



# Insights into the physiological and molecular responses of plants to iron and zinc deficiency

Sushmita Singh<sup>1</sup> · Amritlal Singh<sup>1</sup> · Rinku Dey<sup>1</sup> · Mahesh Mahatma<sup>1</sup> · Kiran Reddy<sup>1</sup> · Anuj Kumar Singh<sup>2</sup> · K. Gangadhara<sup>3</sup> · Sujit K. Bishi<sup>4</sup>

Received: 31 July 2021 / Accepted: 30 September 2021  
© Indian Society for Plant Physiology 2021

**Abstract** Iron (Fe) and Zinc (Zn) are vital micronutrients for plants and their deficiency causes severe impairments in physiological and biochemical responses of plants. In response to stress emerging due to their deficiency, plants evolve different strategies to regulate the homeostasis network to ensure optimum Fe and Zn uptake. Fe and Zn biofortification of food crops offer a promising approach to alleviate the malnutrition caused due to their deficiency. However, the complex mechanism underlying the fine-tuned processes of mineral uptake, transport and accumulation in seeds involve a multitude of regulatory insights including alteration in root morphology, nutrient partitioning and subsequent accumulation in seeds mediated by different transporters, chelators, transcription factors and post transcriptional regulation which act in a coordinated manner to elicit responses in plants regulating Fe and Zn acquisition. These insights into the regulatory mechanisms will provide a better understanding for improving the Fe- and Zn- use efficiencies, maximization of Fe and Zn bioavailability in edible parts, the deficiency tolerance attributes and subsequent Fe and Zn- biofortification in plants.

**Keywords** Iron · Zinc · Root exudations · Hormonal crosstalk · ROS scavenging · Molecular regulations

## Introduction

A balanced human nutrition implies an optimum supply of all the essential nutrients required for overall growth and development. The alarming population demand for food security compromises with the nutritional security. This is due to greater emphasis on cereal production which are inherently low in Iron (Fe) and Zinc (Zn) content as well as bioavailability (Kumar et al., 2017, 2019, 2021; Singh & Mann, 2012; Singh et al., 2017; White & Broadley, 2009). Fe and Zn are the vital micronutrients required for human nutrition, the deficiency of which result in “hidden hunger” having adverse impacts on human health, particularly with severe impairments on the growth and development of children and pregnant and lactating women (Lal et al., 2020; Stein, 2010). Malnutrition due to Fe and Zn deficiency affects more than 2 billion people across the globe and is the major cause of deaths of children below 5 years of age (WHO, 2017). Fe and Zn are equally vital for plant growth and development. Zn plays the role of catalytic and structural cofactors for numerous enzymes (Hambidge et al., 2000). Zn also assists plants in withstanding salinity (Tolay, 2021) through reduction of Na accumulation and improving K/Na ratio and drought (Hassan et al., 2020) by improving cell membrane stability, osmolyte accumulation, stomatal regulation, photosynthesis and water use efficiency (Karim et al., 2012; Singh et al., 2018). On the other hand, Fe is the key component of electron transport chain and chlorophyll synthesis. Fe plays vital roles in most of the metabolic processes namely DNA synthesis,

✉ Sushmita Singh  
sushmitapantnagar@gmail.com

<sup>1</sup> ICAR-Directorate of Groundnut Research, Junagadh, Gujarat, India

<sup>2</sup> Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar, Banaskantha, Gujarat, India

<sup>3</sup> Central Tobacco Research Institute, Regional Station, Kandukur, A.P., India

<sup>4</sup> Indian Institute of Agricultural Biotechnology, Ranchi, Jharkhand, India

respiration, photosynthesis and nitrogen fixation (Rout & Sahoo, 2015; Singh et al., 2003).

The problem of Fe and Zn deficiency is ascribed to a number of factors including soil properties (Alloway, 2009; Singh et al., 2003, 2004), rhizosphere biological activities (Moreno-Lora et al., 2019), solubility and mobility of micronutrients in the soil for plant uptake (Bariya et al., 2015; Rengel, 2015) and nutrient interactions within the soil (Alloway, 2009; Singh, 1999, 2004). The plants exhibit different physiological and biochemical manifestations to cope with such nutritional stress like alteration in root architecture, release of root exudates in the rhizosphere, antioxidant defense activation, rhizospheric acidification, symbiotic associations with microbes in the soil, mobilization of stored nutrient pools, and enhanced nutrient uptake for translocation to the shoot (Sinclair & Kramer, 2012; Singh & Mann, 2012; Theocharis, 2014). The permeability of the root endodermis is also altered in response to nutrient stress, facilitating the uptake of specific nutrient ions through the vasculature (Barberon et al., 2016). The physiological and molecular mechanisms by which plants sense and respond to Fe and Zn deficiency is essential for cultivation of crops with better nutrient use efficiency (Zhang et al., 2019). This review, emphasize on the physiological and molecular insights of sensing, responding and signalling of Fe and Zn deficiencies and their regulations for improving the Fe and Zn homeostasis in plant system.

### Morpho-anatomical responses of plants during Fe and Zn deficiency

Fe is an essential component for cellular redox homeostasis of the cell mediating light reaction of photosynthesis, electron transport system of mitochondria, nitrogen assimilation and chlorophyll biosynthesis. Fe deficiency leads to decline in chlorophyll content resulting in chlorotic leaves, lower photosynthetic rate and subsequent yield reduction (Ramirez et al., 2011; Singh et al., 2003). The anatomical responses of plants to Fe deficiency include development of transfer cells in the root, subapical root hair from epidermal cells, swollen root tips and cluster formation in roots (Schikora & Schmidt, 2002; Schmidt et al., 2000). Zn is a crucial micronutrient involved in carbohydrate metabolism, cell proliferation and forms an integral component of vital enzymes including carbonic anhydrases (CA) and alcohol dehydrogenase (Adh) (Rehman et al., 2012; Rengel, 2015) and enhances photosynthesis and productivity (Singh et al., 2017). The exposure of plants to Zn deficiency results in declined plant growth, enhanced ROS accumulation and impaired photosynthetic electron transport (Bae et al., 2011).

## Physiological responses to Fe and Zn deficiency

### Fe deficiency responses in Strategy I and II plants

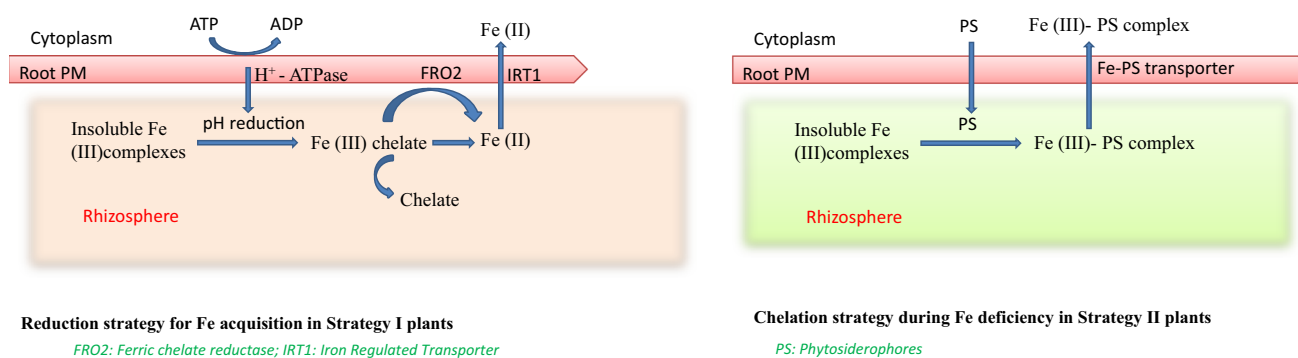
Strategy I and Strategy II plants: There are two distinct strategies for Fe acquisition in plants namely Strategy I, represented by non-graminaceous monocots and dicot plants involving reduction strategy and Strategy II plants, comprising of chelation strategy in graminaceous plants.

#### Root exudations

The solubility of Fe is greatly influenced by soil pH with an increase by 1000 times upon a unit reduction in soil pH (Grotz & Guerinotz, 2006). Strategy I plants including dicots and non-graminaceous monocots respond to Fe deficiency by extruding  $H^+$  in the rhizosphere as the first step to lower the soil pH, increasing Fe (III) solubility in the soil and its availability for plant uptake (Bienfait, 1988; Jolley et al., 1996; Kumar et al., 2021). The Fe deficient plants have been found to have higher  $H^+$ -ATPases than that during Fe-sufficient conditions (Colangelo & Guerinot, 2004). In case of strategy II plants, mainly represented by grasses, the phytosiderophores (PS) secretion is enhanced in the rhizosphere (Lopez-Millan et al., 2012), resulting in Fe (III)-PS complex formation which can readily move across the membranes of roots as mediated by specific transmembrane proteins. However, some studies reveal the presence of strategy I- like mechanism in grasses (Ishimaru, 2006; Zanin et al., 2017). Some characteristic features of strategy I plants like elevated levels of  $H^+$ -ATPase and  $Fe^{3+}$  reductase activities during Fe deficiency in maize (Li et al., 2016) and increased phenolic efflux in rice (Bashir et al., 2011) have been reported to improve Fe acquisition in plants. Figure 1 represent the mechanism of Fe acquisition in Strategy I and II plants.

#### Hormonal crosstalk

A number of hormones act through intricate signalling pathways to modulate the gene expression and root system architecture with an aim to improve Fe acquisition in plants. Each hormone has specific roles in plant system and perception of Fe deficiency induces a cross talk mechanism whereby they regulate the alterations mediating plant's survival during Fe-limited conditions. Auxin, ethylene and nitric oxide (NO) have been suggested as positive regulators of Fe acquisition (Garnica et al., 2018) while cytokinins and jasmonates as the negative regulators (Hindt & Guerinot, 2012). Increased auxin synthesis during Fe deficiency is linked to regulate lateral root growth by affecting AUX-1 transporter in strategy I plants (Giehl



**Fig. 1** Strategies for Fe acquisition during Fe deficiency in plants

et al., 2012) while the strategy II plants are suggested to involve an auxin response factor like, *OsARF12* (in rice) (Qi et al., 2011). Ethylene, in response to Fe deficiency, is reported to act by affecting the interaction of *ETHYLENE INSENSITIVE3* and *ETHYLENE INSENSITIVE3-LIKE1* (*EIN3/EIL1*) directly interacting with *FIT*, wherein they are suggested to aid Fe acquisition by regulating *FIT* stabilization (Lingam et al., 2011). NO is a signalling molecule mediating reversion of chlorotic effects in maize (Graziano & lamattina, 2005) and inducing the *FRO1*, *IRT1*, and *FER* expression in tomato roots (Graziano & lamattina, 2007). A model suggestive of the concerted roles of positive regulators entails that Fe deficiency induces elevated auxin levels that acts upstream, increasing NO levels which acts to upregulate the genes responsible for higher Fe acquisition (Chen et al., 2010). Ethylene production is elevated by NO in roots, and NO and ethylene together act by aiding transcription of genes responsible for Fe acquisition (Garcia et al., 2011).

Another hormone with auxin like activity is melatonin (N-acetyl-5-methoxytryptamine), which modulates the gene expression of a number of receptors and hormone signalling pathways to impart growth promoting attributes in plants (Tiwari et al., 2020). Melatonin, acts by elevating the remobilization of Fe, bound to pectin and hemicellulosic components of cell wall, through polyamine-mediated NO accumulation (Zhou et al., 2016). Abscisic acid (ABA) alleviates Fe deficiency induced chlorosis in *Arabidopsis* by reducing the root apoplastic Fe and elevating the level of shoot Fe content, which is suggestive of improved reutilization and transport of Fe from root to shoot under Fe deficiency (Lei et al., 2014). Gibberellins (GAs) cause reduction in Fe transport and translocation from root to shoots thereby negatively modulating Fe utilization in rice seedlings (Wang et al., 2017). Furthermore, cytokinins (CTK), jasmonic acid (JA) and brassinosteroids (BRs) inhibit the expression of genes regulating Fe acquisition namely *IRT*, *FRO2* and *FIT* (Hindt & Guerinot, 2012; Maurer et al., 2011; Seguela et al., 2008).

### ROS (Reactive oxygen species) scavenging

As the plants perceive any stressful conditions including nutrient stress (like Fe and/or Zn deficiency), generation of reactive oxygen species (ROS) is a common consequence wherein there occurs enhanced production of hydroxyl ( $\bullet\text{OH}$ ), superoxide ( $\text{O}_2^-$ ) radicals and hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) (Del Rio., 2015). A normal metabolic functioning involves a balanced generation and quenching of ROS, thereby preventing the lipid membranes. An increased accumulation of ROS generates enzymatic ROS scavenging mechanism in plants (Singh et al., 2021). However, severe exposure to stressful conditions like nutritional deficiencies causes enhanced ROS production exceeding the quenching capacity of enzymatic and non-enzymatic ROS scavenging mechanisms (Del Rio., 2015). These extremely reactive ROS species, particularly  $\bullet\text{OH}$ , cause severe damage to lipid membranes, protein and nucleic acids. As a part of electron transport chain in chloroplasts and mitochondria, the cellular redox balance is disturbed during Fe deficiency in plants which eventually generates the ROS elevation. The role of ROS scavenging enzymes, particularly Glutathione (GSH) and ascorbate (ASC), are crucial to improve Fe availability and maintaining cellular Fe homeostasis in *Arabidopsis* (Ramirez et al., 2013) and sugar beet (Zaharieva & Abadia, 2003). The induction of ROS signalling has also been demonstrated in sunflower and maize during Fe deficiency. The iron deficiency caused a significant increase in ROS production mainly hydrogen peroxide and superoxide radicals in leaves of maize and sunflower plants (Ranieri et al., 2001; Sun et al., 2007) and peroxides in peanut (Singh & Chaudhari, 1992). The Fe deficiency is also suggested to be regulated by ethylene and NO which is linked to ROS mediated signalling (Xia et al., 2015).

Thus, the Fe deficiency responses in plants comprise of an intricate network of events which includes a number of physiological and biochemical alterations in terms of root

exudations, hormones signalling and their crosstalk and ROS scavenging to preserve the cellular redox balance.

## Zn deficiency responses

### Root exudations

The plants respond to limited Zn availability in soil by release of various root exudates like amino acids, sugars and phenolics (Rasouli-Sadaghiani et al., 2011). These root exudates indicate a strong plant-soil interaction affecting the overall metabolite composition in the rhizosphere. The root exudates constitute low molecular weight organics released as a consequence of their excessive accumulation in the roots during Zn deficient status. This is mainly attributed to the leaky membranes of Zn-deficient plants having higher permeability of root plasma membrane due to  $K^+$  leakage (Cakmak & Marschner, 1988). The elevated exudation of amino acid may be attributed to inhibition of protein synthesis accompanied with increased accumulation of amino acids in roots during Zn deficiency (Cakmak et al., 1989; Shahsavari et al., 2019). The graminaceous plants release phytosiderophores which mobilizes both Fe and Zn and shows similar attributes for both the Fe and Zn deficiencies in the rhizosphere (Kabir et al., 2017; Treeby et al., 1989).

### Hormonal regulations

Plants respond to Zn deficiency by eliciting a signalling cascade that traverses between roots and shoots to maintain nutrient homeostasis (Kabir et al., 2017). Hormone signalling regulates the mineral acquisition by plants during Zn deficit status. Indole-3-acetic acid, the major auxin in plants play critical role in plant development and the Zn status greatly influences the auxin-mediated responses while auxin signalling triggers Zn acquisition efficiency in plants. The Zn transporter genes in rice including *OsIRT1*, *OsZIP4* and *OsZIP1* were expressed upon exposure to auxin inhibitor in roots under Zn deficiency while the absence of auxin inhibitor imparts zinc efficiency attributes in rice (Begum et al., 2016). The auxin signalling is, therefore, crucial for Zn- efficiency in plants under Zn-limited environments. Cakmak et al. (1989) speculated that the low levels of IAA under Zn-deficiency in *Phaseolus vulgaris* L. can be attributed to increased oxidative degradation of IAA due to decline in SOD (*Zn-SOD*) rather than impaired IAA biosynthesis. The level of gibberellic acid in *Zea mays* L. was also recorded low in Zn -deficient plants with variable responses shown by  $GA_1$  and  $GA_{20}$ . The concentration of  $GA_{20}$ , a precursor of  $GA_1$ , showed a lesser reduction while  $GA_1$  recorded 2.6–6.3 folds lower levels in Zn-deficient plants. Thus, Zn is suggested to affect

the conversion of  $GA_{20}$  to  $GA_1$  by interfering with transcription or translation steps (Sekimoto et al., 1997).

A weaker ethylene response was demonstrated in *B. oleracea* plants which can be attributed to slower activation of senescence, since Zn is a component of the receptor for ethylene response and its deficiency may reduce the plant's sensitivity to ethylene (Navarro-Leon et al., 2016).

### ROS scavenging

The Zn-deficient plants experience restrictions in  $CO_2$  uptake and its subsequent fixation as the stomatal conductance is greatly impaired. This leads to reduced utilization of NADPH and a distortion in the NADP: NADPH ratio generates  $O_2^-$  through electron transfer to  $O_2$  (Cakmak, 2000). The oxidative stress in plants during Zn-deficiency has been reported in many plants including mulberry (Tewari et al., 2008), wheat (Sharma et al., 2004) and legumes (Gupta et al., 2011; Michael & Krishnaswamy, 2011) and can be attributed to a decline in Cu–Zn SOD (Saibi & Brini, 2018). The Zn- deficiency elevates the response of a number of antioxidant enzymes like catalase, ascorbate peroxidase and glutathione reductase (Sharma et al., 2004). The non- enzymatic scavenging response including total ascorbic acid (AA), Dehydroascorbate (DHA), reduced glutathione (GSH) and oxidized glutathione (GSSG) were greatly elevated in Zn-deficient maize plants suggesting the activation of ascorbate–glutathione cycle to control ROS levels (Potters et al., 2002).

## Molecular regulation of Fe and Zn homeostasis

The plants have a tightly regulated process for uptake, transport and accumulation of Fe and Zn as they are required in very small amount but are crucial for maintenance of their growth and development. The involvement of Zinc- regulated transporter (*ZRT*) and iron-regulated transporter (*IRT*)- like protein (*ZIP*) family have ubiquitous roles in their uptake and transport (Grotz & Guerinot, 2006). A number of *ZIP* proteins have been characterized in *Arabidopsis* (Maser et al., 2001), rice (Ishimaru et al., 2007; Li et al., 2013), barley (Tiong et al., 2015), wheat (Evens et al., 2017), maize (Li et al., 2013; Xu et al., 2010), soybean (Moreau et al., 2002) and common bean (Astudillo et al., 2013) which are known to maintain the cytosolic homeostasis of Fe and Zn. The *ZIP* and *IRT* transporters regulate the uptake of divalent cations like  $Fe^{2+}$  and  $Zn^{2+}$  ions across cellular membranes into the cytoplasm (Eide, 2005; Krishna et al., 2017). In *Arabidopsis*, the functional complementation of a yeast mutant defective in iron uptake resulted in identification of *AtIRT1* (Iron-regulated

transporter 1), encoding a major Fe transporter at the root surface (Eide et al., 1996; Henriques et al., 2002; Varotto et al., 2002; Vert et al., 2002). The mutant *irt1* exhibited lethal chlorosis indicating the role of *AtIRT1* in Fe translocation in *Arabidopsis* (Nishida et al., 2011). Furthermore, the overexpression of *AtIRT3* caused an elevated accumulation of Zn and Fe in shoots and roots respectively. The overexpression of *OsIRT1* in rice increased Fe and Zn accumulations in shoots, roots and mature seeds, indicating the role of *OsIRT1* as a functional metal transporter (Bugchio et al., 2002; Ishimaru et al., 2006; Lee et al., 2009).

### Fe deficiency sensing and signaling in plants

#### Regulation of Fe- reduction mechanism in Strategy I plants

The Fe reduction mechanism responds to Fe limitation by proton release through H<sup>+</sup> ATPases located on plasma membrane (Santi et al., 2005). The acidification in the soil effected by proton release increases Fe solubility causing reduction of Fe<sup>3+</sup> to Fe<sup>2+</sup> by ferric chelate reductase enzyme, ferric reduction oxidase (*FRO2*). This reduced Fe form (Fe<sup>2+</sup>) is further transported into root system by the transporter *IRT1* (Bariya et al., 2015; Eckhardt et al., 2001). Such responses are accompanied with modified root architecture like more root hair formation, increased lateral root formation and swelling of tips of root (Muller & Schmidt, 2004) enhancing surface area for Fe acquisition. There are a number of genes regulating the transport of Fe from leaf to the root like *FIT1* (*FER-Like Fe Deficiency Induced Transcription factor*), *IRT1*, *OPT3*, and *bZIP23* in peanut (*AhIRT1*; Xiong et al., 2012), *Medicago truncatula* (*MtNRAMP1*; Tejada-Jiménez et al., 2015), soybean (*NRAMP* genes; Qin et al., 2017), lentil (*Ferritin-1*, *BHLH-1*, and *FER*-like transcription factor protein and *IRT1*), and chickpea (*CaFer1*; Parveen et al., 2016). The transcriptional studies in *Arabidopsis* reveals two major regulatory networks aiming for Fe homeostasis in strategy I plants: *FIT* network and *POPEYE* network (Stein & Waters, 2011).

*FIT* (FER-like iron-deficiency-induced transcription factor) transcription factors, are also induced in root epidermis during Fe limitation, and regulates the deficiency response in plants (Colangelo & Guerinot, 2004; Yuan et al., 2005). It regulates *FRO2* at transcriptional level while *IRT1* is regulated both transcriptionally and post transcriptionally (Jakoby et al., 2004). Recent studies on *FIT* regulation suggests that at transcriptional level there occurs accumulation of *FIT* during Fe limited conditions which is turned over by 26S proteasomal degradation to ensure that gene expression is prevented when Fe supply increases (Hindt & Guerinot, 2012).

In addition to the root epidermal tissues wherein *FIT* is the regulatory network, another transcriptional network is represented in the vasculature with two major transcription factors namely bHLH TFs (*bHLH047*) called as *POPEYE* (*PYE*) and *BRUTUS* (*BTS*), an E3- ubiquitin ligase. These TFs show a higher level of expression in pericycle during Fe deficiency (Long et al., 2010). *PYE* targets a number of genes required for metal homeostasis like *FRO6* and *ZIF1* (Curie et al., 2009). *pye-1* mutants show reduced root growth with chlorosis indicating the regulatory role of *PYE* in Fe deficiency response. Through a long term studies a number of Fe-efficient peanut genotypes, showing tolerance of lime induced iron deficiency chlorosis in calcareous soil, have been identified (Samdur et al., 1999, 2000; Singh and Chaudhari, 1991, 1993; Singh et al., 2003) which need to be studied in details for their Fe homeostasis regulation and their mechanism.

#### Regulation of Chelation in Strategy II plants

During Fe deficiency, the graminaceous plants respond by secreting phytosiderophores (PS) in the rhizosphere which form Fe (III)-PS complex to be available for plant uptake (Takagi et al., 1984). The PS are released in the rhizosphere through PS- efflux transporter *TOM1* (Nozoye et al., 2011). Nicotianamine (NA) gets converted to phytosiderophores which associates with Fe (III) form and this aids in Fe transport into roots through yellow stripe- like (*YSL*) family transporters (Table 1). Different transporters belonging to *YSL* family like *YS1* for maize (Curie et al., 2001), *OsYSL15* in rice (Lee et al., 2009) have been identified.

The transcription factor upregulated in response to Fe deficiency is a *bHLH* protein *IRO2* which is expressed both in root and shoot (Ogo et al., 2006). In rice, the overexpression of *OsIRO2* TFs helps the plants withstand Fe deficiency with elevated PS synthesis and transport. It is expressed to regulate uptake and transport of Fe during the vital processes like development of seeds and germination (Ogo et al., 2011). The other positive regulators of responding to Fe deficiency are *OsIDEF1* and 2 (Iron deficiency responsive elements 1 & 2) (Kobayashil et al., 2003).

### Zn deficiency sensing and signalling in plants

The optimum level of Zn is required to ensure nutritional quality of seeds which requires efficient uptake and transport of Zn (Astudillo et al., 2013). The *ZIP* transporters are the most studied forms mediating Zn uptake and transport in a number of plant species including Soybean, Rice, *Medicago* and common bean (Astudillo et al., 2013; Palmgren et al., 2008). The Zn transporters mediate the

**Table 1** Genes regulating mineral acquisition during Fe and Zn deficiency

Mineral deficiency	Genes	Regulatory roles in mineral acquisition
<i>Fe deficiency</i>		
Strategy I plants	<i>AHA 2</i>	Rhizospheric acidification to lower soil pH
	<i>FRO2</i>	Ferric chelate reductase converting Fe <sup>3+</sup> to Fe <sup>2+</sup>
	<i>IRT1</i>	Transport of Fe <sup>2+</sup> to root epidermal cells
Strategy II plants	<i>TOM1</i>	Regulates phytosiderophores efflux in the rhizosphere
	<i>YSL</i>	Transport of PS-Fe <sup>3+</sup> complex into roots
<i>Zn deficiency</i>		
	<i>ZIP &amp; IRT</i>	Transport of Zn into the cytoplasm and subsequent xylem loading
	<i>HMA 2 &amp; 4</i>	Xylem unloading from xylem parenchyma
	<i>ZIF &amp; MTP</i>	Regulate Zn transport to vacuoles
	<i>NRAMP</i>	Zn mobilization from vacuoles
	<i>YSL</i>	Regulates Zn-NA complex unloading from phloem to seeds

uptake and transport of Zn<sup>2+</sup> through low affinity and high affinity membrane transporter systems, depending upon the Zn status of the soil (Kumar et al., 2016). The transport of Zn into the cytoplasm is mostly mediated by *ZIP* and *IRT* transporters (Krishna et al., 2017), which subsequently gets loaded to the xylem (Krishna et al., 2020). The xylem loading from xylem parenchyma is assisted by heavy metal ATPase 2 and 4 (*HMA 2 & HMA 4*) (Hanikenne et al., 2008). The other transporters involved in Zn transport to the vacuoles are zinc induced facilitator (*ZIF*) and metal tolerance protein (*MTP*) (Hussain et al., 2004) and *NRAMPs* (Natural resistance associated macrophage protein) mediate Zn mobilization from the vacuole (Haydon & Cobbett, 2007). The influx of Zn<sup>2+</sup> to leaf and phloem is primarily mediated by *ZIP* family while phloem loading of Zn and Zn-NA complex unloading to the seeds is actively facilitated by *YSL* (Waters & Grusak, 2008) (Table 1).

In *Arabidopsis*, two TFs were found to be vital to induce adaptation response in plants during Zn deficiency. These TFs, namely *bZIP 19* and *23*, members of the F group of the basic-region leucine zipper (*bZIP*) family, showing histidine rich motifs at basic N-terminal region (Assunção et al., 2010), are key regulators of genes including *ZIPs* under deficient Zn status. These proteins exist as monomers under normal conditions while upon Zn deficiency perception, they dimerize leading to *ZIP* genes expression (Lilay et al., 2018). The conserved histidine-rich motif in TFs belonging to F *bZIP* family, are probable Zn sensors (Henriques et al., 2017).

## Conclusion

A lot of progress has been made in understanding the physiological and biochemical mechanisms causing alterations both in plant and in the rhizosphere to facilitate Fe and Zn uptake during their deficiency in the soil. Root

exudations, ROS scavenging and hormonal regulations are the main physiological responses, while number of transporters and transcription factors coordinate at molecular level to improve the acquisition of Fe and Zn. However, the cascade of events taking place within the plants is very complex and are interconnected through crosstalk of diverse pathways which require detail studies focussing on signal perception and its subsequent transduction and how these signals are integrated to impart tolerance and to maintain homeostasis of Fe and Zn in plants. The hormonal regulations especially roles of phytohormones like ABA, JA, BRs and SA in Zn acquisition need a revisit.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Alloway, B. J. (2009). Soil factors associated with zinc deficiency in crops and humans. *Environmental Geochemistry and Health*, 31, 537–548. <https://doi.org/10.1007/s10653-009-9255-4>
- Assunção, A. G., Herrero, E., Lin, Y. F., Huettel, B., Talukdar, S., Smaczniak, C., et al. (2010). *Arabidopsis thaliana* transcription factors *bZIP19* and *bZIP23* regulate the adaptation to zinc deficiency. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 10296–10301. <https://doi.org/10.1073/pnas.1004788107>
- Astudillo, C., Fernandez, A., Blair, M. W., & Cichy, K. A. (2013). The *Phaseolus vulgaris* ZIP gene family: Identification, characterization, mapping, and gene expression. *Frontiers in Plant Science*, 4, 286. <https://doi.org/10.3389/fpls.2013.00286>
- Bae, Y. S., Oh, H., Rhee, S. G., & Do Yoo, Y. D. (2011). Regulation of reactive oxygen species generation in cell signaling. *Molecules and Cells*, 32, 491–509. <https://doi.org/10.1007/s10059-011-0276-3>
- Barberon, M., Vermeer, J. E., De-Bellis, D., Wang, P., Naseer, S., Andersen, T. G., Humbel, B. M., Nawrath, C., Takano, J., Salt, D. E., & Geldner, N. (2016). Adaptation of root function by

- nutrient-induced plasticity of endodermal differentiation. *Cell*, 164, 447–459.
- Bariya, H., Singh, A. L., Vidya Chaudhari. (2015). Measurement of Fe (II) and Fe (III) in groundnut by in-column and post column reactions in ion-chromatography. *Communications in Soil Science and Plant Analysis*, 46, 358–366.
- Bashir, K., Ishimaru, Y., Shimo, H., Kakei, Y., Senoura, T., Takahashi, R., Sato, Y., Sato, Y., Uozumi, N., Nakanishi, H., & Nishizawa, N. K. (2011). Rice phenolics efflux transporter 2 (*PEZ2*) plays an important role in solubilizing apoplasmic iron. *Soil Sci Plant Nutr*, 57, 803–812.
- Begum, M. C., Islam, M., Sarkar, M. R., Azad, M. A. S., Huda, A. K. M., & Kabir, A. H. (2016). Auxin signaling is closely associated with Zn-efficiency in rice (*Oryza sativa* L.). *Journal of Plant Interactions*, 11(1), 124–129. <https://doi.org/10.1080/17429145.2016.1220026>
- Bienfait, H. F. (1988). Mechanisms in Fe-efficiency reactions of higher plants. *Journal of Plant Nutrition*, 11, 605–610.
- Bughio, N., Yamaguchi, H., Nishizawa, N. K., Nakanishi, H., & Mori, S. (2002). Cloning an iron-regulated metal transporter from rice. *Journal of Experimental Botany*, 53(374), 1677–1682.
- Cakmak, I. (2000). Possible roles of zinc in protecting plant cells from damage by reactive oxygen species. *New Phytologist*, 146, 185–205.
- Cakmak, I. and Marschner, H. (1988). Increase in membrane permeability and exudation in roots of zinc deficient plants. *Journal of Plant Physiology*, 132(3), 356–361. ISSN 0176-1617. [https://doi.org/10.1016/S0176-1617\(88\)80120-2](https://doi.org/10.1016/S0176-1617(88)80120-2).
- Cakmak, I., Marschner, H., & Bangerth, F. (1989). Effect of zinc nutritional status on growth, protein metabolism and levels of indole-3-acetic acid and other phytohormones in bean (*Phaseolus vulgaris* L.). *Journal of Experimental Botany*, 40, 405–412.
- Chen, W. W., Yang, J. L., Qin, C., Jin, C. W., Mo, J. H., Ye, T., & Zheng, S. J. (2010). Nitric oxide acts downstream of auxin to trigger root ferric-chelate reductase activity in response to iron deficiency in *Arabidopsis*. *Plant Physiology*, 154, 810–819.
- Colangelo, E. P., & Guerinot, M. L. (2004). The essential *bHLH* protein *FIT1* is required for the iron deficiency response. *The Plant Cell*, 16, 3400–3412.
- Curie, C., Panaviene, Z., Loulergue, C., Dellaporta, S. L., Briat, J. F., & Walker, E. L. (2001). Maize yellow stripe1 encodes a membrane protein directly involved in Fe (III) uptake. *Nature*, 409, 346–349.
- Curie, C., Cassin, G., Couch, D., Divol, F., Higuchi, K., Le Jean, M., Misson, J., Schikora, A., Czernic, P., & Mari, S. (2009). Metal movement within the plant: Contribution of nicotianamine and yellow stripe 1-like transporters. *Annals of Botany*, 103, 1–11.
- Del Rio, L. A. (2015). ROS and RNS in plant physiology: An overview. *Journal of Experimental Botany*, 66, 2827–2837.
- Eckhardt, U., Marques, A. M., & Buchhout, T. J. (2001). Two iron-regulated cation transporters from tomato complement metal uptake-deficient yeast mutants. *Plant Molecular Biology*, 45, 437–448.
- Eide, D., Broderius, M., Fett, J., & Guerinot, M. L. (1996). A novel iron-regulated metal transporter from plants identified by functional expression in yeast. *Proceedings of the National Academy of Sciences of the United States of America*, 93(11), 5624–5628.
- Evens, N. P., Buchner, P., Williams, L. E., & Hawkesford, M. J. (2017). The role of ZIP transporters and group F bZIP transcription factors in the Zn–deficiency response of wheat (*Triticum aestivum*). *The Plant Journal*, 92, 291–304. <https://doi.org/10.1111/tpj.13655>
- Garcia, M. J., Suarez, V., Romera, F. J., Alcantara, E., & Perez-Vicente, R. (2011). A new model involving ethylene, nitric oxide and Fe to explain the regulation of Fe-acquisition genes in Strategy I plants. *Plant Physiology and Biochemistry*, 49, 537–544.
- Garnica, M., Bacaicoa, E., Mora, V., San Francisco, S., Baigorri, R., Zamareño, A. M., & Garcia-Mina, J. M. (2018). Shoot iron status and auxin are involved in iron deficiency-induced phytosiderophores release in wheat. *BMC Plant Biology*, 18, 105. <https://doi.org/10.1186/s12870-018-1324-3>
- Giehl, R. F., Lima, J. E., & Wiren, N. (2012). Localized iron supply triggers lateral root elongation in *Arabidopsis* by altering the *AUX1*-mediated auxin distribution. *The Plant Cell*, 1, 33–49.
- Graziano, M., & Lamattina, L. (2005). Nitric oxide and iron in plants: An emerging and converging story. *Trends in Plant Science*, 10, 4–8.
- Graziano, M., & Lamattina, L. (2007). Nitric oxide accumulation is required for molecular and physiological responses to iron deficiency in tomato roots. *The Plant Journal*, 52, 949–960.
- Grotz, N., & Guerinot, M. L. (2006). Molecular aspects of Cu, Fe and Zn homeostasis in plants. *Biochimica Et Biophysica Acta*, 1763(7), 595–608.
- Gupta, B., Pathak, G. C., & Pandey, N. (2011). Induction of oxidative stress and antioxidant responses in Vigna mungo by zinc stress. *Russian Journal of Plant Physiology*, 58, 85–91.
- Hanikenne, M., Talke, I. N., Haydon, M. J., Lanz, C., Nolte, A., Motte, P., Kroymann, J., Weigel, D., & Krämer, U. (2008). Evolution of metal hyperaccumulation required cis-regulatory changes and triplication of *HMA4*. *Nature*, 453, 391. <https://doi.org/10.1038/nature06877>
- Hassan, M. U., Aamer, M., Chattha, M. U., Haiying, T., Shahzad, B., Barbanti, L., Nawaz, M., Rasheed, A., Afzal, A., Liu, Y., & Guoqin, H. (2020). The Critical Role of Zinc in Plants Facing the Drought Stress. *Agriculture*, 10, 0396. <https://doi.org/10.3390/agriculture10090396>
- Haydon, M. J., & Cobbett, C. S. (2007). Transporters of ligands for essential metal ions in plants. *New Phytologist*, 174, 499–506. <https://doi.org/10.1111/j.1469-8137.2007.02051.x>
- Henriques, R., Jasik, J., Klein, M., Martinoia, E., Feller, U., Schell, J., Pais, M. S., & Koncz, C. (2002). Knock-out of *Arabidopsis* metal transporter gene *IRT1* results in iron deficiency accompanied by cell differentiation defects. *Plant Molecular Biology*, 50(4–5), 587–597.
- Henriques, A., Farias, D., & de Oliveira Costa, A. (2017). Identification and characterization of the bZIP transcription factor involved in zinc homeostasis in cereals. *Genetics and Molecular Research*, 16, 1–10. <https://doi.org/10.4238/gmr16029558>
- Hindt, M. N., & Guerinot, M. L. (2012). Getting a sense for signals: Regulation of the plant iron deficiency response. *Biochimica Et Biophysica Acta*, 1823, 1521–1530.
- Hussain, D., Haydon, M. J., Wang, Y., Wong, E., Sherson, S. M., Young, J., Camakaris, J., Harper, J. F., & Cobbett, C. S. (2004). P-type ATPase heavy metal transporters with roles in essential zinc homeostasis in *Arabidopsis*. *The Plant Cell*, 16, 1327–1339. <https://doi.org/10.1105/tpc.020487>
- Ishimaru, Y., Suzuki, M., Tsukamoto, T., Suzuki, K., Nakazono, M., Kobayashi, T., Wada, Y., Watanabe, S., Matsushashi, S., Takahashi, M., Nakanishi, H., Mori, S., & Nishizawa, N. K. (2006). Rice plants take up iron as an Fe<sup>3+</sup>-phytosiderophore and as Fe<sup>2+</sup>. *The Plant Journal*, 45(3), 335–346.
- Ishimaru, Y., Masuda, H., Suzuki, M., Bashir, K., Takahashi, M., Nakanishi, H., Mori, S., & Nishizawa, N. K. (2007). Overexpression of the *OsZIP4* zinc transporter confers disarrangement of zinc distribution in rice plants. *Journal of Experimental Botany*, 58(11), 2909–2915.
- Jakoby, M., Wang, H. Y., Reidt, W., Weissarr, B., & Bauer, P. (2004). *FRU(BHLH029)* is required for induction of iron mobilization genes in *Arabidopsis thaliana*. *FEBS Letters*, 577, 528–534.

- Jolley, V. D., Cook, K. A., Hansen, N. C., & Stevens, W. B. (1996). Plant physiological responses for genotypic evaluation of iron efficiency in strategy I and strategy II plants—A review. *Journal of Plant Nutrition*, 19(8–9), 1241–1255. <https://doi.org/10.1080/01904169609365195>
- Kabir, A.H., Hossain, M.M., Khatun, M.A., Sarkar, M.R. and Haider, S.A. (2017). Biochemical and molecular mechanisms associated with Zn deficiency tolerance and signaling in rice (*Oryza sativa* L.). *J. Plant Interactions*, 12(1): 447–456. DOI: <https://doi.org/10.1080/17429145.2017.1392626>
- Karim, M., Zhang, Y. Q., Zhao, R. R., Chen, X. P., Zhang, F. S., & Zou, C. Q. (2012). Alleviation of drought stress in winter wheat by late foliar application of zinc, boron, and manganese. *Journal of Plant Nutrition and Soil Science*, 175, 142–151.
- Kobayashil, T., Nakayama, Y., Itai, R. N., Nakanishi, H., Yoshihara, T., Mori, S., & Nishizawa, N. K. (2003). Identification of novel cis-acting elements, *IDE1* and *IDE2*, of the barley *IDS2* gene promoter conferring iron-deficiency-inducible, root-specific expression in heterologous tobacco plants. *The Plant Journal*, 36, 780–793.
- Krishna Ajeesh, T. P., Maharajan, T., Roch, G. V., Ignacimuthu, S., & Ceasar, S. A. (2020). Structure, function, regulation and phylogenetic relationship of ZIP family transporters of plants. *Frontiers in Plant Science*, 11, 662. <https://doi.org/10.3389/fpls.2020.00662>
- Krishna, T. P. A., Ceasar, S. A., Maharajan, T., Ramakrishnan, M., Duraipandiyar, V., Al-Dhabi, N., & Ignacimuthu, S. (2017). Improving the zinc-use efficiency in plants: A review. *SABRAO J. Breed. Genet*, 49, 221–230.
- Kumar, L., Meena, N. L., & Singh, U. (2016) Zinc Transporter: Mechanism for Improving Zn Availability. In U. Singh, C. Praharaaj, S. Singh, N. Singh (eds) *Biofortification of Food Crops*. New Delhi: Springer. [https://doi.org/10.1007/978-81-322-2716-8\\_11](https://doi.org/10.1007/978-81-322-2716-8_11).
- Kumar, A., Sahu, C., Panda, P. A., Biswal, M., Sah, R. P., Lal, M. K., Baig, M. J., Swain, P., Behera, L., & Chattopadhyay, K. (2019). Phytic acid content may affect starch digestibility and glycemic index value of rice (*Oryza sativa* L.). *Journal of the Science of Food and Agriculture..* <https://doi.org/10.1002/jsfa.10168>
- Kumar, A., Nayak, S., Ngangkham, U., Sah, R. P., Lal, M. K., TP, A., & Sharma, S., (2021). A single nucleotide substitution in the SPDT transporter gene reduced phytic acid and increased mineral bioavailability from Rice grain (*Oryza sativa* L.). *Journal of Food Biochemistry..* <https://doi.org/10.1111/jfbc.13822>.
- Kumar, A., Lal, M. K., Kar, S. S., Nayak, L., Ngangkham, U., Samantaray, S., & Sharma, S. G. (2017). Bioavailability of iron and zinc as affected by phytic acid content in rice grain. *Journal of Food Biochemistry*, 41(6), e12413. <https://doi.org/10.1111/jfbc.12413>
- Kumar, A., Singh, B., Raigond, P., Sahu, C., Mishra, U. N., Sharma, S., & Lal, M. K. (2021a). Phytic acid: Blessing in disguise, a prime compound required for both plant and human nutrition. *Food Research International*, 142, 110193. <https://doi.org/10.1016/j.foodres.2021.110193>
- Lal, M. K., Kumar, A., Kardile, H. B., Raigond, P., Changan, S. S., Thakur, N., et al. (2020). Biofortification of vegetables. In T. R. Sharma, R. Deshmukh, & H. Sonah (Eds.), *Advances in agri-food biotechnology*. Singapore: Springer. [https://doi.org/10.1007/978-981-15-2874-3\\_5](https://doi.org/10.1007/978-981-15-2874-3_5).
- Lee, S., & An, G. (2009). Over-expression of *OsIRT1* leads to increased iron and zinc accumulations in rice. *Plant, Cell and Environment*, 32(4), 408–416.
- Lee, S., Chiecko, J. C., Kim, S. A., Walker, E. L., Lee, Y., Guerinot, M. L., & An, G. (2009). Disruption of *OsYSL15* leads to iron inefficiency in rice plants. *Plant Physiology*, 150, 786–800.
- Lei, G. J., Zhu, X. F., Wang, Z. W., Dong, F., Dong, N. Y., & Zheng, S. J. (2014). Abscisic acid alleviates iron deficiency by promoting root iron reutilization and transport from root to shoot in *Arabidopsis*. *Plant, Cell and Environment*, 37, 852–863. <https://doi.org/10.1111/pce.12203>
- Li, S., Zhou, X., Huang, Y., Zhu, L., Zhang, S., Zhao, Y., et al. (2013). Identification and characterization of the zinc-regulated transporters, ironregulated transporter-like protein (ZIP) gene family in maize. *BMC Plant Biology*, 13, 114. <https://doi.org/10.1186/1471-2229-13-114>
- Li, S., Zhou, J., Chen, J., & Chen, R. (2016). Is there a strategy I iron uptake mechanism in maize? *Plant Signaling & Behavior*. <https://doi.org/10.1080/15592324.2016.1161877>
- Lilay, G. H., Castro, P. H., Campilho, A., & Assunção, A. G. (2018). The *Arabidopsis* bZIP19 and bZIP23 activity requires zinc deficiency—insight on regulation from complementation lines. *Frontiers in Plant Science*, 9, 1955. <https://doi.org/10.3389/fpls.2018.01955>
- Lingam, S., Mohrbacher, J., Brumbarova, T., Potuschak, T., Fink-Straube, C., Blondet, E., Genschik, P., & Bauer, P. (2011). Interaction between the *bHLH* transcription factor *FIT* and *ETHYLENE INSENSITIVE3/ETHYLENE INSENSITIVE3-LIKE1* reveals molecular linkage between the regulation of iron acquisition and ethylene signaling in *Arabidopsis*. *The Plant Cell*, 23, 1815–1829.
- Long, T. A., Tsukagoshi, H., Busch, W., Lahner, B., Salt, D. E., & Benfey, P. N. (2010). The *bHLH* transcription factor *POPEYE* regulates response to iron deficiency in *Arabidopsis* roots. *The Plant Cell*, 22, 2219–2236.
- Lopez-Millan, A. F., Grusak, M. A., & Abadia, J. (2012). Carboxylate metabolism changes induced by Fe deficiency in Barley, a strategy II plant species. *Journal of Plant Physiology*, 169, 1121–1124.
- Maser, P., Thomine, S., Schroeder, J. I., Ward, J. M., Hirschi, K., Sze, H., Talke, I. N., Amtmann, A., Maathuis, F. J., Sanders, D., et al. (2001). Phylogenetic relationships within cation transporter families of *Arabidopsis*. *Plant Physiology*, 126(4), 1646–1667.
- Maurer, F., Müller, S., & Bauer, P. (2011). Suppression of Fe deficiency gene expression by jasmonate. *Plant Physiol Bioch.*, 49(5), 530–536.
- Michael, P. I., & Krishnaswamy, M. (2011). The effect of zinc stress combined with high irradiance stress on membrane damage and antioxidative response in bean seedlings. *Environmental and Experimental Botany*, 74, 171–177.
- Moreau, S., Thomson, R. M., Kaiser, B. N., Trevaskis, B., Guerinot, M. L., Udvardi, M. K., Puppo, A., & Day, D. A. (2002). *GmZIP1* encodes a symbiosis-specific zinc transporter in soybean. *Journal of Biological Chemistry*, 277(7), 4738–4746.
- Moreno-Lora, A., Recena, R., & Delgado, A. (2019). *Bacillus subtilis* QST713 and cellulose amendment enhance phosphorus uptake while improving zinc biofortification in wheat. *Applied Soil Ecology*, 142, 81–89. <https://doi.org/10.1016/j.apsoil.2019.04.01>
- Muller, M., & Schmidt, W. (2004). Environmentally induced plasticity of root hair development in *Arabidopsis*. *Plant Physiology*, 134, 409–419.
- Navarro-Leon, E., Albacete, A., Torre-Gonzalez, A. T., Ruiz, J. M., & Blasco, B. (2016). Phytohormone profile in *Lactuca sativa* and *Brassica oleracea* plants grown under Zn deficiency. *Phytochemistry*. <https://doi.org/10.1016/j.phytochem.2016.08.003>
- Nishida, S., Tsuzuki, C., Kato, A., Aisu, A., Yoshida, J., & Mizuno, T. (2011). *AtIRT1*, the primary iron uptake transporter in the root, mediates excess nickel accumulation in *Arabidopsis thaliana*. *Plant and Cell Physiology*, 52(8), 1433–1442.



- Nozoye, T., Nagasaka, S., Kobayashi, T., Takahashi, M., Sato, Y., Sato, Y., Uozumi, N., Nakanishi, H., & Nishizawa, N. K. (2011). Phytosiderophore efflux transporters are crucial for iron acquisition in graminaceous plants. *Journal of Biological Chemistry*, *286*, 5446–5454.
- Ogo, Y., Itai, R. N., Nakanishi, H., Inoue, H., Kobayashi, T., Suzuki, M., Takahashi, M., Mori, S., & Nishizawa, N. K. (2006). Isolation and characterization of *IRO2*, a novel iron regulated *bHLH* transcription factor in graminaceous plants. *Journal of Experimental Botany*, *57*, 2867–2878.
- Ogo, Y., Itai, R. N., Kobayashi, T., Aung, M. S., Nakanishi, H., & Nishizawa, N. K. (2011). *OsIRO2* is responsible for iron utilization in rice and improves growth and yield in calcareous soil. *Plant Molecular Biology*, *75*, 593–605.
- Palmgren, M. G., Clemens, S., Williams, L. E., Krämer, U., Borg, S., Schjørring, J. K., & Sanders, D. (2008). Zinc biofortification of cereals: Problems and solutions. *Trends in Plant Science*, *13*, 464–473. <https://doi.org/10.1016/j.tplants.2008.06.005>
- Parveen, S., Gupta, D. B., Dass, S., Kumar, A., Pandey, A., Chakraborty, S., & Chakraborty, N. (2016). Chickpea ferritin *cafer1* participates in oxidative stress response, and promotes growth and development. *Science and Reports*, *6*, 31218.
- Potters, G., de Gara, L., Asard, H., & Horemans, N. (2002). Ascorbate and glutathione: Guardians of the cell cycle, partners in crime? *Plant Physiology and Biochemistry*, *40*, 537–548.
- Qi, Y., Wang, S., Shen, C., Zhang, S., Chen, Y., Xu, Y., Liu, Y., Wu, Y., & Jiang, D. (2011). *OsARF12*, a transcription activator on auxin response gene, regulates root elongation and affects iron accumulation in rice (*Oryza sativa*). *New Phytologist*, *193*, 109–120.
- Qin, L., Han, P., Chen, L., Walk, T. C., Li, Y., Hu, X., et al. (2017). Genome-wide identification and expression analysis of NRAMP family genes in soybean (*Glycine Max L.*). *Frontiers Plant Science*, *8*, 1436.
- Ramirez, L., Simontacchi, M., Murgia, I., Zabaleta, E., & Lamattina, L. (2011). Nitric oxide, nitrosyl iron complexes, ferritin and frataxin: A well- equipped team to preserve plant iron homeostasis. *Plant Science*, *181*(5), 582–592.
- Ramírez, L., Bartoli, C. G., & Lamattina, L. (2013). Glutathione and ascorbic acid protect *Arabidopsis* plants against detrimental effects of iron deficiency. *Journal of Experimental Botany*, *64*, 3169–3178. <https://doi.org/10.1093/jxb/ert153>
- Ranieri, A., Castagna, A., Baldan, B., & Soldatini, G. F. (2001). Iron deficiency differently affects peroxidase isoforms in sunflower. *Journal of Experimental Botany*, *52*, 25–35. <https://doi.org/10.1093/jexbot/52.354.25>
- Rasouli-Sadaghiani, M. H., Sadeghzadeh, B., Sepehr, E., & Rengel, Z. (2011). Root exudation and zinc uptake by barley genotypes differing in Zn efficiency. *Journal of Plant Nutrition*, *34*(8), 1120–1132. <https://doi.org/10.1080/01904167.2011.558156>
- Rehman, H., Aziz, T., Farooq, M., Wakeel, A., & Rengel, Z. (2012). Zinc nutrition in rice production systems: A review. *Plant and Soil*, *361*, 203–226.
- Rengel, Z. (2015). Availability of Mn, Zn and Fe in the rhizosphere. *Journal of Soil Science and Plant Nutrition*, *15*, 3970–4409. <https://doi.org/10.4067/S0718-95162015005000036>
- Rout, G. R., & Sahoo, S. (2015). Role of iron in plant growth and metabolism. *Reviews in Agricultural Science*. <https://doi.org/10.7831/ras.3.1>
- Saibi, W. and Brini, F. (2018). Superoxide dismutase (SOD) and abiotic stress tolerance in plants: An overview. In Magliozzi, S. (Ed.), *Superoxide dismutase. Structure, synthesis and applications*. Nova Science Publishers, Hauppauge, NY, USA, (pp. 101–142).
- Samdur, M. Y., Mathur, R. K., Manivel, P., Singh, A. L., Bandyopadhyay, A., & Chikani, B. M. (1999). Screening of some advanced breeding lines of groundnut for tolerance of lime-induced iron-deficiency chlorosis. *Indian Journal of Agricultural Sciences*, *69*, 722–725.
- Samdur, M. Y., Singh, A. L., Mathur, R. K., Manivel, P., Chikani, B. M., Gor, H. K., & Khan, M. A. (2000). Field evaluation of Chlorophyll meter for screening groundnut (*Arachis hypogaea L*) genotypes tolerant of iron-deficiency chlorosis. *Current Science*, *79*(2), 211–214.
- Santi, S., Cesco, S., Varanini, Z., & Pinton, R. (2005). Two plasma membrane H<sup>+</sup>-ATPase genes are differentially expressed in iron-deficient cucumber plants. *Plant Physiology and Biochemistry*, *43*, 287–292.
- Schikora, A., & Schmidt, W. (2002). Formation of transfer cells and H(+)-ATPase expression in tomato roots under P and Fe deficiency. *Planta*, *215*, 304–311.
- Schmidt, W., Tittel, J., & Schikora, A. (2000). Role of hormones in the induction of iron deficiency responses in *Arabidopsis* roots. *Plant Physiology*, *122*, 1109–1118. <https://doi.org/10.1104/pp.122.4.1109>
- Séguéla, M., Briat, J. F., Vert, G., & Curie, C. (2008). Cytokinins negatively regulate the root iron uptake machinery in *Arabidopsis* through a growth-dependent pathway. *The Plant Journal*, *55*(2), 289–300.
- Sekimoto, H., Hoshi, M., Nomura, T., & Yokota, T. (1997). Zinc Deficiency affects the levels of endogenous gibberellins in *Zea mays L*. *Plant and Cell Physiology*, *38*(9), 1087–1090.
- Shahsavari, F., Khoshgofarmanesh, A. H., Maibody, S. A. M. M., Shariatmadari, H., & Massah, A. (2019). The role of root plasma membrane ATPase and rhizosphere acidification in zinc uptake by two different Zn-deficiency tolerant wheat cultivars in response to zinc and histidine availability. *Archives of Agronomy and Soil Science*. <https://doi.org/10.1080/03650340.2019.1572881>
- Sharma, P. N., Kumar, P., & Tewari, R. K. (2004). Early signs of oxidative stress in wheat plants subjected to zinc deficiency. *Journal of Plant Nutrition*, *27*, 451–463.
- Sinclair, S. A., & Krämer, U. (2012). The zinc homeostasis network of land plants. *Biochimica Et Biophysica Acta*, *1823*, 1553–1567.
- Singh, A. L. (1999). Mineral nutrition of groundnut. In *Advances in Plant Physiology* (Ed.), Hemantranjan, A., vol II. Scientific Publishers (India), Jodhpur, India, (pp. 161–200).
- Singh, A. L. (2004). Mineral nutrient requirement, their disorders and remedies in Groundnut. In *Groundnut Research in India* (Eds.), Basu, M. S., Singh, N. B. National Research center for groundnut (ICAR), Junagadh, India, (pp. 137–159).
- Singh, A. L., Mann, A. (2012). Recent advances in plant nutrition. In *Proc Natl Seminar of Plant Physiology on “Physiological and molecular approaches for development of climatic resilient crops”*, 12–14 Dec 2012, ANGRAU, Hyderabad, India, (pp. 6–22).
- Singh, A. L., Basu, M. S., & Singh, N. B. (2003). *Iron-chlorosis and its management in groundnut* (p. 30). National Research Center for Groundnut (ICAR), Junagadh.
- Singh, A. L., Basu, M. S., Singh, N. B. (2004). Mineral disorders of groundnut. National Research center for groundnut (ICAR), Junagadh India, (p 85).
- Singh, S., Prakash, P., & Singh, A. K. (2021). Salicylic acid and hydrogen peroxide improve antioxidant response and compatible Osmolytes in wheat (*Triticum aestivum L.*) under water deficit. *Agric Res*, *10*, 175–186. <https://doi.org/10.1007/s40003-020-00490-3>
- Singh, A. L., Bishi, S. K., Mahatama, M. K., Chaudhari, V., Thawait, L. K., Sushmita. (2017). High zinc density crop genotypes are a solution in alleviating zinc malnutrition in India Indian. *Journal of Agricultural Biochemistry*, *30*(2), 107–114

- Singh, A. L., Nakar, R. N., Chaudhari, V., Chakraborty, K., Kalariya, K. A., Gangadhara, K., Bishi, S. K., Sushmita, Patel, C. B. (2018). Photosynthetic efficiency among Indian peanut cultivars and influence of seasonal variation and zinc. *Indian Journal of Plant Physiology*, 23(2), 325–341.
- Singh, A. L., & Chaudhari, V. (1991). Screening of groundnut varieties tolerant to iron chlorosis. *Indian Journal of Agricultural Sciences*, 61(12), 925–927.
- Singh, A. L., & Chaudhari, V. (1992). Enzymatic studies in relation to micronutrient deficiencies and toxicities in groundnut. *Plant Physiology and Biochemistry*, 19, 107–109.
- Singh, A. L., & Chaudhari, V. (1993). Screening of groundnut germplasm collection and selection of genotypes tolerant of lime-induced iron-chlorosis. *Journal of Agricultural Science*, 121, 205–211.
- Stein, A. (2010). Global impacts of human mineral malnutrition. *Plant and Soil*, 335, 133–154.
- Stein, R. J., & Waters, B. M. (2011). Use of natural variation reveals core genes in the transcriptome of iron-deficient *Arabidopsis thaliana* roots. *Journal of Experimental Botany*, 63, 1039–1055.
- Sun, B., Jing, Y., Chen, K., Song, L., Chen, F., & Zhang, L. (2007). Protective effect of nitric oxide on iron deficiency-induced oxidative stress in maize (*Zea mays*). *Journal of Plant Physiology*, 164, 536–543. <https://doi.org/10.1016/j.jplph.2006.02.011>
- Takagi, S., Nomoto, K., & Takemoto, S. (1984). Physiological aspects of mugineic acid, a possible phytosiderophore of gramineous plants. *Journal of Plant Nutrition*, 7, 469–477.
- Tejada-Jiménez, M., Castro-Rodríguez, R., Kryvoruchko, I., Lucas, M. M., Udvardi, M., Imperial, J., et al. (2015). *Medicago truncatula* natural resistance-associated macrophage protein1 is required for iron uptake by rhizobia-infected nodule cells. *Plant Physiology*, 168, 258–272. <https://doi.org/10.1104/pp.114.254672>
- Tewari, R. K., Kumar, P., & Sharma, P. N. (2008). Morphology and physiology of zinc-stressed mulberry plants. *Journal of Plant Nutrition and Soil Science*, 171, 286–294.
- Theocharis, C. (2014). Plant responses to iron, manganese, and zinc deficiency stress. In *Emerging Technologies and Management of Crop Stress Tolerance*, Academic Press. ISBN 9780128008768. <https://doi.org/10.1016/B978-0-12-800876-8.00013-8>, (pp. 293–311).
- Tiong, J., McDonald, G., Genc, Y., Shirley, N., Langridge, P., & Huang, C. Y. (2015). Increased expression of six ZIP family genes by zinc (Zn) deficiency is associated with enhanced uptake and root-to-shoot translocation of Zn in barley (*Hordeum vulgare*). *New Phytologist*, 207, 1097–1109. <https://doi.org/10.1111/nph.13413>
- Tiwari, R. K., Lal, M. K., Kumar, R., Chourasia, K. N., Naga, K. C., Kumar, D., & Zinta, G. (2020). Mechanistic insights on melatonin mediated drought stress mitigation in plants. *Physiologia Plantarum*. <https://doi.org/10.1111/ppl.13307>
- Tolay, I. (2021). The impact of different Zinc (Zn) levels on growth and nutrient uptake of Basil (*Ocimum basilicum* L.) grown under salinity stress. *PLoS ONE*, 16(2), e0246493. <https://doi.org/10.1371/journal.pone.0246493>
- Treeby, M., Marschner, H., & Romheld, V. (1989). Mobilization of iron and other micronutrient cations from a calcareous soil by plant borne, microbial and synthetic metal chelators. *Plant and Soil*, 114, 217–226.
- Varotto, C., Maiwald, D., Pesaresi, P., Jahns, P., Salamini, F., & Leister, D. (2002). The metal ion transporter *IRT1* is necessary for iron homeostasis and efficient photosynthesis in *Arabidopsis thaliana*. *The Plant Journal*, 31(5), 589–599.
- Vert, G., Grotz, N., Dedaldechamp, F., Gaymard, F., Guerinot, M. L., Briat, J. F., & Curie, C. (2002). *IRT1*, an *Arabidopsis* transporter essential for iron uptake from the soil and for plant growth. *The Plant Cell*, 14(6), 1223–1233.
- Wang, B., Wei, H., Xue, Z., & Zhang, W. H. (2017). Gibberellins regulate iron deficiency-response by influencing iron transport and translocation in rice seedlings (*Oryza sativa*). *Annals of Botany*, 11, 945–956. <https://doi.org/10.1093/aob/mcw250>
- Waters, B. M., & Grusak, M. A. (2008). Whole-plant mineral partitioning throughout the life cycle in *Arabidopsis thaliana* ecotypes Columbia *Landsberg erecta*, Cape Verde Islands, and the mutant line ysl1ysl3. *New Phytologist*, 177, 389–405. <https://doi.org/10.1111/j.1469-8137.2007.02288.x>
- White, P. J., & Broadley, M. R. (2009). Biofortification of crops with seven mineral elements often lacking in human diets -iron, zinc, copper, calcium, magnesium, selenium and iodine. *New Phytologist*, 182, 49–84.
- WHO. (2017). The double burden of malnutrition: Policy brief. Available online at: <http://www.who.int/nutrition/publications/doubleburdenmalnutrition-policybrief/en/>.
- Xia, X. J., Zhou, Y. H., Shi, K., Zhou, J., Foyer, C. H., & Yu, J. Q. (2015). Interplay between reactive oxygen species and hormones in the control of plant development and stress tolerance. *Journal of Experimental Botany*, 66, 2839–2856. <https://doi.org/10.1093/jxb/erv089>
- Xiong, H., Kobayashi, T., Kakei, Y., Senoura, T., Nakazono, M., Takahashi, H., et al. (2012). *AhNRAMP1* iron transporter is involved in iron acquisition in peanut. *Journal of Experimental Botany*, 63, 4437–4446. <https://doi.org/10.1093/jxb/ers117>
- Xu, Y., Wang, B., Yu, J., Ao, G., & Zhao, Q. (2010). Cloning and characterisation of *ZmZLP1*, a gene encoding an endoplasmic reticulum-localised zinc transporter in *Zea mays*. *Functional Plant Biology*, 37(3), 194–205.
- Yuan, Y. X., Zhang, J., Wang, D. W., & Ling, H. Q. (2005). *AtbHLH29* of *Arabidopsis thaliana* is a functional ortholog of tomato *FER* involved in controlling iron acquisition in Strategy I plants. *Cell Research*, 15, 613–621.
- Zaharieva, T. B., & Abadia, J. (2003). Iron deficiency enhances the levels of ascorbate, glutathione, and related enzymes in sugar beet roots. *Protoplasma*, 221, 269–275.
- Zanin, L., Venuti, S., Zamboni, A., et al. (2017). Transcriptional and physiological analyses of Fe deficiency response in maize reveal the presence of *Strategy I* components and Fe/P interactions. *BMC Genomics*, 18, 154. <https://doi.org/10.1186/s12864-016-3478-4>
- Zhang, X., Zhang, D., Sun, W., & Wang, T. (2019). The adaptive mechanism of plants to iron deficiency via iron uptake, transport, and homeostasis. *International Journal of Molecular Sciences*, 20, 2424. <https://doi.org/10.3390/ijms20102424>
- Zhou, C., Liu, Z., Zhu, L., Ma, Z., Wang, J., & Zhu, J. (2016). Exogenous melatonin improves plant iron deficiency tolerance via increased accumulation of polyamine-mediated nitric oxide. *International Journal of Molecular Sciences*, 17, 1777. <https://doi.org/10.3390/ijms17111777>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.