REVIEW

Carbon Monoxide Modulates Auxin Transport and Nitric Oxide Signaling in Plants under Iron Deficiency Stress

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ABSTRACT

Carbon monoxide (CO) and nitric oxide (NO) are signal molecules that enhance plant adaptation to environmental stimuli. Auxin is an essential phytohormone for plant growth and development. CO and NO play crucial roles in modulating the plant's response to iron deficiency. Iron deficiency leads to an increase in the activity of heme oxygenase (HO) and the subsequent generation of CO. Additionally, it alters the polar subcellular distribution of Pin-Formed 1 (PIN1) proteins, resulting in enhanced auxin transport. This alteration, in turn, leads to an increase in NO accumulation. Furthermore, iron deficiency enhances the activity of ferric chelate reductase (FCR), as well as the expression of the Fer-like iron deficiency-induced transcription factor 1 (FIT) and the ferric reduction oxidase 2 (FRO2) genes in plant roots. Overexpression of the long hypocotyl 1 (HY1) gene, which encodes heme oxygenase, or the CO donor treatment resulted in enhanced basipetal auxin transport, higher FCR activity, and the expression of FIT and FRO2 genes under Fe deficiency. Here, a potential mechanism is proposed: CO and NO interact with auxin to address iron deficiency stress. CO alters auxin transport, enhancing its accumulation in roots and up-regulating key iron-related genes like FRO2 and IRT1. Elevated auxin levels affect NO signaling, leading to greater sensitivity in root development. This interplay promotes FCR activity, which is crucial for iron absorption. Together, these molecules enhance iron uptake and root growth, revealing a novel aspect of plant physiology in adapting to environmental stress.

KEYWORDS

Carbon monoxide; nitric oxide; auxin; iron deficiency; signal molecule; plants

Abbreviations

ABA	Abscisic acid
bHLH	Basic helix-loop-helix
CO	Carbon monoxide
FCR	Ferric chelate reductase
FIT1	Fer-like iron deficiency-induced transcription factor 1
FRO2	Ferric reduction oxidase 2

GSH   Glutathione
IRT   Iron-regulated transporter gene
HO   Heme oxygenase
hy1   Long hypocotyl 1
NADH   Nicotinamide adenine dinucleotide
NO   Nitric oxide
NR   Nitrate reductase
PIN1   Pin formed 1
PIN2   Pin formed 2
RNS   Reactive nitrogen species
XOR   Xanthinine oxidoreductase

1 Introduction

Iron is a micronutrient indispensable for the growth and development of plants. It plays a pivotal role within plant organisms [1], encompassing crucial functions such as chlorophyll synthesis [2], DNA replication [3], nitrogen metabolism [4], and antioxidant defense [5]. Insufficient iron levels can detrimentally impact photosynthesis, resulting in diminished growth and reduced yields [6]. Furthermore, iron deficiency impedes fundamental biological processes, including cell division and the development of new tissues [7]. Iron deficiency also exerts adverse effects on protein synthesis in plants [8]. Iron plays a pivotal role in enabling plants to mitigate oxidative damage [9] and is essential for root development and nitrogen fixation—processes intimately linked to the growth and viability of plants [10]. Consequently, the investigation of how plants adapt to iron deficiency stands as a matter of paramount significance in the realm of academic research.

CO and NO hold substantial significance in the physiological reactions of plants to iron deficiency (ID). Recent research has elucidated the mechanisms by which CO and NO contribute to plants' responses to ID. Under conditions of ID, an increase in heme oxygenase (HO) activity, responsible for CO generation, has been observed [11]. The increased CO production subsequently affects auxin transport by altering the polar subcellular distribution of PIN1 proteins. Additionally, NO has a discernible impact on auxin signaling. This phenomenon was observed in *Arabidopsis* plants subjected to a 12-h period of cadmium-induced stress, wherein a reduction in the accumulation of PIN1 protein and the stability of AXR3/IAA17 protein (which acts as an inhibitor of IAA signaling) were observed [12]. The occurrence of ID has been associated with an elevation in nitric oxide (NO) levels and an upregulation of FCR activity. FCR is a key enzyme involved in iron absorption, as substantiated by experiments conducted on pear trees [13]. Furthermore, the expression of critical genes associated with iron homeostasis, including Fer-like ID-induced transcription factor 1 (FIT), has also been upregulated [14]. Recent research has underscored that the absence of FIT function leads to a reduced capacity of plants to efficiently uptake iron, ultimately culminating in their mortality [15,16].

In recent times, there has been an increasing fascination among researchers regarding the exploration of signal molecules and their pivotal functions in enabling plants to adapt to a multitude of environmental stressors. Within this realm of signal molecules, carbon monoxide (CO) and nitric oxide (NO) have emerged as indispensable regulators, orchestrating the plant's responses to a wide spectrum of environmental stimuli [17]. Moreover, auxin, a widely recognized phytohormone, plays a pivotal role in regulating the growth and development of plants. There has been a lot of interest in learning how CO, NO, and auxin interact to control how plants react to environmental stress, especially iron deficiency (ID) [18].

For many decades, CO has been predominantly recognized as a toxic gas, presenting significant harm to both humans and animals when present in elevated concentrations. Likewise, NO has primarily been the subject of research within the realm of mammalian physiology and pathology. Elevated levels of CO have been found to significantly hinder cellular activity and increase the responsiveness of cancer cells to chemotherapy [19]. In mammals, NO functions as a widely distributed signaling molecule, that assumes multifaceted roles encompassing vasodilation, platelet function, neurotransmission, immunity, and metabolism [20]. On the contrary, in the field of botany, there has been a scarcity of research on the functions of CO and NO, leading to an incomplete comprehension of their roles. Nonetheless, recent studies have unveiled the intricate and multifarious roles of CO and NO in plant biology. In plants, CO and NO primarily regulate plant iron homeostasis through their ability to induce the expression of ferritin transcription factors [21]. These molecules have shown their importance in orchestrating different facets of plant biology, including the regulation of plant growth, development, and responses to an array of environmental stressors such as drought, salinity, high temperature, cold, nutrient deficiency, and exposure to heavy metals.

The purpose of this review is to delve into the interactions among NO, CO, and Auxin, aiming to unveil novel mechanisms of their involvement in plant physiological regulation. While past research has elucidated the significance of these signaling molecules in plant physiological processes, further investigations are required to understand how they influence each other and collaborate at different growth stages. The objective of this paper is to consolidate existing literature, emphasizing the pivotal roles of NO, CO, and Auxin throughout the entire course of plant growth and development. Additionally, we aim to introduce new insights into how they collectively govern plant adaptability and growth performance. Through this review, our intention is to inspire future research and lay the foundation for further exploration and innovation in the field of plant biology.

2 The Roles of Carbon Monoxide, Nitric Oxide, and Auxin in Plant Physiology

Within the field of plant physiology, there has been a significant surge in attention towards small-molecule compounds like CO, NO, and auxin in recent times [22]. As signaling molecules, they play pivotal roles in plant growth and development and how plants respond to environmental stresses, nutrient uptake, and root development [23]. Iron, a crucial element for plants, is central to processes such as chlorophyll synthesis and cellular respiration [24]. CO finely tunes plant iron metabolism, ensuring an adequate supply of this essential element and contributing to plant health [25].

NO, acting as a signaling molecule, plays a pivotal role in regulating plant growth and development [26]. It regulates cell growth, differentiation, and organ formation, enabling plants to adapt to environmental stressors such as drought, diseases, and salt stress [27]. This regulatory mechanism equips plants to cope with various challenges, safeguarding their survival and growth [24].

Additionally, the plant hormone auxin influences root development [28], organ formation [29], and overall growth [30]. Small molecules like CO and NO fine-tune auxin transport and distribution, enhancing plant adaptability and survival [31].

In summary, CO and NO's interplay is central to coordinating and regulating critical physiological processes in plants, ensuring their ability to thrive and adapt to diverse conditions while managing stressors, ultimately contributing to plant health and adaptability [24,25].

2.1 Carbon Monoxide

In plants, CO can trigger a series of physiological responses and has thus become an important signaling molecule. It has a positive impact on seed germination, root development, and stomatal closure. Furthermore, CO typically enhances the plant's resistance to abiotic stress by strengthening the antioxidant defense system [32]. In plants, endogenous CO is generated through HO converting heme into biliverdin IXa (BV), CO, and

free iron (Fe^{2+}) [33]. This conversion occurs through a series of reduction and oxygenation reactions, which take place in the presence of molecular oxygen, with electrons supplied by NADPH [34] (Fig. 1). The involvement of HO in regulating iron homeostasis may be considered a pivotal factor in the modulation of cell death [22]. In *Arabidopsis*, four *HO* genes have been characterized and studied, including *HY1*, *HO2*, *HO3*, and *HO4*. However, it has been determined that only the enzyme encoded by the *HY1* gene is responsible for CO production [35].
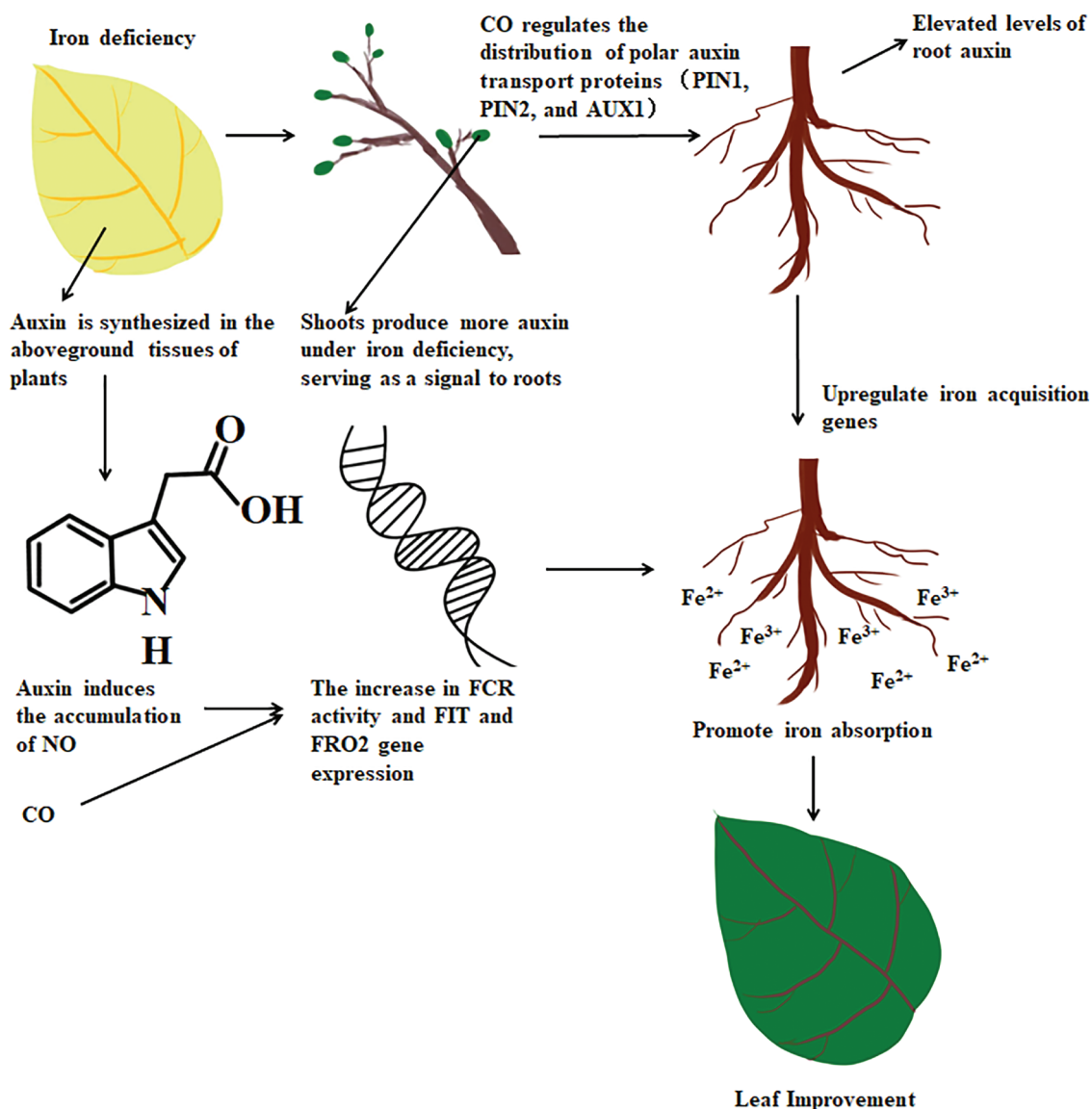
Figure 1: Pathways of CO generation in plants

2.2 Nitric Oxide

NO is a gaseous signaling molecule that functions as a molecular messenger in both animal and plant cells. In eukaryotes, it is typically produced endogenously, whereas in higher plants, its production is mediated by a number of redox pathways [36]. NO has a crucial role in regulating several growth and

developmental processes in plants, such as seed germination and flowering. Additionally, it is involved in the plant's response to environmental stresses such as drought, high temperature, and salinity [37]. It is necessary for the symbiotic relationship between legumes and nitrogen-fixing bacteria [38]. According to recent studies, NO and ethylene signals enhance salt-alkali resistance in tomatoes, with NO acting as an upstream regulatory factor within the ethylene signaling pathway [39]. In *Arabidopsis*, the shoot apical meristem serves as a crucial organ for sensing high temperatures, as it exhibits a rapid release of NO in response to heat stress. Following that, the S-nitrosoglutathione (GSNO) molecule, which is a relatively stable active molecule of NO, functions as a mobile signaling molecule [40]. NO is also transported from the aboveground part of the plant to the roots through the vascular bundle [41]. This transport process subsequently initiates the response to high temperatures and establishes heat tolerance over the entire plant [42]. Furthermore, researchers have explored the impact of melatonin (MT) on pepper plants' responses to salt stress (SS) and ID, revealing potential signal crosstalk between NO and H2S in MT-induced tolerance [43].

2.3 Auxin

Auxin is an endogenous hormone characterized by the presence of an unsaturated aromatic ring and an acetic acid side chain. It is a small molecule with a low molecular weight widely present in plants, playing key roles in several physiological processes, including growth stimulation, the regulation of plant organ formation, stem elongation, lateral root generation [44], fruit development [45], and response to environmental stimuli. Even at low concentrations, auxin can regulate gene expression through the activation of specific transcription factors and proteins [46]. Recent research has revealed the role of iron in regulating root hair growth under phosphorus deficiency conditions; iron may influence auxin signal transduction by modulating vacuolar transport [47]. Auxin can be synthesized via two distinct pathways: tryptophan (Trp)-dependent and non-Trp-dependent pathways [48,49]. The Trp-dependent auxin synthesis pathways encompass a range of intermediates that give rise to pathways such as the indole-3-pyruvic acid (IPA) pathway, tryptamine (TAM) pathway, indole-3-acetonitrile (IAOx) pathway, and indole-3-acetamide (IAM) pathway [48,50]. In the IPA pathway, the conversion of Trp into indole acetic acid (IAA) occurs through a two-step process. Initially, Trp forms IPA, and then, under the action of a specific dehydrogenase, it oxidizes into indoleacetic acid. In the TAM pathway, Trp is first transformed into TAM by tryptophan decarboxylase [51]. Then, through a series of enzymatic reactions, TAM is transformed into indole-3-acetaldehyde (IAAld), which is ultimately oxidized into IAA by a specific dehydrogenase. In the indole-3-acetaldehyde oxime (IAOx) pathway, Trp is initially transformed into IAOx [52], IAOx is further converted into indole-3-acetonitrile (IAN), and finally, IAN is transformed into IAA by nitrilase [53]. In the IAM pathway, Trp is first converted into IAM and subsequently into IAA [48,54]. Although non-Trp-dependent auxin synthesis pathways have been confirmed in maize and *Arabidopsis* yet, their specific mechanisms remain unclear. This auxin synthesis pathway plays a crucial role in the different developmental stages of various species [50].

As a signaling molecule, auxin's signal transduction pathway is relatively simple. Most auxins form a receptor-enzyme complex by binding to their respective receptors [55], which leads to the direct hydrolysis of specific transcription inhibitors, thereby activating downstream auxin response genes [56]. Additionally, it has been suggested that there may be a potential interaction among CO, NO, and auxin signaling in plants under ID conditions [57]. NO negatively regulates auxin signal transduction by inhibiting the degradation of the IAA17 protein [58]. Increasing evidence indicates that NO and NO-mediated S-nitrosylation play a vital role in auxin signal transduction. These components are involved in various aspects of auxin-induced cellular processes, such as the cell division cycle, the formation of primary roots, lateral root development, adventitious root formation, and root hair development [59].

3 Nutrient Deficiency in Plants

Plants require a diverse array of nutrients to facilitate their growth and ensure their survival. These nutrients can be categorized into two main groups: non-mineral and mineral [60]. Hydrogen, carbon, and oxygen are classified as non-mineral, whereas nitrogen, phosphorus, potassium, calcium, magnesium, sulfur, iron, boron, copper, chloride, manganese, molybdenum, and zinc minerals are obtained from the soil through the roots [61]. Plant development can be limited in natural soils due to the scarcity of certain mineral nutrients. The ability of plants to perceive alterations in nutrient levels is a phenomenon that remains inadequately elucidated at the molecular level. Recent studies show the importance of NO and CO in nutrient absorption by plants [62].

During plant growth, auxin, through ARF, regulates nutrient absorption and distribution in plants, leading to the formation of distribution centers where auxin concentration is high [50,63]. A study found that IAA regulates iron chelate reductase and iron transport genes, impacting iron uptake by cucumber roots [64]. This suggests IAA is involved in the regulation of root responses to iron stress [65]. In mild nitrogen deficiency, *Arabidopsis thaliana* produces local auxin to boost lateral root growth, thus enhancing plants' nutrient absorption [66]. Phosphorus deficiency in plants results in primary root growth stagnation and increased auxin content in lateral root formation [67]. In *A. thaliana*, *OsAUX1* regulates auxin transport from the root tip to the differentiation zone [68]. In rice, *OsPIN1b* responds to phosphorus deficiency by regulating the activity of the root tip meristem, and participating in the elongation of rice SR (seminal root) [69,70].

3.1 Iron Deficiency

Iron (Fe) plays a crucial role in plant growth, particularly in chlorophyll synthesis. However, the solubility of crystalline Fe minerals in soil is typically low [71]. The primary reason for iron deficiency in plants is the insolubility of iron (III) oxides in the soil [72]. The main factors that alter the solubility of iron in the soil include redox processes and the presence of chelators [73]. Plants adopt two distinct strategies for iron acquisition (Fig. 2): Enhancing the reduction of ferric iron in the roots to promote absorption in non-graminaceous plants such as *Arabidopsis*, and employing plant-specific iron transporters in graminaceous plants like barley [74]. The strategy I adopted by dicotyledonous plants to acquire iron from the external medium is based not only on the reduction of Fe^{3+} but also involves the acidification of the external medium and the secretion of several compounds, including organic acids and phenols. In most non-graminaceous plants, key transcription factors such as FER in tomato and its homolog FIT in *Arabidopsis* are responsible for the activation of FCR. This process induces soil acidification around roots, hence facilitating the transport of iron by the iron-regulated transporter gene (IRT) into the roots. Recently, a novel iron transporter, ZmIRT2, was discovered in maize, providing additional support to the previously reported research findings [75]. Remarkably, despite possessing distinct iron absorption systems, both *Arabidopsis* and rice employ a dual-molecular module (FIT-bHLH Ib) to initiate the iron uptake process under ID conditions [76]. Researchers have elucidated that bHLH transcription factors play a pivotal role in enabling plant cells to establish a photoprotective mechanism [77]. This mechanism, in turn, induces alterations in chloroplast morphology, thereby mitigating the generation of deleterious reactive oxygen species (ROS) while concurrently facilitating the restoration of photosystem II functionality [78]. These research findings unveil a compelling convergence: under iron stress, both of these plant species harness analogous molecular modules to govern iron absorption. This strategic response enhances their resilience to environmental stressors by modulating chloroplast status.
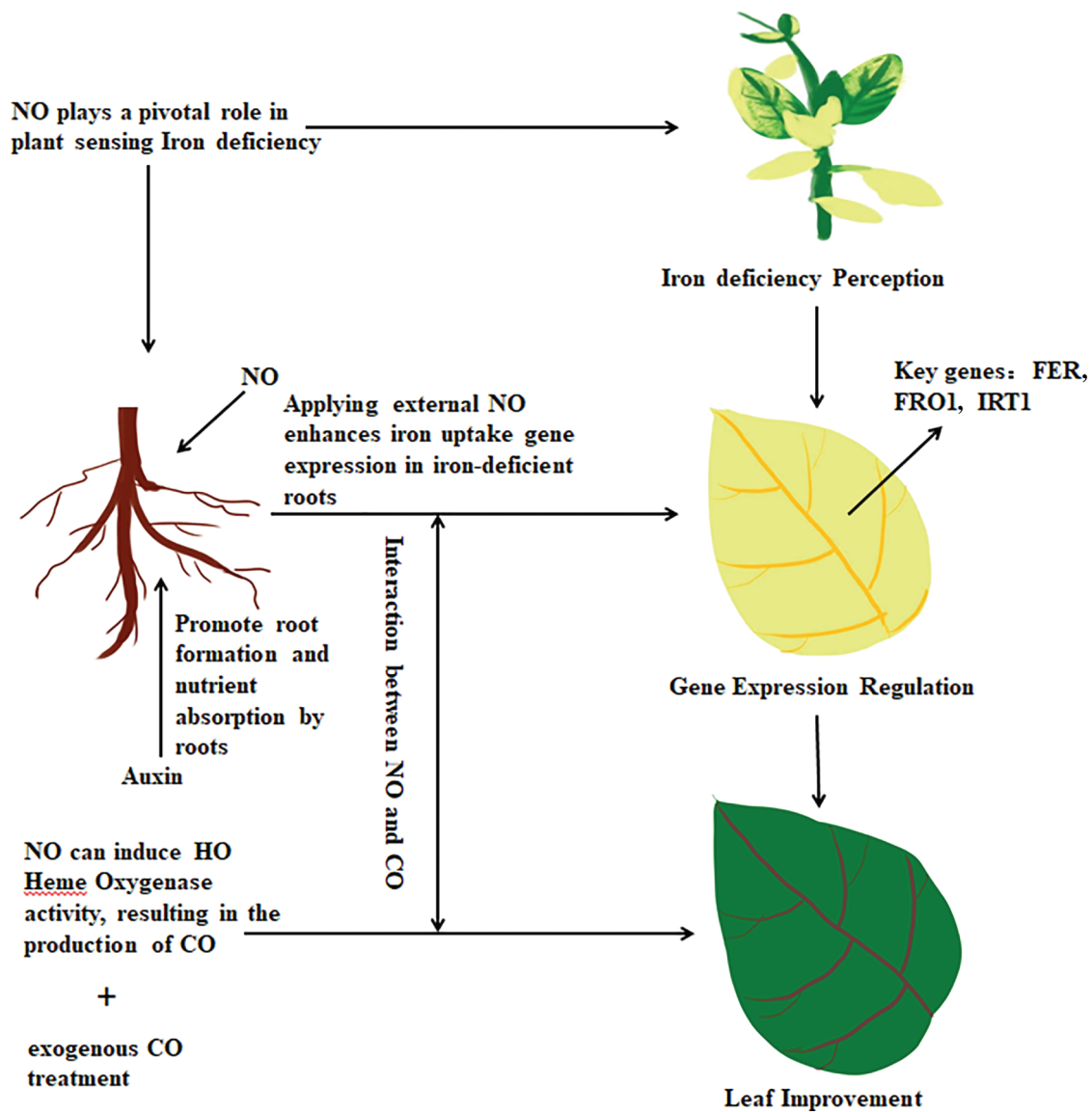
Figure 2: Strategies for Iron acquisition and adaptation in plants

3.2 The Roles of Carbon Monoxide and Nitric Oxide in Plant Response to Iron Deficiency

Numerous research state that NO is essential for plants to sense ID and controls the uptake of Fe. ID causes NO to build up, and exogenous NO applied to tomato roots lacking in iron boosts the expression of iron-uptake-related genes. These genes include the divalent cation transporter IRT1, the transcription factor FER, and the iron chelate reductase FRO1 [79]. Previous research has indicated that elevating NO levels in rice promotes the development of lateral roots and increases HO activity [80], hence increasing the plant's resistance to ID [57]. Cucumber adventitious roots require the formation of CO, which is produced when NO stimulates the action of the HO enzyme [81].

Both NO and CO have been identified as crucial regulators of plant cell metabolism, participating in various stages of plant development, including maturation, seed dormancy and germination, hypocotyl elongation, and root development [82,83]. Research has indicated that ID elevates endogenous CO levels

in *Arabidopsis* [84]. In *Populus*, the expression of PtIRT1 significantly increases during iron deficiency [85]. The same is true in *Arachis hypgaea*, with a significant increase in the expression of *AhIRT1* during iron deficiency [86]. Additionally, exogenous CO application to iron-deficient *Arabidopsis* has been found to mitigate leaf chlorosis and increase chlorophyll accumulation, iron levels, and NO accumulation in the root tips.

Both NO and CO are required for FIT expression and FRO activity in plants under ID [87]. NO is reported to regulate target protein stability during the hormone response. NO can also stabilize the FIT protein in *Arabidopsis* [88]. However, it is unknown whether CO directly controls FIT and its associated protein degradation during ID or whether it requires interaction with the NO signal. In regulating environmental stress, over-accumulation of NO leads to the generation of reactive nitrogen species (RNS) damage, initiating the modification of proteins through S-nitrosylation, which plays a role in plant sensing abscisic acid (ABA) [89,90]. It is reported that CO can reduce RNS damage in recalcitrant seed germination [91]. Further work is required to determine whether the FIT protein undergoes post-translational modification by NO-mediated S-nitrosylation or if CO can affect this alteration. These studies indicate that the interaction between CO, NO, and their crosstalk may play important roles in improving plant tolerance to ID (Fig. 3).

When the exogenous concentration of CO is 8 mM in an Fe-deficient medium, it has been observed that there is an increase in the accumulation of iron in *C. mydomonas reinhardtii*, which subsequently prevents the yellowing induced by ID and promotes the accumulation of chlorophyll. Additionally, the expression levels of FOX1, FTR1, and iron redox protein were up-regulated under these conditions. This upregulation further enhances the accumulation of NO in the plant. However, it should be noted that the presence of the NO scavenger may inhibit the effects of NO accumulation [92]. Cyg11, a Guanylate Cyclase in *C. reinhardtii*, has been suggested as a potential CO sensor and is believed to be involved in the CO-dependent recovery pathway that is activated under iron-deficient growth conditions [93]. AtHO1's catabolism of iron homeostasis is linked with the production of CO. The CO generated by AtHO1 catalysis may promote the transport of iron in iron-containing components and increase its bioavailability to tissues that require iron [94]. Additionally, the application of an exogenous concentration of 50 μM CO can promote chlorophyll accumulation and greening in *A. thaliana* [95]. Similar observations were also found in corn [96], indicating that CO plays a certain role in maintaining Fe homeostasis in plants.

3.3 Role of Auxin during Iron Deficiency

Previous studies have indicated that the plant hormone auxin stimulates FCR activity in response to ID. Exogenous introduction of auxin can increase FCR activity as well as FIT and FRO2 expression [87]. Such effects could be impaired by auxin transport inhibitor NPA treatment or in the presence of auxin transport mutant, such as aux1-7. In contrast to wild-type plants, the *Arabidopsis* yuc1 mutant, which exhibits elevated auxin levels, showed higher FCR activity under ID conditions [57]. This suggests that the transportation of auxin from the shoot to the root is necessary for FCR activity and iron uptake during ID [97]. Sucrose can increase root-ward auxin transport, and the sucrose accumulation induced by Fe deficiency acts along with auxin in transmitting ID signals in *Arabidopsis* [98]. Scholars recent investigations have shown that Fe stimulates the elongation of lateral roots through the upregulation of the auxin influx carrier AUX1 expression, increasing the auxin content at the tips of lateral roots, and serving as a prerequisite for lateral root elongation [99]. According to a recent study, it has been found that Fe may regulate vacuolar transport, hence affecting auxin's signal transduction [47]. Guo et al. have studied the role of PbrSAUR72 in regulating the response of pear trees to ID and found the modulation of auxin signal transduction promoted iron uptake and reduced oxidative stress in those species [100].
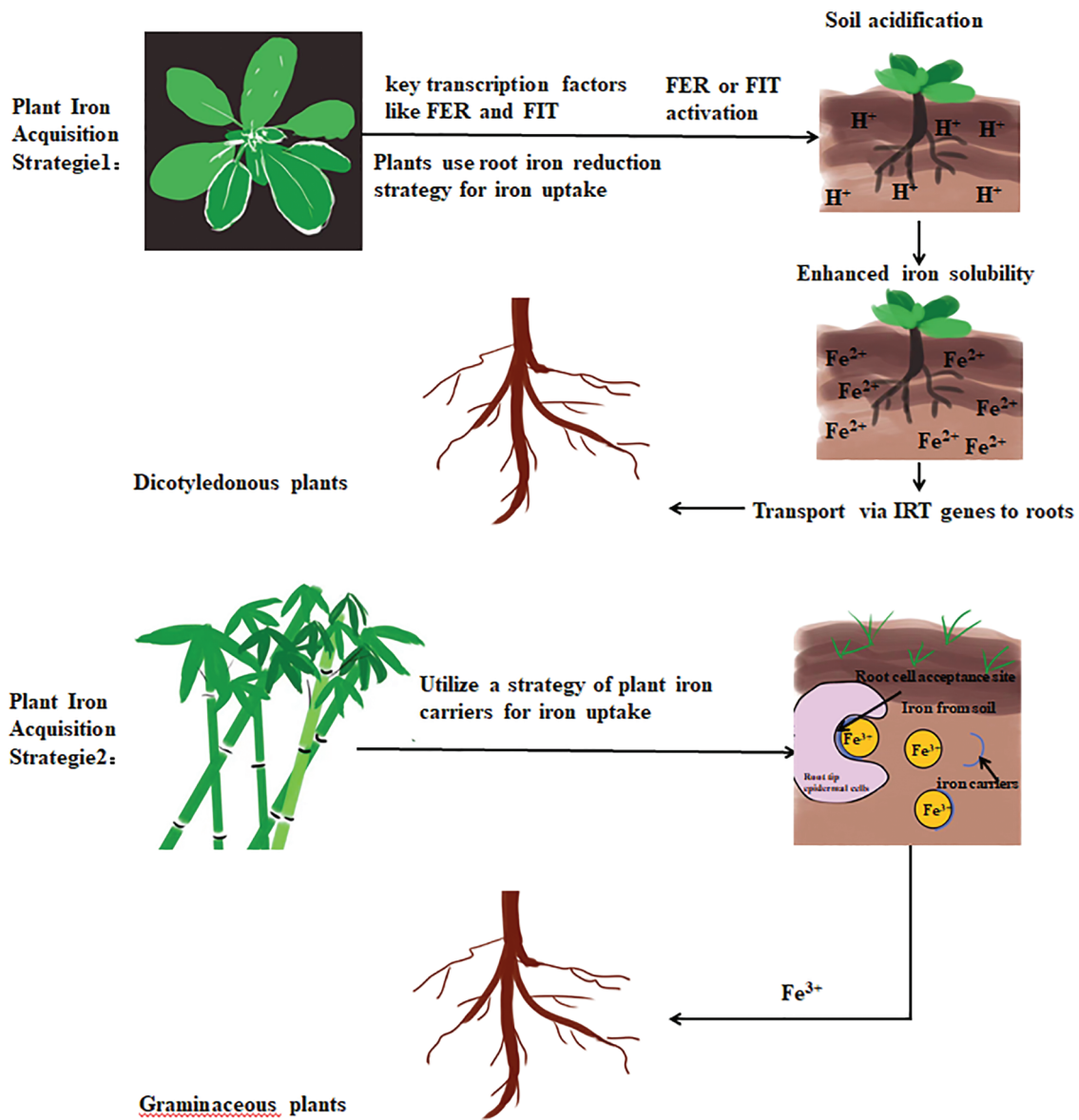
Figure 3: Interplay of NO and CO in enhancing plant tolerance to iron deficiency

In summary, both NO and CO act as signaling molecules to enhance FCR activity and facilitate Fe uptake during ID in plants. Auxin transmission from the shoot to the root triggers the biosynthesis of NO, which further upregulates FCR activity to enhance Fe uptake. During this process, ID also induces HY1 activity, which is responsible for CO biosynthesis [22,101]. It is possible that CO promotes basipetal polar auxin transport into the root tip by altering the asymmetric accumulation of PIN and AUX proteins. Further investigations are needed to gain a comprehensive understanding of the mechanisms behind the interaction between CO and the NO signal in the regulation of the asymmetric stability of PIN and AUX proteins, which are crucial for auxin transport during iron deprivation (Fig. 4).
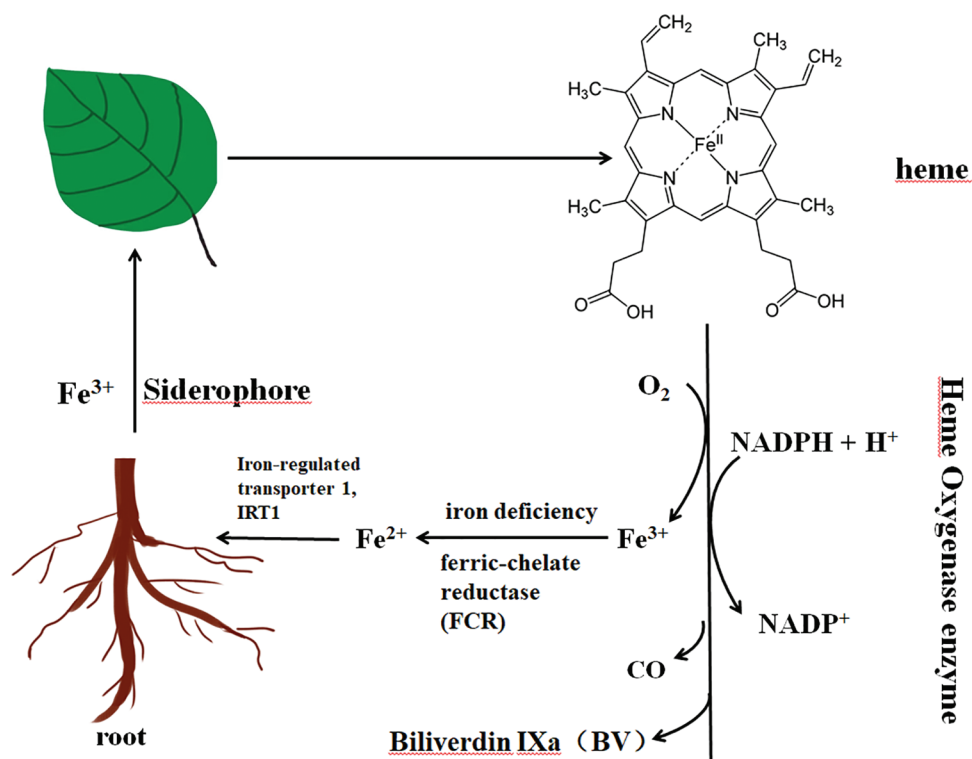
Figure 4: CO-mediated signaling pathway model in plants under ID

3.4 The Connection between CO, NO, and Auxin in Plant Responses to ID Stress

Iron deficiency triggers an increase in HO activity, leading to the production of CO. CO, in turn, enhances the expression of key genes such as FRO2 and FIT, promoting iron reduction and uptake. In *Arabidopsis*, CO alters the asymmetric accumulation of PIN1 and PIN2, facilitating polar auxin transport in the root tip and elevating auxin levels. Consequently, this upregulates the expression of FIT1 and FRO2 genes, enhancing iron absorption [84].

Concurrently, the accumulation of NO also promotes an upregulation of FCR activity, a crucial step in iron absorption. The levels of NO significantly increase under iron-deficient conditions, which can be achieved through the enhanced activity of enzymes such as nitric oxide synthase (NOS) [102]. NO exerts a significant influence on Auxin signal transduction, possibly achieved by reducing the accumulation of PIN1 protein and stabilizing the AXR3/IAA17 protein (the latter being an inhibitor of the Auxin signal), contributing to an increased sensitivity of the roots to Auxin.

Auxin plays a crucial role in root elongation and branching, which is closely related to iron absorption in plants. In cucumbers, NO and Auxin can interact to induce the formation of adventitious roots [103]. Furthermore, Auxin can also induce the accumulation of NO, thereby enhancing FCR activity. Therefore, the synergistic interactions among CO, NO, and Auxin regulate a complex array of physiological processes under iron deficiency stress. These processes include iron reduction and uptake, root development, and Auxin signaling. CO, NO, and Auxin may interact by influencing different signaling pathways, thus co-regulating plant responses to iron deficiency. This may involve affecting plant hormone signaling pathways such as gibberellin, ethylene, and abscisic acid, as well as activating relevant signaling protein kinases (MAPK), among others [104]. CO and NO can also work together with Auxin to enhance the plant's antioxidant defense system. This can be achieved by regulating the expression and activity of antioxidant enzymes, thereby alleviating the oxidative stress caused by iron deficiency.

4 The Use of CO, NO, and Auxins in Plants with Iron Deficiency

CO, NO, and Auxin are crucial signaling molecules that regulate iron absorption in plants, leading to a multitude of effects, enhancing plant resilience, and increasing crop yield [105]. Here are the multiple applications of these signaling molecules in plant iron metabolism:

Adaptation to various environmental stressors [106]: The application of CO, NO, and Auxin can bolster a plant's ability to adapt to a wide range of environmental stressors, including drought, high temperatures, pests, and soil quality issues. By optimizing iron uptake and distribution, plants are better equipped to cope with these pressures, reducing crop losses, ensuring stable agricultural yields, and contributing to the protection of ecosystems.

Enhancement of nutrient utilization efficiency: CO and NO promote the absorption of iron by plants while simultaneously reducing the demand for other nutrients in crops [107]. Improvement of fruit quality [108]: CO, NO, and Auxin have a significant impact on the size, shape, and sugar content of fruits through their influence on iron absorption and distribution [109]. This is crucial for the quality and commercial value of fruits, vegetables, and nuts. Adjusting the levels of these signaling molecules can improve the overall quality of agricultural produce, making it more competitive in the market. Enhancement of the immune system: CO, NO, and Auxin not only affect iron uptake but also play a role in strengthening a plant's immune system. They enhance resistance to pathogens [110], reducing the need for pesticides. This is essential for maintaining ecological balance and environmental protection.

In summary, the application of CO, NO, and Auxin in plant iron metabolism offers multiple benefits, including increased crop yields, improved food quality, reduced environmental stress, and a contribution to sustainable agriculture. In the future, research and application of these signaling molecules are expected to continue driving innovation and advancements in the field of agriculture.

5 Conclusions

Grasses (*Poaceae*) and non-grass plants employ different strategies when facing iron deficiency. Grasses have the ability to directly uptake trivalent iron ions, while non-grass plants need to employ FCR to convert trivalent iron ions in the soil into divalent iron ions for absorption. The interaction between CO, NO, and auxin enhances FCR activity to cope with iron deficiency stress in plants. ID triggers an increase in HO activity, leading to the production of CO, which, in turn, influences auxin transport by modulating the subcellular distribution of PIN1 proteins. Simultaneously, NO levels surge, enhancing FCR activity and upregulating the expression of crucial genes in plant roots, such as FIT and FRO2. Auxin promotes root growth and, in turn, iron absorption in plants while also stimulating NO accumulation, thereby boosting FCR activity. The process of iron uptake, facilitated by the interaction of CO, NO, and auxin, also relies on the expression of relevant genes, such as FER, FRO, and IRT, among others.

These recent discoveries collectively elucidate the interplay between CO, NO, and auxin, which collectively assist plants in adapting to ID stress. Beyond advancing our understanding of how plants respond to ID, these findings offer hope for potential applications in crop improvement, forestry production, and nutrient management strategies. The future holds exciting prospects for utilizing this knowledge to enhance plant productivity and resilience.

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