strategies to access soil Fe, including acidification–reduction–transport (Strategy I, non-grass plants) and Fe^{3+} chelation by hexadentate chelators and phytosiderophores (Strategy II, grass plants) [Figure 3] [9,20]. Plants under calcisol conditions tend to exploit these strategies to access Fe.

In Strategy I, hydrogen (H^+) is extruded by the enzyme H^+ -ATPase (HA1), which acidifies the rhizosphere and allows the solubilization of insoluble Fe^{3+} complexes. Then, phenolic compounds (mainly coumarins excreted by PLEIOTROPIC DRUG RESISTANCE 9 transporter, PDR9) or organic acids chelate the Fe^{3+} , producing a “zone of optimum concentration” in the rhizosphere. The chelated Fe^{3+} complex is then reduced to Fe^{2+} by ferric reduction oxidase (FRO), and finally, the Fe^{2+} is transported into the plant by the zinc (Zn)-regulated transporter- and iron-regulated transporter (IRT)-related protein (ZIP) family, mainly IRT1, or by natural resistance-associated macrophage protein 1 (NRAMP1). These components are overexpressed in the outer membrane and in the early endosomes of the root system [4,9,18,21–24]. Transcription factors, such as the FER-like iron deficiency-induced transcription factor (FIT), basic helix–loop–helix (bHLH), and myeloblastosis (MYB), promote the activation of this strategy [25].

In Strategy II, the 2'-deoxymugineic acid secreted by the protein transporter of mugineic acids 1 (TOM1) chelates the Fe^{3+} to obtain a Fe^{3+} -phytosiderophore complex. Subsequently, the transporter yellow stripe-like 1 (YSL1) located in the root epidermis and IRT1/2 capture the complex and mobilize it toward the root cells [4,9,10,21,24].

Excretion of the catecholic metabolite sideretin from the coumarin fraxetin functions as an annex mechanism in Fe uptake by a redox cycle (electron transport) in the root system of plants (probably in a greater proportion in Strategy I than Strategy II plants) [26].

In the root epidermis, Fe is mobilized through the apoplastic pathway (where the Caspary band and endodermis regulate its mobilization) until it is loaded into the xylem (mainly by transporters of the YSL family) or loaded into the phloem (as Fe^{2+} nicotianamine by YSL transporters) for subsequent translocation and histolocalization through a source-sink mechanism in chelated form – that is, Fe citrate, Fe cysteine, Fe histidine, Fe malate, Fe nicotianamine, Fe aspartate, Fe glutathione, and Fe glutamate – or with IMAI peptides (IRON MAN) [4,21,24,27]. In leaf tissue, it is loaded into the mesophyll cells, probably by YSL and IRT1. In addition, FRO may

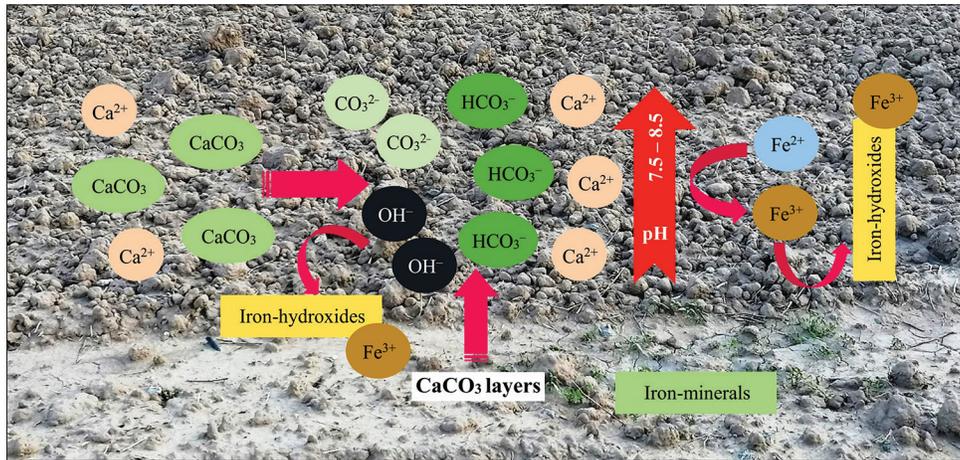


Figure 2: Behavior of iron in calcisol soils.

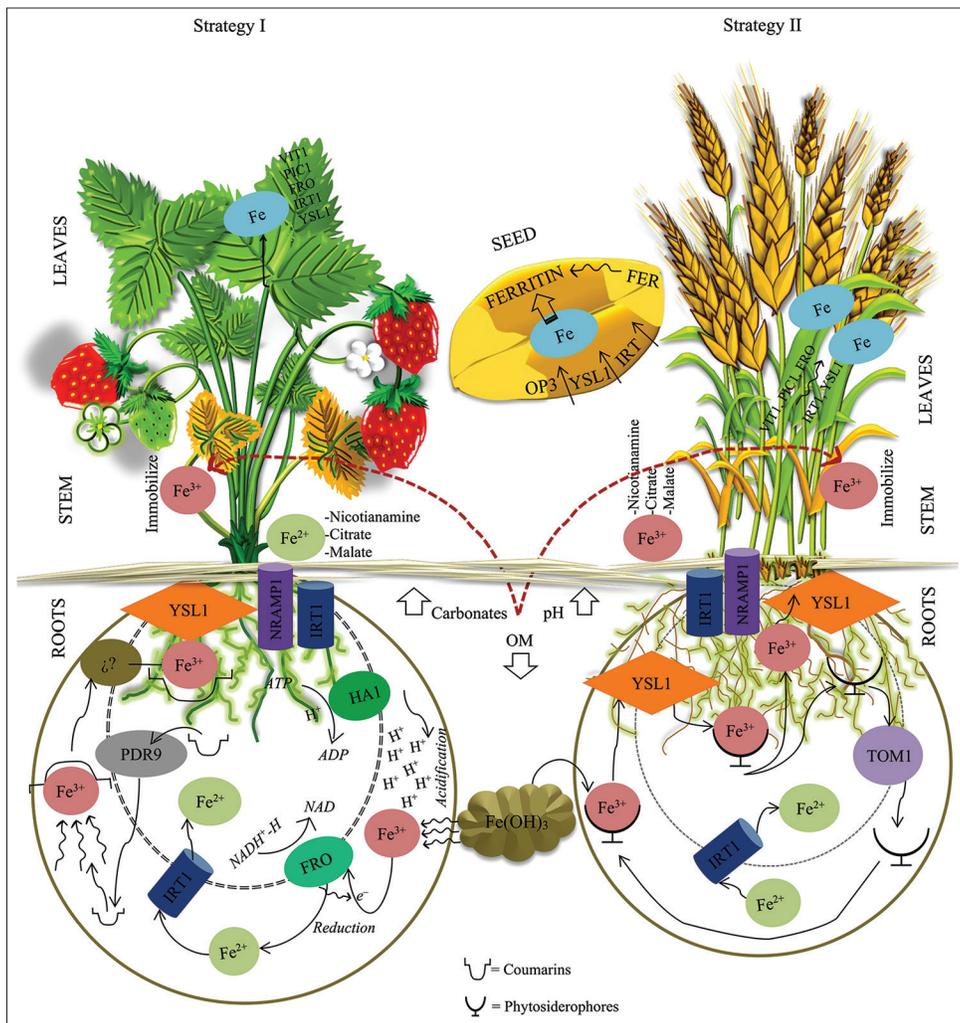


Figure 3: Mechanisms of iron uptake and transport in plants.

be activated to reduce the chelated complex. Once inside the cell, it can be redirected and stored mainly in the chloroplast by the protein components complex containing permease in chloroplast 1, a nickel-cobalt transporter, and mitoferrin-like 1; in the vacuole by vacuolar iron transporter (VIT1), VIT-like, and NRAMP; into the mitochondria by FRO and mitoferrins; or be redirected to the seed by oligopeptide

transporter 3 (OPT3) and YSL1, where it is stored as FERRITIN in the vacuole by B3 transcription factors, including FUSCA3 (FUS3), leafy cotyledon2, and abscisic acid insensitive 3 [13,28]. Similarly, in the chloroplasts and mitochondria, the enzyme ferrochelatase allows the binding of Fe^{2+} in protoporphyrin IX, producing heme proteins or Fe-sulfur (S) groups [24,28,29].

With foliar Fe application, the presence of negative charges on the cuticle facilitates the diffusion of Fe (which has a positive charge) or FeO (nanoparticles [NPs]) through the cell wall. There is a certain degree of similarity between the van der Waals radius of chelates and Fe sulfate (FeSO_4) and the aqueous pores, such that the Fe can penetrate through the stomata as easily as through the apparent free spaces. The Fe then rapidly penetrates into the vascular bundles, where, depending on the cell pH, it binds to anions and/or ligands (nicotianamine, deoxymugineic acid, and Fe transport proteins) or reacts with nitric oxide, forming nitrosyl, and dinitrosyl complexes (mainly under Fe-deprived conditions) for subsequent cell compartmentalization, as mentioned above [20].

The characteristics of calcisol soils (mainly their high pH and high HCO_3^- contents) and their Fe-deprived conditions significantly affect the plant physiology because the reduction in tissue Fe content generates a decrease in chlorophyll synthesis and alters the carbonic anhydrase, ribulose-1,5-bisphosphate carboxylase activase and phosphoenolpyruvate carboxylase (PEPC) activity, gas exchange (net photosynthesis), and chlorophyll fluorescence [30-34], and these alterations impair plant growth rate and production.

Iron deficiency in plants grown in calcisol soil leads to oxidative stress through an increase in the synthesis of ROS (H_2O_2 , O_2^\bullet , HO) and malondialdehyde [33]. This oxidative environment promotes proline concentration while reducing the synthesis of catalase, superoxide dismutase, and peroxidase because Fe is a constituent of these enzymes [30]. This enzymatic response varies according to the genetic resource and strategy used in Fe management.

The physiological and biochemical response observed in plants with IDC varies according to the level and timing of the Fe deprivation, both in Strategies I and II. In both cases, there is a molecular response that allows the mechanisms of Fe acquisition to be regulated. In this sense, transcription factors allow signaling and modulation. In plants developed in calcisol soils, the transcription factors FER, FIT, bHLH, and MYB, and the transcript expression of NRAMP3 and yellow stripe 1 (YS1)/YSL, are crucial for detecting Fe deprivation in the plant, thereby allowing this promotion and modulation of the signaling [25]. These transcription factors regulate the expression of the gene AHAs (encoding the ATPase protein in the plasma membrane), FRO (encoding the FRO protein), IRI1 (encoding the IRT protein), PEPC (synthesizing the PEPC1), YS1/YSL (encoding the Fe(III)-phytosiderophore complex transporter), and TOM1 (synthesizing the phytosiderophore transporters) [35-38]. These authors cited differential modifications in the expression of the genes in tomato (LeIRT1, LeFRO1, LePEPC1), rice (OsIRT1), barley (HvYS1), and maize (ZmYSI), as well as their heterologous nature in different plant organs.

4. MANAGEMENT STRATEGIES

To mitigate the incidence and levels of IDC in crops and to avoid inadequate plant development, different alternatives for its management have been investigated and implemented that can contribute to sustainable crop production in calcisols [9,10].

4.1. Grafting

Grafting is a practice based on the union of a plant of particular interest (graft) on another plant (rootstock) that presents resistance characteristics and is compatible with grafting. This technique has been reported in grapevine cultivars developed in calcisols to avoid IDC (given that grafting + quality rootstock \rightarrow Fe accessibility and

uptake and thus \downarrow IDC) by promoting Fe uptake strategies through the modification of 3-hydroxymugineic acid, 3-desoxymugineic acid, and steryl ferulate exudation patterns [39]. For example, in a pear cultivar (*Pyrus bretschneideri* cv. Rehd) grafted onto a dwarf quince (*Cydonia oblonga* cv. Molino) grown in a calcisol, a high susceptibility to IDC was found, whereas a *P. bretschneideri* cv. Rehd grafted onto a *Pyrus betulifolia* showed a mechanism of Fe activation in the leaves [40].

The positive response to the use of grafting in the management of Fe nutrition may be due to an alteration in the FRO activity or by exudation of low-molecular-weight compounds from the root system of the rootstock. However, in calcisols, the high bicarbonate concentration may lead to alkalization of the pH in the xylem, causing inefficiency in the Fe transport or precipitation. This condition increases the concentration of inactive Fe in the apoplast of Fe-deficient leaves compared to non-deficient leaves (Fe-chlorosis paradox). In this context, using rootstocks can minimize the increase in apoplastic pH, stabilize the FRO activity, and mitigate the Fe precipitation in the leaf tissue. An appropriate selection of the rootstock-cultivar combination is necessary to initially facilitate the greatest survival and enhance the characteristics of the plant species; for example, the use of various *Prunus* rootstocks has led to agronomic alterations and modifications in the quality of the graft fruit in addition to a differential response in IDC and the foliar Fe content [41-44]. The graft's physiological response may have resulted from histological and genetic interactions with the rootstock [45]. The graft-rootstock behavior, Fe content, yield, and incidence of chlorosis depend on the level of CaCO_3 in the soil [46].

4.2. Intercropping Systems

Intercropping systems (a method that consists of sowing/developing more than one crop in a given area at the same time) have positive effects on the Fe nutrition derived from the interrelationships occurring in the root system of the plants. In an intercrop of peanut (*Arachis hypogea* L. cv. Luhua14) and maize (*Zea mays* L. cv. 4 Nongda108), the Fe content was improved by facilitating the root acquisition of Fe through modifications in the Fe transporter (AhNRAMP1) and divalent metal ion transporter [47]. Those authors pointed to an increase in methionine synthesis (derived from increased homocysteine S-methyltransferase and serine acetyltransferase 1) possibly related to an increased release of phytosiderophores. In another study, the intercropping of peanut (Strategy I) and maize (Strategy II) led to reductions in IDC and an increase in Fe in the peanut. This response was due to the AhYSL1 gene expressed in the root system of the peanut allowing the uptake of the Fe(III) phytosiderophore complex located in the rhizosphere of the maize [48]. Similarly, planting wheat, alfalfa, and maize in calcareous soil, in combination with chemical fertilization or manure, modified and increased the concentration of available Fe (mainly in the alfalfa) and promoted higher concentrations of Fe associated with CaCO_3 and OM and lower contents of Fe associated with soil minerals [49]. Contrastingly, a peanut-corn intercropping system, developed in calcareous soil (pH 7.92), showed strong interspecific interactions that promoted both N and Fe acquisition, which may be because the corn root system under a Fe deficit increased the release of Fe phytosiderophore complexes in the rhizosphere zone. This availability allowed the peanut to absorb Fe, increasing the activity of FRO and specific transporters [50].

Intercropping systems positively promote the physicochemical and biochemical characteristics of the soil, rhizosphere, and microbiome [51], improving Fe absorption processes in calcisols, with crop₁ + crop₂ + crop_n stimulated plant-plant relationships leading

to stability of the plant-soil system, and thus to Fe bioavailability. However, for this strategy to be more efficient, it is necessary that the plants used present only slight complementation to avoid competition (e.g., combining a species with a high solar radiation demand with a species that demands less), that the water requirements are adequate, and, above all, that the allelopathy is analyzed, with the objective of enhancing the combination of crops beyond leguminous–non-leguminous pairs.

4.3. Fertilizers

The use of fertilizers is common practice in relation to ferric nutrition due to their rapid response. However, the qualities of the fertilizer must be verified to avoid its precipitation when it comes into contact with soil particles. Likewise, its relationship with S must be accounted for, and excessive applications of copper (Cu) and Mn must be avoided because Fe absorption can decrease if there is an accumulation in the roots [52,53].

Due to its solubility and acceptable cost, the most widely used inorganic fertilizer for supplying Fe is FeSO_4 . Several studies have demonstrated the benefit of its use, with applications of 12 kg/ha on flour wheat in soils with pH 7.5–7.7 improving the Fe and starch content in the grain, while a combination of 12 kg/ha FeSO_4 and 10 kg/ha ZnSO_4 increased productivity and the Zn, Fe, Ca, and starch content [2]. Similarly, the use of foliar-applied FeSO_4 has been effective in reducing IDC in the leaves of orange trees (*Citrus sinensis* L. cv. Thomson Navel, grafted on *Citrus limon* L.) grown in calcareous soil (pH 7.9) due to the remobilization of inactivated Fe in the apoplast, thus avoiding its oxidation and precipitation [54]. *Paspalum scrobiculatum* cv. CO_3 plants developed under calcisols did not show IDC when 50 kg/ha of FeSO_4 was applied to the soil in addition to foliar spraying at 0.5% at 30 and 50 days after planting [55]. Another example is the combined use of FeSO_4 and biochar, which promoted root biomass and photosynthesis by improving the Fe and ferritin content and possibly reducing the soil pH [56]. Similarly, applications of S and bentonite granules to calcisol soil (inoculated with *Thiobacillus thioparus*) reduced the soil pH (by ≈ -0.3 units) by *Thiobacillus*-mediated S oxidation, thereby improving the growth parameters and increasing the Fe uptake, in addition to the Mn, Cu, S, and phosphorus (P) in corn plants [57].

In addition to ferrous sulfate, using nitrogen fertilizers (ammonium $[\text{NH}_4^+]$ sulfate, NH_4^+ nitrate, or urea) allows localized soil acidification, promoting greater Fe availability [58]. However, it should be taken into account that the uptake of N-NO_3^- is associated with H^+ cotransport systems or OH^- antiporters, so the rhizospheric pH could increase, reducing the Fe availability, and the excreted H^+ could be neutralized by HCO_3^- [18]. When N-NH_4^+ encounters the soil, it is deprotonated (loses a H^+), inducing a localized reduction in pH; however, the resulting ammonia (NH_3) can easily volatilize. In this situation, a $\text{N-NO}_3^-/\text{N-NH}_4^+$ balance is suggested to allow the proper activity of nitrate transporter 1, which makes the reuse of apoplastic Fe more efficient [59].

The combined application of mineral fertilizers in saline-alkaline soils can be a management strategy for stimulating soil aggregation, the content of amorphous Fe oxides, and the distribution of C-aromatic, the latter being capable of forming Fe-aromatic complexes [60]. Another alternative is the application of ceramic frits (of fused, tempered, and granulated ceramic composition) that can increase the available Fe content in the soil (pH 8.25). Using these frits on kiwifruit, melon, and zucchini plants increased the foliar Fe content in the melon plants [61]. According to these authors, Fe release

increased under alkaline conditions, suggesting its potential use as a slow-release inorganic fertilizer in calcisol soils. Recently, fertilizers coated with organic acids and amino acids (citric, humic, fulvic, and salicylic acids, and glycine) have been developed to allow a controlled release of nutrients, with granules coated with citric acid (10% w/v), especially allowing a greater availability of S and micronutrients, such as Fe, in calcisols [62].

To achieve sustainable Fe administration in calcisols, the 4Rs perspective is recommended. The 4Rs nutrient stewardship framework is based on four interrelated principles – the right source, right rate, right time, and right place [63]. This involves selecting the most adequate source for providing the Fe (preferably acid-reaction fertilizer/s), verifying the ideal dose based on the plant developmental stage, establishing the adequate moment(s) for application, and determining whether drench, edaphic, or foliar application should be used. This method can provide greater certainty in reducing IDC in the plants developed in this type of soil. Similarly, using biodegradable materials (palm and pistachio cellulose) to coat slow-release Fe fertilizers is effective and plausible [64].

4.4. Chelates and Novel Chelates

The application of conventional synthetic chelates, such as ethylenediaminetetraacetic acid (EDTA), ethylenediamine-N-N'-bis(o-hydroxyphenyl acetic) acid (EDDHA) in different racemic ratios, and N-N'-bis(hydroxyphenyl) ethylenediamine-N-N'-diacetic acid (HBED), is a common and effective agricultural practice used to prevent and/or mitigate IDC [21,65]. However, different application times are required for its efficiency, and ideally, before the first symptoms of IDC have manifested [18]. Applying HBED/ Fe^{3+} chelate in the early stages of plant development is the most appropriate time for achieving a greater accumulation of Fe in the plant and in the soil [66]. In *A. hypogea* L., the foliar application of Fe-EDTA (0.1 mM) at 45, 60, and 90 days after sowing improved the pod number in plants developed in calcisols due to a possible reduction in the apoplastic pH that allowed Fe stabilization, mobilization, and metabolism [5]. Alternatively, applying Fe chelates to date palms grown in calcisols improved their fruit yield [67]. Similarly, the foliar application of Fe-EDDHA to tomato plants (in a calcisol with pH 7.9) improved their growth and yield [68], while applications of 4.8% of the same chelate to the tomato plants led to increased efficiency in Fe uptake. Thus, this may be a useful way of mitigating IDC, while a dose of 6.0% may serve as a long-term nutrition strategy [69]. To achieve efficiency in the use of chelates, the pH and carbonate content (buffering capacity) of the soil must be considered; otherwise, only short-term results will be obtained. Some chelates, such as EDDHA, lose stability due to the retention of their isomers in the soil particles [18].

Another alternative is the combined application of chelates and fertilizers, for example, applications of Ca nitrate ($[\text{Ca}[\text{NO}_3]_2]$) (50 g/tree) and Fe chelate (6%, 30 mL/tree) in *Malus domestica* Borkh cv. Red Delicious grown in calcisols improved the yield and fruit quality by optimizing the postharvest quality [70]. In addition, ferric fertilizer sprays (particularly citric acid + $\text{Fe}_2[\text{SO}_4]_3$ + Fe-EDTA-Na) can increase the yield and Fe content in potato tubers grown on alkaline soil (pH 8.3–8.4), improving the photosynthetic pigments and leaf gas exchange [71]. In addition, in Italian lemon, the direct soil application of Fe-EDDHA + urea (1 month after the onset of sprouting) was found to increase the Fe content in the leaf tissue and the yield [72]. Although the use of these chelates increases the Fe content, reduces the IDC, and improves the fruit quality, their efficiency may be reduced by

precipitation in the soil, and the low translocation or accumulation in the cuticle through foliar application [19].

Considering that conventional chelates can be highly persistent in the environment, alternative molecules have been sought to chelate the Fe. In this sense, N,N-dihydroxy-N,N'-diisopropyl hexanediamide (DPH) and azotochelin have been applied to soybean to investigate their stability in improving Fe nutrition as a long-term source of Fe, and inducing dissolution in calcareous soil [73]. It has also been reported that ethylenediamine disuccinic acid ([S,S]-EDDS/Fe) chelate applied to calcisol increased the Fe content in soybean plants similarly to the application of a Fe-EDTA chelate [74]. One of the qualities of the EDDS chelate is its low durability in soil, although this causes it to have a lower reactivity with the Ca in CaCO_3 , such that Fe is made available. In another study, it was found that the use of Fe chelate tris (3-hydroxy-1-(H)-2-methyl-4-pyridinonate) Fe(III), applied to soybean grown in calcisols on two occasions (the V3 and V4 phenological stages) at a dose of 5.5 mM, improved the chlorophyll content and root biomass in addition to the Fe content in the trifoliolate leaves by promoting a system of absorption, redistribution, and accumulation of Fe in the plant, correcting the IDC [75].

In other studies, knowledge of the functionality of 2'-deoxymugineic acid (Strategy II) has been used to synthesize a more stable and economically accessible analog. In this sense, the compound proline-2'-deoxymugineic acid + Fe can be mobilized toward the plant as a Fe chelate by Fe(III)-2'-deoxymugineic acid transporters, reducing the Fe chlorosis in rice plants, and even applications of proline-2'-deoxymugineic acid chelate Fe found in calcisols enhanced its effect by up to 10-fold compared to Fe-EDDHA [76]. This molecule has also been tested on Strategy I plants (e.g., cucumber) grown in calcareous substrates (pH 9.1), where a reduction in IDC was observed along with an increase in Fe in the shoots due to its high reducibility [77]. Similarly, its application as proline-2'-deoxymugineic acid in peanuts grown in this type of soil can dissolve the insoluble Fe in the rhizosphere and stimulate AhYSL1 gene expression, thus improving the Fe nutrition, yield, and nutrient content in the grain [78]. Finally, the application of deferoxamine combined with Fe^{3+} to the roots of *Cinnamomum camphora* grown in saline-calcisol soil (pH 8.2) alleviated the IDC by increasing the leaf Fe content by stimulating its uptake and transport system (CcbHLH, CcFRO, CcNramp, CcOPT, CcLRT, and CcVIT), as well as generating a higher solubility and mobility of the Fe in the plant due to the reduced activity of pectinesterase, which fixes Fe in cell walls [79].

Conventional chelates can cause contamination due to their high persistence in the soil and water fields, so their use in the context of the 4Rs is recommended, for example, selecting the right chelate source, right dose, right time, and right place. It is also to reduce and/or mitigate interesting to promote the use of novel chelates under a similar approach in both cases to reduce and/or mitigate plant IDC sustainably.

4.5. OM

Given that soil OM plays a crucial role in increasing Fe availability, the addition of organic sources (such as humic complexes) can stimulate soil microbial activity and/or induce the reduction of microsites – phenomena that can lead to bioavailable and stable Fe concentrations for prolonged periods in the soil and in the soil solution. A widely studied source of OM in soils is leonardite. In this context, applications of Fe fulvate (fulvic acid + Fe_2SO_4) in serrano chili grown in calcareous soil improved the growth and fruit quality in addition

to inducing conditions for an optimal Fe content [80]. In the same context, humic substances adsorbed on weakly crystalline Fe oxides (ferrihydrite) can stabilize Fe in the soil, favoring its uptake. However, their effect varies depending on the type of strategy used by the plant. In wheat (Strategy II), an increase in Fe uptake was observed to result from the mobilization of Fe from the oxides in comparison to white lupin (Strategy I) [81]. In *Glycine max*, the application of a 2:1 mixture of Fe leonardite humates plus a chelating agent (Fe-HBED) provided available Fe to the chelating agent and subsequently to the plants, inducing a synergistic effect. Unlike the chelates, the Fe leonardite mixture maintained a stable humate supply. The same authors [81] noted an increase in the shuttle effect from a synergistic application of these compounds derived from the solubilization of the Fe^{3+} present in the soil and provided by the leonardite, as well as its subsequent chelation [82]. This was because humic substances can stabilize, solubilize, and provide plant-available ferric complexes [83].

Alternatively, weekly applications of humic complexes to calcareous soil (pH 8.5, 0.2% OM, 5 mg/kg Fe), in combination with a Fe-EDTA or Fe-EDDHA chelate, improved the Fe content in tomato plants [84]. In a study conducted over the course of 3 years (2017–2019) on *Vitis vinifera* L. cv. Tempranillo grafted on 41-B rootstocks and developed in calcareous soil (pH 8.265, 1.195% OM), applications of leonardite supplemented with ferrous sulfate heptahydrate increased the soil OM content, favoring root growth, slightly reducing the soil pH (≈ -0.2 units), and improving the nutrient content of the soil [P, potassium (K), Fe, Mn, Cu, and Zn] and petiole (P, K, Fe, and Zn) [85]. The authors pointed out that the reduction in soil pH was because the Fe^{2+} in the sulfate was very labile in soils with good aeration and high pH because it reacted with oxygen (O_2) to generate Fe^{3+} , which hydrolyzed to form $\text{Fe}(\text{OH})_3$, releasing three H^+ into the soil for each Fe^{3+} . The $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$ produced H_2SO_4 , $\text{Fe}(\text{OH})_3$ formed $\text{Fe}_2\text{O}_3 \cdot n\text{H}_2\text{O}$, and H_2SO_4 was neutralized by CaCO_3 , thereby releasing Ca^{2+} , SO_4^{4-} , and HCO_3^- , the latter of which was able to dissociate into CO_3^{3-} and H^+ . Finally, the foliar spraying of humic acid plus Fe on rice, soybean, and lettuce crops in soils with a pH of 8.44 resulted in increased growth, higher yields, better Fe accumulation in the aerial parts, and increased Fe mobilization to the seeds (rice and soybean) [86].

Using animal manure amendments (at an application rate of 10%) on pearl millet improved the Fe availability in calcareous soil (pH 8.5) and stimulated its uptake and accumulation in the plant. A reduction in IDC symptoms by stimulating photosynthesis and plant growth has also been reported [34].

4.6. Amino Acids and Low-Molecular-Weight Compounds

Amino and organic acids are molecules that allow metabolic activation in plants; their exogenous application can be a tool in managing Fe nutrition. Foliar applications of sulfate plus organic acids to *Platanus orientalis* (0.7% FeSO_4) showed a better response than soil applications because they were able to influence the root system and rhizosphere of the trees [87]. In the same way, foliar applications of amino chelates (2.0% N-amino acids, 2.5% Zn, 2.0% Fe, 1.5% Mn, and 0.4% Cu) to *Solanum lycopersicum* L., *Cucumis sativus* L., and *Phaseolus vulgaris* L., grown on calcareous soils, improved the chlorophyll index and yield [88]. Contrastingly, applications of organic acids (1 mmol citrate, malate, and oxalate) and flavonoids can mobilize Fe in calcareous soils, inducing the dissolution of amorphous fractions, and allowing illite formation in *C. sativus* grown in calcareous soils (pH 8.0) [89].

To increase the biodegradation rate (concerning synthetic chelates), new complexes have been reported, such as the compound Fe^{3+}

heptagluconate (in equimolar and 1:2 ratios), which gave greater stability to the Fe in the soil at high pH values as a result of the formation of polynuclear complexes [90]. Alternatively, FeSO₄·7H₂O, Fe glycine, Fe tyrosine, and Fe chitosan complexes have been developed. These were applied to the soil (20 mg Fe/kg) or leaves (0.25% w/v) of wheat in soil at pH 7.8 and were found to have improved the yield in addition to promoting Fe and N uptake and increasing the Fe concentration in the shoots. This response was derived from an improvement in the transport systems [91]. Applying these compounds implies lower energy costs for Strategy II plants, in addition to the fact that amino acids can participate in protein synthesis (e.g., Fe transport). Likewise, ferrous glycinate and ferrous citrate increased the Fe content through foliar application. Ferrous glycinate, in particular, induced greater chlorophyll biosynthesis and improved photosynthesis in *Vigna* [92]. Applying amino acids to soil-developed tomato (pH 7.17, available Fe 1.48 mg/kg) under greenhouse conditions promoted better yields, fruit weights and diameters, and higher concentrations of N, P, Fe, and Mn [93].

The application of various Fe sources to soybean grown in a calcisol can be considered a sustainable alternative in the management of Fe deficiency. Mining byproducts (Fe oxide and Fe-FeS₂ oxide), in combination with thiols (glutathione, dithiothreitol, and thiophenol), increased the Fe in the plant and modified the content of reduced-oxidized glutathione, ascorbate, and antioxidant enzymes [94]. Mining byproducts are more effective than Fe-EDDHA chelate, probably due to their ability to release Fe, which can be solubilized and absorbed by the plant acquisition mechanism. Similarly, in tomato grown on calcisols, the foliar spraying of Fe glutamate improved the plant height and shoot and root fresh weights and increased the fruit number, yield, and quality, indicating that Fe glutamate can improve Fe nutrition by acting as a biostimulant [95].

Drench applications of nutrient solutions containing organic acids (citric or salicylic acid) and chelates (Fe-EDTA or Fe-EDDHA) to pot-grown tomato in calcisol soil (pH 8.5, 0.2% OM, and 5 mg/kg Fe) promoted Fe content in the shoot tissue. It increased the yield per plant [85,96]. Finally, applications of ascorbic and oxalic acid to cucumber plants grown in calcisol soil (pH 8, 10% CaCO₃) appeared to reduce abiotic stress by histologically modifying the xylem duct and cortical cells [97].

4.7. Microorganisms

Plants tend to interact strongly with the rhizospheric microbiome to aid in their Fe uptake strategy. Likewise, some microorganisms under Fe deprivation can produce siderophores that chelate Fe³⁺ and induce its bioavailability. In this sense, the selection, propagation, and application of such microorganisms is a strategy that can contribute to Fe uptake in calcisols [98]. It has been shown that *Azotobacter vinelandii* and *Bacillus subtilis*, in combination with FeCl₃·6H₂O, can be a viable way to reduce IDC in soybean plants grown in calcisols [75,99]. The simultaneous application of growth-promoting rhizobacteria (*Pseudomonas fluorescens* T17-24 and *B. subtilis* P96) and Fe chelate (10 mg Fe-EDTA/kg soil) to sorghum grown in calcisol showed improvements in the morphological characteristics of the crop due to the dissolution of insoluble compounds, which increased the availability of Fe in the rhizosphere and expanding the Fe, Mn, Zn, Cu, and K contents in the plant [65].

Alternatively, microorganisms such as *Pantoea agglomerans*, *Pseudomonas plecoglossicida*, and *Lactococcus lactis* can synthesize pyoverdine siderophores (ferripyoverdines), catecholate, hydroxamate,

and carboxylate, so that their application, in addition to modifying the plant ionome, can chelate Fe, facilitating its absorption, and increasing its content in the plant [100,101]. Similarly, soil applications of inocula of *Glomus* spp. microorganisms, *Trichoderma asperellum*, and *Streptomyces avermitilis* on strawberry plants (Strategy I) in calcisol were found to reduce IDC symptoms by increasing the Fe content in the different tissues. This was explained by an increase in Fe availability by the siderophores of the microorganisms [102]. In a 1:1 mixture of vermiculite and calcisol (pH 7.8), the individual or combined inoculation of *Sphingobium fuliginis* ZR 1-6 and *Pseudomonas jessenii* ZR 3-8 in soybean plants increased the FRO activity, allowing Fe³⁺ reduction, and improving Fe uptake and concentration in the tissues. This action was due to the production of indole-2-acetic acid, 1-aminocyclopropane-1-carboxylic acid deaminase, siderophores, and organic acids [103].

Rahnella aquatilis JZ-GX1 applied to *C. camphora* induced a substantial improvement in the chlorophyll and Fe²⁺ content in the leaves, in addition to increasing the activity of the superoxide dismutase, peroxidase, catalase, and ascorbate peroxidase enzymes [104]. The same authors pointed out the probability that this strain could secrete desferrioxamine in the rhizosphere and promote increased abundances of *Glomus*, *Mortierella*, *Trichoderma*, and *Penicillium* in calcisols at pH 8.2. Recently, it was found that the coinoculation of *Piriformospora indica* (phytopromotional fungus) and *Azotobacter chroococcum* WR5 (rhizobacterium) in *Triticum aestivum* L. altered the root system and enhanced Fe accumulation in plant tissues by increasing the root, stem, leaf, and grain transfer factors and the Fe transfer factors in the root-stem, root-leaf, and root-grain systems, as well as increasing the overexpression of ZIP-family transporter genes in the root system [105]. Similarly, *Thiobacillus thiooxidans* and *Thiobacillus ferrooxidans* in calcisols can increase the Fe concentration in soybean shoots [106].

The joint application of *Bacillus megaterium* and Ca superphosphate (69, 207, and 345 kg/ha) led to a reduction in the damage caused by a high soil carbonate content (10.8–11.3%, pH 7.19–7.77), and improved the content of Fe, Cu, Zn, and Ca in the leaf and root tissues [107]. Similarly, biochar applied with plant growth-promoting rhizobacteria and mycorrhizal fungi under wheat seed at sowing under rhizobox conditions improved the availability of Fe, Zn, and P in the soil, thereby increasing the OM [108]. The increase in Fe bioavailability was due to the synthesis of microbial siderophores that could promote Fe solubility and stability, with the biochar functioning as a niche for microbial proliferation due to its high porosity and through the interaction of different Fe fractions with the biochar and soil [109]. Microbiome-soil-plant-root interactions under Fe-deficient conditions may depend on coumarin excretion [110].

4.8. Bioengineering: Plant Breeding

Selective crop management allows desirable and interesting traits to be obtained (conventional breeding). However, genetic engineering (gene manipulation) allows a more efficient and rapid response. In both cases, the objective is to understand and improve the mechanisms of Fe uptake, translocation, and utilization at the transcriptomic level in IDC-tolerant/resistant genotypes [18,111,112]. For example, the introduction of barley genome fragments containing the OsIRT1-refre1/372 promoter (increased chelate reductase capacity) and the 35S-OsIRO2 promoter (increased phytosiderophore secretion) into an Fe deficit-tolerant rice crop allowed enhancement of the gene expression related to phytosiderophore synthesis and ferric chelate reductase activity, enabling the efficient acquisition of the Fe present in

a calcisol (pH 8.9), which allowed a 9-fold increase in yield compared to non-transgenic rice plants [113].

Some plant species or cultivars show a higher tolerance to Fe deficiencies. For example, *Medicago truncatula* line TN8.20 showed better performance when grown in a calcisol than the Jemalong line, which is possibly due to the differential capacity for Fe allocation to nodules, thereby enabling their symbiotic N-fixing functionality and the higher enzymatic activity of superoxide dismutase, catalase, and peroxidase [16]. Likewise, a higher relative tolerance to Fe deprivation conditions was found in the calcisols of durum wheat cultivars due to a higher Fe uptake and translocation capacity together with its efficient use [112]. In this regard, genetic engineering strategies have been proposed to exacerbate the synthesis of certain genes as well as their promoters (YS1 controlled by the heavy metal ATPase 2 promoter, transporter of mugenic acid 1 controlled by ferric reductase defective like 1 promoter, ferritin, and nicotianamine synthase), which may correspond to an increased Fe content in maize and rice seeds [114]. The combined introduction knockdown of the OsHRZ and OsIRT1-Rfre1/372 promoter (artificial gene) can lead to improved tolerance of Fe deficiency without reducing its accumulation. This approach has allowed plants to exhibit increased reductase activity at elevated pH levels (in calcisols), leading to Fe accumulation in rice seed and rice straw. Thus, the augmentation of transcription factors is a feasible tool [115].

Further potential for the genomic improvement of plants could be the genetic mapping of IDC-tolerant plants [116] or wild plants. The latter plants (Strategy I) developed in calcisols have been reported as presenting a different absorption and assimilation mechanism because they did not show a strong effect at high carbonate concentrations and soil pH values. This suggests the exudation of specific chemical reductants [117]. Consequently, genetic mapping techniques, and even clustered regularly interspaced short interspaced palindromic repeats (Cas9) [118], could present a way to improve the metabolic pathways that comprise such chemical reductants or exacerbating genes related to their uptake, transport (FRO and IRT1), and storage (Ferritin).

4.9. Nanotechnology

Nanotechnology (a tool that uses compounds <100 nm in size) allows environmentally friendly applications because very low concentrations are required to deliver the nutrient, which, due to its specific characteristics, will have completely different morphological and physiological effects than a particle at its normal scale [119]. Nanoscale Fe (nanoiron) shows rapid penetration, its release, and distribution being controlled and specific. When applied foliarly, it enters the plant through the stomata, hydathodes, and apparent free spaces, whereas, when applied to the roots, it enters through the youngest root cells. In both cases, it is mobilized, through apoplastic and symplastic pathways, to the vascular bundles for translocation by Fe transporters or by phagocytosis, pinocytosis, or endocytosis, can accumulate in the cell. This accumulation results in the supply of Fe for the required metabolic processes and stimulation of the plant antioxidant system [120,121].

Applications of Fe nanofertilizers synthesized from leonardite and containing ferrihydrite in their structure have produced a slow and continuous supply of Fe to soybean plants under calcisol conditions (pH 7.9) [122], while the application of nanoiron (15 mg Fe/kg) to soybean grown in slightly alkaline soil (pH 7.81) induced an increase in shoot-and-root fresh and dry weights, as well as higher leaf numbers, due to a high nutrient-use efficiency with respect to $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$

and Fe-EDDHA [123]. Similarly, under calcisols, cumin (*Cuminum cyminum* L.) plants responded positively to foliar applications (before flowering) of 1 g/L nanochelated Fe, which improved the yield and plant height [124]. Contrastingly, the application of 10% diammonium phosphate, nanocoated with KFeO_2 and urea and 25% K_2SO_4 , to wheat under calcisol-alkaline soil conditions appears to be promising, having improved the growth and development and increased the Fe uptake in plants [125]. These authors pointed out that the positive responses may have resulted from the nanocoating causing a slow release of nutrients. In another case, foliar nutrition with Zn oxide (ZnO) NPs (1000 mg/L) and ascorbic acid (250 mg/L) in sweet potato plants (Beauregard) grown in calcisols (pH 7.19–7.77) promoted higher Fe, Mn, P, and Cu contents and improved tuber yields, perhaps by stimulating the root area, phytohormone synthesis, and ROS scavenging, possibly triggered by the high carbonate content (10.8–11.3%) in the soil [126]. The application of green Fe NPs to the soil increases Fe release and thus its uptake, as well as the growth and photosynthetic pigment content of sorghum plants. This behavior is due to Fe polyphenol complexes (from green NPs) and the reduction of Fe^{3+} to Fe^{2+} , causing high Fe availability in the soil while reducing the precipitation of Fe oxides-hydroxides in the roots [127].

Using nanotechnology in conjunction with humic substances may be a promising way of reducing Fe-deficiency problems in calcisols and alkaline-reactive soils, in addition to presenting low to no toxicity levels in the environment and maximizing the physiological changes caused by humic substances [83]. In this sense, the foliar application of Fe oxide NPs supplemented with humic acid (Fe-NPs-HA) to geranium plants grown in alkaline soils (pH 7.66) improved their yield and stimulated metabolite accumulation as a result of a higher Fe content, which caused an increase in cellular energy and activation of the enzyme nitrate reductase. This prevents alterations caused by Fe deficiency to a greater extent than sprays of EDDHA, ferrous sulfate, and even Fe NPs [31]. Similarly, foliar applications of fulvic substances in combination with Fe in the form of nanoferrihydrate to spinach improved the total leaf Fe and chlorophyll contents, and the plant fresh weight [32]. This combination allowed for a faster penetration into the leaf. In plant tissues, these substances can induce morphological changes and affect the activity related to nutrient uptake by the plasma membrane [83], which is maximized by Fe at the nanometer scale [31]. The use of zero-valent nanoiron could be an alternative strategy for managing Fe nutrition in these soils, as opposed to FeSO_4 and Fe-EDDHA applications, for improving grain Fe concentrations [128].

The foliar application of $\gamma\text{-Fe}_2\text{O}_3$ nanomaterials to soybean has been presented as a sustainable and highly efficient strategy for mitigating Fe deficiency; this nanomaterial induces significantly greater growth than Fe-EDTA by increasing the biomass, nodules, N fixation, yield, and free amino acid content in the seed [129]. These positive effects may be due to an increase in energy supply, reduction in ROS, and phytohormonal modulation. However, it will be necessary to apply this technology at the field level in calcisols soils. It should be noted that through the reduction of Fe NPs through the Maillard reaction, efficient, and environmentally friendly systems that are highly tolerant to alkaline environments have been developed [130].

Combinations of these strategies have been reported as being suitable tools for improving plant Fe nutrition by promoting Fe availability in calcisols [131–139] [Table 1]. Plant chlorosis can be alleviated by organic management practices, coupled with proper water management. This method reduces the soil pH, which affects the

Table 1: Summary of research on the combination of strategies for ferric nutrition management in calcareous soils.

Strategies	Findings	References
Biochar impregnated with Fe.	Increases Fe availability, Fe content, and fresh and dry weight of the soybean plant.	[131]
Foliar spraying of Fe + no-tillage system or flattening soil without the use of mulch.	Promotes the FRO activity of the root system, alleviating chlorosis on bread wheat plant.	[132]
Manure applications plus aeration system.	Improve soil Fe and its use in the leaves of pears plants.	[133]
Irrigation with carbonated water.	Improves the morphological development of the plant and nutraceutical quality of the grape berry.	[134]
Foliar and basal application of FeSO ₄ together with citric acid sprays and applications of enriched organic compounds	Yield promotion, improved availability of Fe, in groundnut.	[135]
NPK in combination with Fe (as enriched farmyard manure) and <i>Bacillus</i> .	Improve peanuts yield.	[136]
Trunk injection and FeSO ₄ .	Increased chlorophyll and active iron content in leaves, improving weight, volume, and yield on peach trees.	[137]
Biochar with foliar chelate and nano chelate.	Induces positive response of vegetative attributes and photosynthetic pigments of spikenard plants.	[138]
Inoculation (bacterial strains) and grafting.	Increased plant growth, leaf area, and iron of peach plants.	[139]

availability, mobilization, and uptake mechanisms of Fe [132-136]. It is possible that these practices can supply Fe to plants in the form of natural chelates, slowly and continuously [136], generating an increase in active Fe in the plant tissues. This increase, mainly in the apoplast, alters the source-sink distribution rate, alleviating IDC [137].

However, because agroecosystems are network-responsive systems [140], it is necessary to verify the pH and the Fe, carbonate, and OM contents of calcisols, in addition to determining the crop(s) of interest for an adequate selection of the most relevant strategies for enhancing interactions for sustainable Fe nutrition management.

5. CONCLUSION

In this review, we have summarized the present knowledge concerning calcisol conditions, including management strategies for minimizing the prevalence and/or incidence of IDC in crops. These included grafting, intercropping, the use of fertilizers and chelates (both conventional and novel), organic molecules, engineering, and nanomaterials. Each strategy has its complexities, but each offers the sustainable management of Fe nutrition in these types of soils.

The presented studies demonstrated how modifications are carried out at both the structural and functional levels in the soil-plant system, in terms of promoting Fe nutrition, increasing its bioavailability, stimulating microbiome activity, improving enzymatic activity, and stabilizing Fe for adequate absorption, transport, and assimilation.

Signaling molecules, such as hydrogen sulfide and nitric oxide, have been studied as alternatives to Fe nutrition, but need to be tested under calcisol conditions. In this context, we recommend implementing one or more strategies to improve plant growth and development in calcisols by reducing IDC, generating better-quality food, and improving soil sustainability.

6. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to the conception, design, acquisition of data, analysis, and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be an author as

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