

MINI-REVIEW



Is there a strategy I iron uptake mechanism in maize?

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ABSTRACT

Iron is a metal micronutrient that is essential for plant growth and development. Gramineous and nongramineous plants have evolved different mechanisms to mediate Fe uptake. Generally, strategy I is used by nongramineous plants like *Arabidopsis*, while gramineous plants, such as rice, barley, and maize, are considered to use strategy II Fe uptake. Upon the functional characterization of *OsIRT1* and *OsIRT2* in rice, it was suggested that rice, as an exceptional gramineous plant, utilizes both strategy I and strategy II Fe uptake systems. Similarly, *ZmIRT1* and *ZmZIP3* were identified as functional zinc and iron transporters in the maize genome, along with the determination of several genes encoding Zn and Fe transporters, raising the possibility that strategy I Fe uptake also occurs in maize. This mini-review integrates previous reports and recent evidence to obtain a better understanding of the mechanisms of Fe uptake in maize.

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Iron is an essential micronutrient in plants

Iron plays an essential role in plant growth and development, as it serves as a cofactor in many physiological and biochemical processes, such as photosynthesis and respiration. Fe deficiency leads to growth arrest and reduced grain quality. On the other hand, Fe excess is toxic to plants, as a high cellular Fe level may elevate the rate of $\text{Fe}^{3+}/\text{Fe}^{2+}$ redox reactions, resulting in high oxidation-reduction potential and damage to cells.¹ Therefore, a strictly regulated mechanism is required for plants to maintain Fe homeostasis, which includes the uptake, utility, and storage of Fe. As an initial process, the regulation of Fe uptake is the key step to maintain Fe homeostasis in plants.

Two mechanisms of Fe uptake in plants

Gramineous and nongramineous plants utilize different strategies of Fe uptake. Strategy I is used by nongramineous plants, such as *Arabidopsis*, which take up Fe(II) as their main source of iron.^{2,3} The whole process is divided into several steps. First, insoluble ferric compounds in soil are acidified by protons exported from the root cells via H^+ ATPase.⁴⁻⁶ Then, a membrane-bound ferric-chelate reductase, AtFRO2, reduces ferric ions into ferrous ions, which are subsequently taken up into root epidermal cells by a transmembrane transporter, AtIRT1.^{7,8} In contrast, gramineous plants, such as barley, rice, and maize, use strategy II to take up Fe, which is a chelation strategy that includes a series of steps. Primarily, this involves mugineic acids (MAs) that are synthesized by a conserved pathway, which begins with the trimerization of 3 molecules of S-adenosyl-L-methionine into nicotianamine (NA) by nicotianamine synthase (NAS).^{9,10} Then, nicotianamine aminotransferase (NAAT) and

deoxymugineic acid synthase (DMAS) further converted NA into 2'-deoxymugineic acid and MAs,^{11,12} which are secreted into the rhizosphere by the transporter of mugineic acid family phytosiderophores 1 (TOM1). MAs serve as phytosiderophores (PSs), which chelate insoluble Fe in soil, and the Fe(III)-MA complexes are subsequently translocated into root cells by the yellow stripe-like family transporters.^{13,14}

Rice is thought to utilize a combined Fe uptake strategy

Recently, it was proposed that rice utilizes a combined strategy to absorb Fe, as both strategy I and strategy II proteins have been functionally characterized in rice. For instance, OsNAS1, OsNAS2, OsNAAT1, and OsDMAS1 were demonstrated to be key components in the biosynthesis of MAs; TOM1 transports MAs out of cells; while OsYSL15 was reported to take part in the uptake of Fe(III)-MAs into root cells.^{12,15-23} It was also revealed that Fe(II) can be directly absorbed into rice roots by OsIRT1 and OsIRT2. Although there is a lack of evidence for proton extrusion and Fe(III)-chelate reductase activity,^{24,25} these results suggest that the strategy I mechanism is active to some extent in rice. Therefore, rice is considered to be an exceptional gramineous plant that possesses a combined Fe uptake strategy.

Strategy I Fe uptake mechanism may also be present in maize

Although the Fe uptake mechanism has not been as well characterized in maize as in rice, it was generally believed that maize, as a gramineous plant, utilizes strategy II to take up Fe. The evidence supporting this includes the

Table 1. The predicted genes participated in the strategy I mechanism of Fe uptake in maize.

Gene name	Gene ID	Chromosome no.	CDS length	Protein length
<i>ZmFIT</i> (FER like)	103641578	10	1038	345
<i>H⁺ATPase 2</i> (<i>MHA2</i>)	542048	2	2856	951
<i>ZmFRO2</i>	100281526	2	2280	759

following: *ZmYS1* was reported to transport Fe-PS from the soil into root epidermis.^{13,26} In addition, 2 classes of *ZmNAS* genes were identified in the maize genome and the complementary expression pattern of class I and II *ZmNAS* suggests that they may play different roles in the uptake and transport of iron.²⁷ As observed in rice, several genes involved in strategy I were also identified in maize. Nine *ZmZIP* genes were cloned by genome mining and their functions were preliminarily confirmed by a yeast complementation test.²⁸ Moreover, the divalent cation transporting

activity of *ZmIRT1* and *ZmZIP3* was confirmed in plants, as the levels of Zn and Fe were increased in *ZmIRT1*- and *ZmZIP3*-overexpressing Arabidopsis.²⁹ Although there is a lack of evidence regarding whether the strategy I system is intact in maize, several genes encoding transcription factors, plasma membrane H⁺ATPase, and ferric reductases that participate in strategy I were identified in the maize genome. As shown in Table 1, the putative maize orthologs of FIT, H⁺ATPase (MHA), and FRO were identified by BLAST searches using Arabidopsis genes as queries. It was reported that the transcript factor AtFIT regulates the expression of *FRO* and *IRT1* in Arabidopsis,³⁰⁻³² while AtAHA and AtFRO are responsible for increasing Fe(III) solubility and reducing ferric ions into ferrous ions, respectively.^{2,3} The existence of *FRO* and *MHA* genes in maize, which are absent from the rice genome, indicates that maize may have a regulatory mechanism similar to that in Arabidopsis, and the strategy I Fe uptake mechanisms retained in maize and rice may differ from each other.

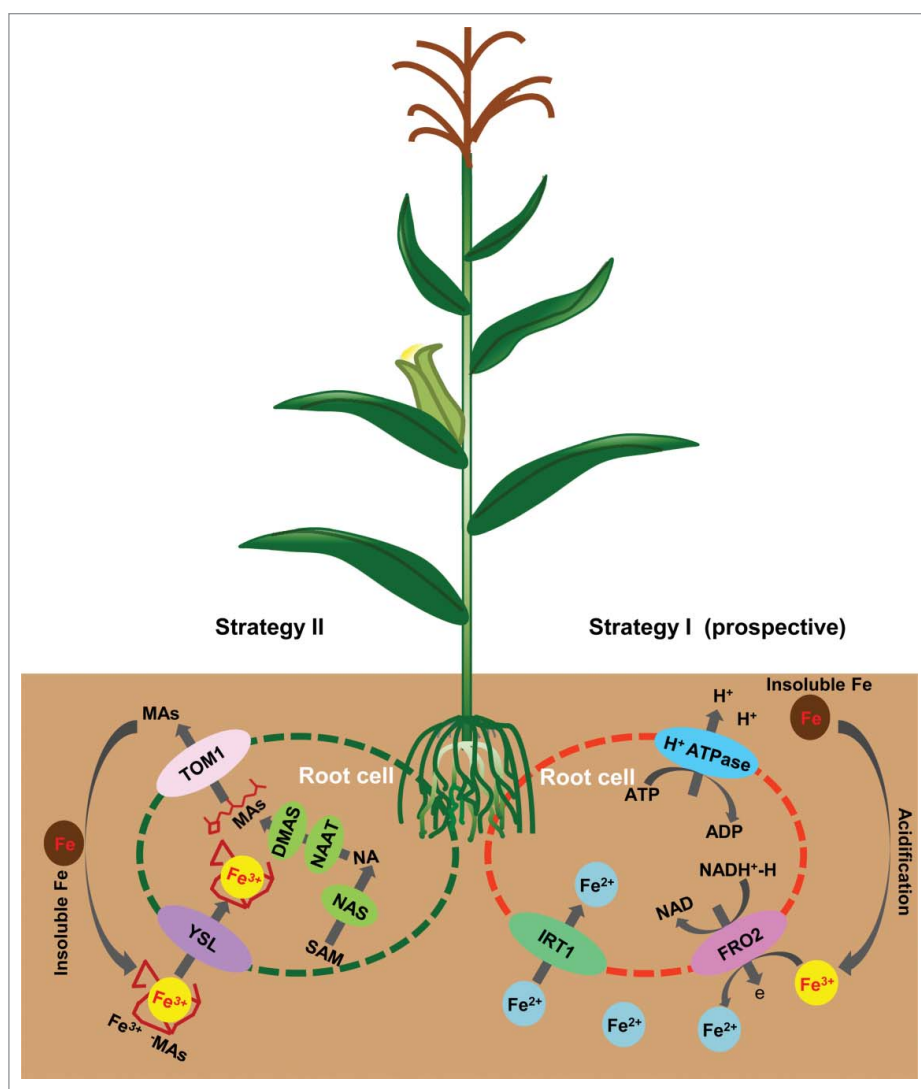


Figure 1. A hypothetical scheme showing the co-existence of strategy I and strategy II Fe uptake system in maize. In strategy II, MAs are synthesized in root cells by NAS, NAAT and DMAS, and MAs are secreted into rhizosphere by TOM1. Then, Fe(III)-MAs are transported in to cells by YSLs. Strategy I may serve as a complementary mechanism in maize, which involves the direct acquisition of Fe(II) by *ZmIRT1* on root surface. The genes corresponding for acidification and ferric reduction are still uncovered in maize. MAs, mugineic acids; NAS, nicotianamine synthase; NAAT, nicotianamine aminotransferase; DMAS, deoxymugineic acid synthase; YSL, yellow strip like; TOM1, transporter of mugineic acid family phytosiderophores 1; IRT1, iron regulated transporter 1.

Conclusions and perspectives

An understanding of the Fe uptake mechanism in maize may help to explain the regulation of Fe assimilation in graminaceous plants, and provide genetic resources for the biofortification of maize varieties that are valuable due to their levels of essential metal micronutrients. In this mini-review, we have summarized the functionally characterized transporters and pathways involved in Fe uptake in maize and identified putative strategy I genes in maize, such as *ZmFIT*, *ZmMHA*, and *ZmFRO* by homolog searching. From our results, we hypothesize that strategy I may act as a complementary mechanism for Fe uptake in maize (Fig. 1). Further studies regarding the physiological functions of putative *ZmFIT*, *ZmFRO*, and *ZmMHA* should be undertaken to clarify their roles in mediating Fe uptake, and to confirm whether the strategy I mechanism is active in maize or whether the findings simply represent a group of functionally degenerate genes that are an evolutionary artifact.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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