

Fe Uptake and Transport

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The mode of iron (Fe) uptake and transport in cereal species is distinguished from that in other plant species by the synthesis and utilization of phytosiderophores, which are a group of Fe chelators involved in Fe mobilization from the environment as well as within the plant body. In this entry, the overview of the molecular mechanisms behind the Fe uptake and transport is presented, highlighting the commonality and diversity among cereal species.

Keywords: Iron ; Strategy I ; Strategy II ; Nicotianamine ; Phytosiderophore ; YSL

1. Fe Uptake and Transport in Cereals

In this section, we provide a concise overview of the mechanisms underlying Fe homeostasis in cereal crops, highlighting their diversity among cereal species and recent insights. Readers interested in a detailed review on the mechanisms, especially with an extensive graphical illustration, are referred to preceding articles [\[1\]\[2\]\[3\]\[4\]](#).

1.1. Fe Uptake System and Phytosiderophore Synthesis

In aerobic soil conditions, Fe is mostly present as sparingly soluble ferric oxides, which cannot be taken up by plants as such. So as to take up sufficient Fe from the soil, graminaceous species employ a mode of Fe acquisition called Strategy II [\[5\]\[6\]](#). In Strategy-II Fe uptake, plants secrete a group of Fe(III) chelators called mugineic-acid family phytosiderophores (PS) from the roots via TRANSPORTER OF MUGENEIC ACID 1 (TOM1) [\[7\]](#). The resultant Fe(III)–PS complex are taken up by the cereal plants through YELLOW STRIPE 1 (YS1) or YS1-LIKE (YSL) transporters, such as maize (*Zea mays*) YS1 (ZmYS1), barley (*Hordeum vulgare*) YS1 (HvYS1), or rice YSL15 (OsYSL15) [\[8\]\[9\]\[10\]\[11\]](#).

PS are produced from S-adenosyl methionine (SAM; AdoMet), which originates from the methionine cycle through a sequence of enzymatic reactions [\[12\]\[13\]\[14\]](#) (Figure 1), putatively in an intracellular vesicle derived from rough endoplasmic reticulum (rER) [\[15\]\[16\]\[17\]\[18\]\[19\]\[20\]](#). Firstly, nicotianamine (NA) is synthesized via trimerization of SAM by NA SYNTHASE (NAS) [\[21\]](#). Then, deoxymugineic acid (DMA) is synthesized from NA in the reactions mediated by NA AMINOTRANSFERASE (NAAT) and DMA SYNTHASE (DMAS) [\[22\]\[23\]](#) (Figure 1). DMA is the only type of PS produced by rice, wheat (*Triticum aestivum*), and maize [\[24\]\[25\]](#), whereas barley and some other graminaceous species can further convert DMA into other members of PS, some of which have stronger Fe(III)-binding capability than DMA [\[26\]\[27\]\[28\]\[29\]](#). The amount of PS secreted from roots also varies among graminaceous species, positively correlating with the crops' tolerance to Fe deficiency—barley is the most tolerant crop with the largest PS secretion, whereas rice is the least tolerant with the smallest PS secretion [\[30\]](#).

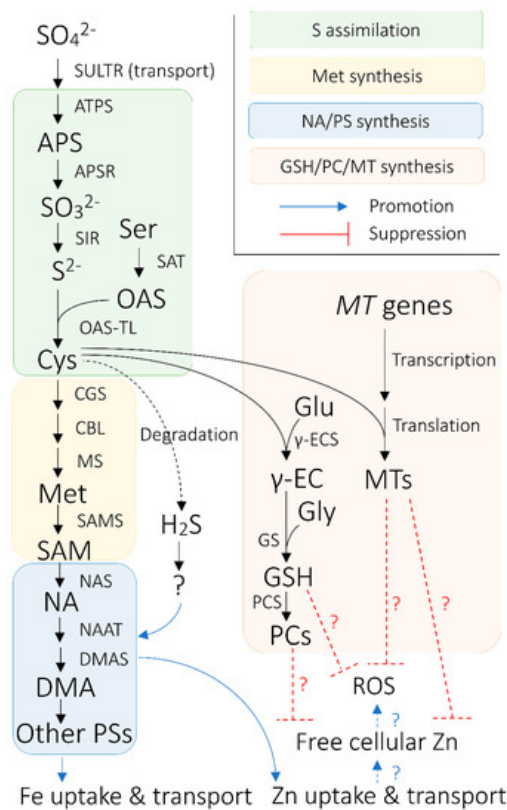


Figure 1. Overview of the connection between sulfur (S) nutrition and iron (Fe) nutrition in cereal plants. Black arrows indicate enzymatic synthetic reactions, unless otherwise indicated. Blue arrows signify promotional effects between biological processes, whereas red bars with flat ends indicate suppressive effects between biological agents and processes. Arrows and bars with dotted lines indicate relationships between biological processes/agents that are hypothetically pronounced in Fe-biofortified crops. Hydrogen sulfide (H_2S) is hypothesized to regulate nicotianamine (NA)/phytosiderophores (PS) synthesis via unknown biological mechanisms or agents. Abbreviations are as follows: APS: ADENOSINE PHOSPHOSULFATE; APSR: APS REDUCTASE; ATPS: ATP SULFURYLASE; CBL: CYSTATHIONINE β -LYASE; CGS: CYSTATHIONINE γ -SYNTHASE; Cys: cysteine; DMA: deoxymugineic acid; DMAS: DMA SYNTHASE; Glu: glutamate; Gly: glycine; GS: GLUTATHIONE SYNTHETASE; GSH: glutathione; Met: methionine; MS: Met synthase; MT: METALLOTHIONEIN; NAAT: NA AMINOTRANSFERASE; NAS: NA SYNTHASE; OAS: O-acetylserine; OAS-TL: OAS (THIOL) LYASE; PC; phytochelatin; PCS: PC synthase; ROS: reactive oxygen species; S^{2-} : sulfide; SAM: S-adenosyl methionine; SAMS: SAM SYNTHASE; Ser: serine; SO_3^{2-} : sulfite; SO_4^{2-} : sulfate; SULTR: SULFATE TRANSPORTER; Zn: zinc; γ -EC: glutamylcysteine; γ -ECS: γ -EC SYNTHETASE.

Relatively modest level of PS secretion from rice may be associated with the environment to which rice and its relatives have adapted [31][32]. Rice is commonly cultivated in water-logged paddy fields, where anaerobic soil conditions prevail. In deoxygenated soil, Fe is reduced to soluble Fe(II) and is fairly available for plant uptake [33]. Thus, in contrast to other cereal species [34], rice partially adopts Strategy-I Fe uptake, in which Fe(II) ions are directly taken up by IRON-REGULATED TRANSPORTERS (IRTs) [31][35]. Although a functional Strategy-II uptake system is present in rice, when Fe(II) ions are abundant in the rhizosphere, Fe acquisition is mainly achieved through Strategy-I uptake, and genes involved in Strategy-II Fe uptake are down-regulated [33][36].

1.2. Potential Diversity in the Manner of Fe Uptake and Radial Fe Transport in Roots

Among cereal species, there are also variations in root anatomy that possibly affect the site of Fe uptake in roots, as well as the fashion of subsequent within-root radial Fe transport required for xylem Fe loading.

The number of Casparian strips, which block apoplastic flow of water and nutrients across the root cell layers, is one of such anatomical variations. Almost all vascular plants have endodermis, a cell layer with a Casparian strip surrounding the root stele [37]. Moreover, the majority of the plants investigated possess exodermis, another cell layer with a Casparian strip beneath the epidermis [38]. Although rice and maize are commonly found to possess both endodermal and exodermal Casparian strips (exodermal species), wheat and barley tend to be void of exodermis (non-exodermal species), though these characteristics may vary depending on the type of roots, genotype, and stress conditions [38][39][40][41][42]. In exodermal species, nutrients should be taken up either by epidermal or exodermal cells because they are the only cell layers contacting the soil solution [37]. In non-exodermal species, on the other hand, cortical and endodermal cells can

contribute to the uptake due to the absence of a barrier for the apoplastic flow of nutrients into the cortex from the external environment [37]. In line with this notion, the expression of Fe(III)-PS uptake transporter in maize, ZmYS1, is confined to epidermal cells [43].

Subsequent to uptake from the rhizosphere, Fe should be radially transported to the root stele for xylem loading. The manner of such within-root Fe transport may also differ, especially between rice and other cereal species, owing to the difference in root anatomy. As a species well adapted to flooded conditions, rice has a highly developed aerenchyma between the endodermis and exodermis, through which air is supplied for the root cells [45]. Because only a small number of cells are alive in rice aerenchyma, there is little symplastic connection between the rice epi/exodermis and stele [46]. This distinct root internal structure in rice requires the nutrients to be apoplastically transported across the cortex before entering the stele, which is putatively mediated by a pair of efflux and influx transporters at the exodermis and endodermis, respectively [47][48]. Rice Fe transporters involved in this transport are currently unknown, but the fact that OsYSL15 is induced not only in epidermis but also in cortex upon Fe deficiency [11][49], even though rice is an exodermal species, suggests the potential involvement of OsYSL15 in radial Fe transport in roots.

Owing to its high redox activity and low solubility, Fe has to be chelated by organic ligands for its solubilization and transport in plants [50]. The main chelators for Fe long-distance transport in cereals are considered to be citrate, NA, and PS [51][52][53][54][55][56][57][58]. In xylem Fe transport, citrate seems to be the major chelator [51][52][54][55], whereas DMA plays a supplementary role, especially under Fe deficiency (Figure 2) [52][53]. As citrate is considered to be loaded onto xylem via FERRIC REDUCTASE DEFECTIVE LIKE 1 (FRDL1) transporter in a form unbound to Fe, there can be a transporter that mediates unchelated Fe loading onto xylem, which is yet to be identified [55]. The loading of DMA and NA onto xylem may be undertaken by TOM2 and EFFLUX TRANSPORTER OF NA 1 (ENA1), respectively [59][60].

Figure 2. Graphical summary of important cereal iron (Fe) biofortification strategies. Proteins surrounded with blue squares are those whose modulation leads to increase in grain Fe concentration. Blue underlines indicate the molecules whose genes are up-regulated in rice lines overaccumulating nicotianamine (NA) or overexpressing *NA SYNTHASE* (*NAS*). Red underscores refer to the complexes whose amount is putatively increased in *NAS*-overexpressing lines. Black arrows indicate the movement of molecules unless otherwise noted, whereas green arrows signify synthetic enzymatic reactions. In the inset for Fe homeostasis regulation, blue arrows and red bars with flat ends indicate promotional and suppressive effects between molecular agents and/or processes, respectively. In the same inset, black arrows pointing to the bin indicate proteasomic degradation of proteins. Abbreviations are as follows: AtNRAMP3: NATURAL RESISTANCE-ASSOCIATED MACROPHAGE PROTEIN 3 from *Arabidopsis thaliana*; bHLH156: BASIC HELIX-LOOP-HELIX 156; DMA: deoxymugineic acid; DMAS: DMA SYNTHASE; FER: FERRITIN; HRZ: HEMERYTHRIN MOTIF-CONTAINING REALLY INTERESTING NEW GENE- AND ZINC-FINGER PROTEIN; IBP1: IDEF1-BINDING PROTEIN 1; IDEF1: IRON

DEFICIENCY-RESPONSIVE ELEMENT-BINDING FACTOR 1; IRO2/3: IRON-RELATED TRANSCRIPTION FACTOR 2/3; IRT1: IRON-REGULATED TRANSPORTER 1; PRI: POSITIVE REGULATOR OF IRON DEFICIENCY RESPONSE; TOM1: TRANSPORTER OF MUGENIC ACID 1; VIT: VACUOLAR IRON TRANSPORTER; YSL2/15: YELLOW STRIPE-1 LIKE 2/15.

In phloem, NA and/or DMA are likely to be the primary chelators for Fe (Figure 2) ^{[51][56][61]}. A Fe(II)-NA transporter YSL2, and possibly a Fe(III)-DMA transporter YSL18, contribute to Fe transport via phloem in rice ^{[61][62][63]}, which suggests that Fe is primarily loaded onto phloem in a chelated form. It remains to be examined whether or not there is a phloem loading of chelator-free Fe.

Fe transferred from roots to shoots is once accumulated in stem nodes and distributed to various aboveground tissues, probably via phloem ^[64]. This implies that there is a mechanism mediating xylem-to-phloem Fe transfer in stem nodes (Figure 2), an organ that plays a central role in intervascular nutrient transfer and nutrient delivery to various aboveground tissues in graminaceous species ^{[65][66]}. The transporters mediating this putative xylem-to-phloem Fe transfer at stem nodes are yet to be identified. Besides being a hub for nutrient distribution, stem nodes pool nutrients in their apoplastic regions ^{[67][68][69]}. The role of citrate and citrate transporter FRDL1 in remobilizing Fe deposited in the apoplastic regions of the nodes has been described ^[70].

Graminaceous plants can also accumulate Fe in apoplastic spaces in roots, which can serve as a reservoir for Fe, especially under Fe-limiting conditions ^{[71][72][73][74][75]}. Phenolic compounds can contribute to solubilizing Fe precipitated in the root apoplastic regions. In rice, PHENOLICS EFFLUX ZERO1 (PEZ1) is identified as a transporter responsible for mobilizing precipitated Fe in the root xylem by pumping in protocatechuic acid (PCA) in the xylem sap ^[74]. In addition, PEZ2 provides phenolics to solubilize Fe in the apoplasm in the roots ^[75].

Route for Fe loading onto the grains may differ among cereal species as well. In wheat and barley, xylem is discontinued towards the grain ^{[76][77]}. On the other hand, there is no discontinuity of xylem towards developing rice grains ^{[78][79]}. This implies that the relative contribution of phloem-mediated source-to-sink Fe translocation to grain Fe concentration may differ among cereals.

In cereal species including rice, there is no symplastic connection between the maternal tissue and the filial tissues in grains ^{[76][80]}. Therefore, Fe must be transported through a pair of unknown efflux and influx transporters in order to be loaded onto the grain. After grain loading, Fe tends to accumulate at a higher concentration in the aleurone layer than in the endosperm ^{[81][82]}. In aleurone layer, Fe is often associated with phytic acids, which makes Fe unavailable for humans ^{[81][83]}. Fe transfer between endosperm and embryo seems to be mediated by YSL9 transporter in rice ^[84].

1.4. Fe Intracellular Homeostasis

Given the reactive nature of Fe, surplus Fe has to be sequestered in vacuole in plant cells ^[85]. On the other hand, organelles such as mitochondria and chloroplasts should be supplied with ample Fe to fulfill their physiological roles involving many redox reactions ^{[86][87]}. To meet these somewhat dilemmatic needs, Fe transport and storage in these organelles are tightly controlled. In the last decade, roles of transporters and Fe-binding agents in the regulation of intracellular Fe homeostasis have been gradually revealed in cereals, especially in rice.

MITOCHONDRIAL IRON TRANSPORTER (MIT) assumes a critical role in providing Fe for mitochondria ^[88]. As Fe importers for chloroplasts, Fe DEFICIENCY-RELATED 3 (FDR3) and FDR4 transporters were identified in maize ^{[89][90]}. Fe storage in plastids, particularly under sufficient or excess Fe conditions, is likely to be mediated by Fe storage protein FERRITIN (FER), whose genes encode transit peptides for plastid localization at its N-terminus ^{[91][92][93]}. In addition to FER, VACUOLAR IRON TRANSPORTERS (VITs) on the tonoplast promote compartmentalization of surplus Fe into vacuoles ^{[94][95]}. In rice, knockdown of a tonoplast-localized DMA influx transporter VACUOLAR MUGENIC ACID TRANSPORTER (VMT) leads to higher root cell sap Fe concentration as well as lower xylem Fe concentration ^[96]. This implies that Fe once sequestered in vacuoles is stored as Fe(III) and can be exported again as Fe(III)-DMA. Moreover, it has been postulated that FERRIC REDUCTASE OXIDASE 1 (FRO1) localized on rice tonoplast can contribute to increasing the Fe availability for cytoplasm by reducing Fe(III) to Fe(II) in vacuoles ^[97]. Therefore, there may also be an unknown Fe(II) export mechanism from the vacuoles, in addition to the Fe(III)-DMA export machinery.

1.5. Fe Homeostasis Regulation

Genes involved in Fe uptake are up-regulated in response to Fe deficiency in graminaceous species, whereas they are down-regulated under Fe sufficiency [33][98][99][100][101]. An elaborate network of regulatory factors underlying such an adaptive response has been delineated recently in rice, which may be transferrable to other cereal crops. The factors that assume a pivotal role in the regulatory network in rice are IRON DEFICIENCY-RESPONSIVE ELEMENT-BINDING FACTOR 1 (IDEF1) and HEMERYTHRIN MOTIF-CONTAINING REALLY INTERESTING NEW GENE- AND ZINC-FINGER PROTEINS (HRZs), which are classified into Fe sensors by virtue of their putative capacity to alter their function to regulate Fe homeostasis by directly sensing the Fe availability in the cells [102].

IDEF1 is a positive regulator of Fe uptake-related genes, which can sense the Fe availability in cells by binding to Fe and other metal ions (Figure 2) [103][104][105]. IDEF1 interacts with a *cis*-element IDE1 in the promoter regions of Fe deficiency-responsive genes to up-regulate them [103][106]. As there is a diversity in amino acid sequence in the metal-binding region of IDEF1 among different graminaceous species, there may also be an inter-species functional diversity for IDEF1 [105]. *IDEF1* gene is expressed irrespective of the Fe status of the plant, but its protein is prone to 26S proteasome-dependent degradation under Fe-sufficient conditions (Figure 2) [107][108]. In Fe-deficient conditions, its degradation is prevented by IDEF1-BINDING PROTEINS (IBPs), and as a result, genes involved in Fe deficiency response are induced (Figure 2) [107]. *IBP* genes have many IDE1 motifs in their promoter regions and are positively regulated by IDEF1, thereby constituting a positive feedback loop between IDEF1 and IBP1 for Fe deficiency response (Figure 2) [107]. In rice, IDEF1 is known to positively regulate another transcription factor governing Fe deficiency response, called IRON-RELATED TRANSCRIPTION FACTOR 2 (IRO2) (Figure 2) [103][109]. IRO2 can induce genes involved in Strategy-II Fe uptake upon Fe deficiency by binding to their promoter regions [110]. It has been recently revealed that IRO2 requires another transcription factor BASIC HELIX-LOOP-HELIX 156 (bHLH156) to localize in the nucleus and regulate gene expression (Figure 2) [111].

In contrast to IDEF1, HRZ1 and HRZ2 are identified as negative regulators of Strategy-II Fe uptake in rice, especially when there is sufficient external Fe available [112]. Supposedly, HRZs sense Fe availability also by binding with Fe and other metal ions (Figure 2) [112]. Like IDEF1, HRZs are as well susceptible to 26S proteasome-dependent degradation in roots, but contrary to IDEF1, they are so regardless of the Fe status (Figure 2) [112]. HRZs negatively regulate Fe uptake and translocation by contributing to the proteasomic degradation of POSITIVE REGULATORS OF IRON HOMEOSTASIS (PRIs) through their ubiquitination (Figure 2) [113][114]. PRIs positively regulate the expression of *IRO2* and also *YSL2*, which is not regulated by *IRO2* [114][115].

Interestingly, *HRZs* are positively regulated by IDEF1 (Figure 2) [112]. Moreover, PRIs, which are deemed overall as positive regulators of Fe uptake and translocation, induce the expression of *IRO3*, which codes for a negative transcription factor for Fe deficiency response in rice (Figure 2) [113][114][116]. These interrelations between antagonistic regulatory factors could be part of a sophisticated machinery to prevent excessive Fe deficiency response.

There are several other characterized regulatory factors involved in Fe homeostasis regulation in rice, whose association with the abovementioned regulation network, with IDEF1 and HRZs at its core, is absent or unknown. In parallel to IDE1 and IDEF1, a pair of *cis*-element and *trans*-factor, namely, IDE2 and IDEF2, were found to positively regulate Fe deficiency response [106][117]. Moreover, rice bHLH133 is a transcription factor that contributes to Fe retention in roots under Fe-deficient conditions [118]. Rice homologues of IRON MANs (IMAs), which are regulatory factors identified in *Arabidopsis* (*Arabidopsis thaliana*) as a positive regulator of systemic Fe deficiency signaling, are also likely to have similar roles in rice [119].

One rare exception of a transcription factor related to Fe transport identified first in wheat is NO APICAL MERISTEM B-1 (NAM B-1) [120]. Wheat NAM B-1 promotes the senescence of vegetative tissues, which leads to increased translocation of Fe from leaves to grains along with other nutrients [120]. Although NAM B-1 homologue is identified in rice, it does not have an identical role as the wheat counterpart [121].

In addition to transcription factors, signal transduction through phytohormones such as auxin or jasmonates are suggested as being important components of Fe deficiency response [122][123]. NA is also speculated as being a possible Fe deficiency signaling molecule [19][102][124], given that the genes involved in Fe acquisition and translocation are up-regulated in rice lines accumulating increased NA [18][125][126].

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