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Iron transport in plants: better be safe than sorry

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Iron is essential for plant cell function and more specifically for photosynthesis. Plants have evolved highly efficient systems to take up iron from the soil. However, activating iron uptake is a double jeopardy: not only iron itself is toxic but iron uptake systems are poorly selective and allow the entry of other potentially toxic metals. Plants therefore tightly control iron uptake at the transcriptional and post-translational level and have evolved mechanisms to cope with the concomitant entry of toxic metals. In plant cells, iron has to be distributed to chloroplasts and mitochondria or may be stored safely in vacuole. Distinct transcriptional networks regulating uptake and intracellular distribution are being uncovered, while iron sensing mechanisms remain elusive.

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Introduction

A large number of cellular enzymes depend on iron for their biological function, making of iron an essential element for basic cellular processes in most living organisms including plants. Iron can alternate between two oxidation states, Fe^{3+} or ferric iron and Fe^{2+} or ferrous iron. Cell metabolism uses iron-containing cofactors under the forms of heme or Fe–S clusters to transfer electrons, such as in mitochondial respiration or chloroplast photosynthesis. Although quite abundant in soils, iron tends to be poorly available to plants. All living organisms have thus evolved very efficient strategies to acquire iron. The ability to gain and loose electrons also renders iron potentially toxic. In the presence of oxygen, iron engages in the Fenton chemistry which generates highly toxic reactive oxygen species.

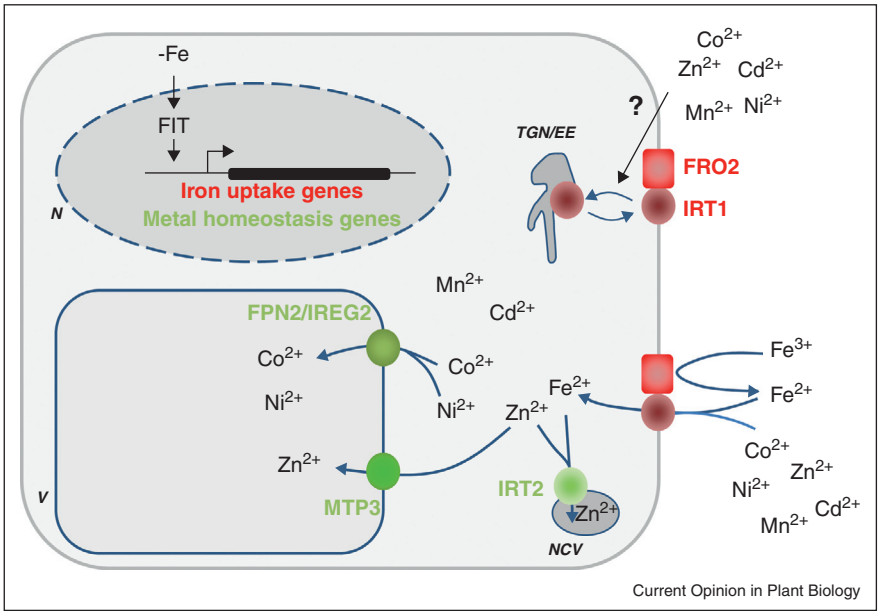
The absolute requirement of iron for life and its biological reactivity are the basis for the complex networks of transport systems and regulatory mechanisms targeting transporters to ensure proper and safe delivery of iron to its final destination. These transport activities include iron uptake from the environment, iron distribution to various organs and tissues and organelles. In this review, we will highlight recent findings on the mechanisms of iron uptake in root cells and intracellular partitioning, but will not address long-distance transport. The complex regulation of these transporters in the context of iron and metal nutrition will be discussed.

Iron uptake

The non-specific diffusion of nutrients including iron between root cells is kept in check by two cell layers harboring waxy compounds on their surface, that are, the exodermis and the endodermis [1]. Iron uptake from the soil occurs in cells layers external to such diffusion barriers. Non-graminaceous plants, including *Arabidopsis thaliana*, take up iron by the sequential acidification-reduction-transport strategy (strategy I). The Arabidopsis *FRO2* and *IRT1* genes encode the ferric reductase and the iron transporter involved in iron acquisition from the soil, respectively [2]. Both genes are specifically expressed in the root epidermis and are critical for iron uptake and plant growth. IRT1 shows low selectivity when expressed in yeast and mediates Zn, Mn, Co, Ni and Cd uptake in addition to Fe transport [3] (Figure 1). Recently, the *AHA2* gene was shown to account for rhizosphere acidification in response to low iron [4]. It is quite obvious that the three core components of the root iron uptake system have to work in a coordinated fashion and in close proximity to maximize the efficiency of reduction-based transport of iron. Other metal transporters such as NRAMP1 have been implicated in iron uptake from the soil, although marginally [5]. Its specific contribution to iron nutrition is still unclear and may reside in its relative affinity for iron and its expression profile in response to intrinsic and environmental signals.

Grass plants have evolved a distinct mechanism to acquire Fe from the soil, known as the chelation strategy or Strategy II. The chelation is achieved by strong Fe(III) chelators from the mugineic acid (MA) class named phytosiderophores [3]. Analysis of genes induced by low iron in rice identified a putative efflux transporter of small molecules, TOM1 [6]. TOM1 mediates efflux of deoxymugineic acid when expressed in xenopus oocyte, and is expressed in rice root cells. A natural mutation in maize called yellow stripe3 (*ys3*) impairs phytosiderophore secretion even though phytosiderophores synthesis is not compromised [7]. Further work will determine if *ys3* is a loss-of-function mutation of the TOM1 ortholog in maize. The Fe(III)-phytosiderophore complex is then

Figure 1



Integrated control of iron and metal homeostasis in Arabidopsis root epidermal cells. Iron deficiency triggers transcriptional activation of genes encoding the iron uptake machinery (FRO2 and IRT1) in the nucleus (N) to maximize iron absorption. Genes encoding metal transporters (IRT2, IREG2/FPN2, MPT3) are co-regulated with IRT1 to compartmentalize potentially toxic metals in the vacuole (V) or non-characterized intracellular vesicles (NCV) upon high metal influx conditions. The localization of IRT1 protein between the cell surface and the *trans*-Golgi Network/Early endosomes is controlled by ubiquitination and may be under the control of non-iron metals transported by IRT1, thus providing another layer of control for metal uptake.

taken up into root cells via YELLOW STRIPE1 and YELLOW STRIPE-Like transporters in different grasses [3].

Rice is atypical because it absorbs iron using features of both strategy I and II plants, including a ferrous iron transporter OsIRT1 and the Fe(III)-phytosiderophore based uptake using OsYSL15 [8–10]. Rice roots however display very low ferric reductase activity [9]. Rice thus appear to have evolved and adapted to its growth habitat where oxygen is low due to flooding, thus favoring the existence of iron into its Fe(II) form.

Changes in morphology

Iron deficiency increases not only the absolute quantity of transporters facing the rhizosphere, but also the exchange surface of the root system and its foraging capacity [11–13]. This is of particular importance for the uptake of immobile nutrients such as iron. Iron limitation affects the root system architecture by promoting lateral root elongation in zones where Fe is available, a process dependent on auxin and the AUX1 auxin influx transporter [14••]. The shortage in iron also triggers the formation of ectopic root hairs at positions normally occupied by non-hair cells in an ethylene-dependent and auxin-dependent manner [13], and leads to bifurcated root hairs with two tips. This peculiar phenotype requires the ubiquitin-conjugating enzyme UBC13 [15], although the precise molecular events are unknown.

Partitioning of iron

After iron has been taken up from the soil by plant roots, it has to be distributed to plant tissues and organs by long distance transport. Within plant cells, the quantitatively most important sites for iron use are chloroplasts and mitochondria [16]. Chloroplast Fe accounts for 70–90% of cellular iron in mesophyll cells [16]. Iron compartmentalization varies greatly between cell types and organs. For example, in Arabidopsis mature embryo, a major fraction of total iron is localized in the vacuoles of endodermal cells [17–19]. Recently, iron was also detected at high concentrations in the nucleolus in Arabidopsis leaves and pea embryo [20•]. However, the function of nucleolar iron or the mechanisms that allow accumulation in this nuclear domain remains to be discovered.

Vacuole

The role of vacuoles in iron storage has been clearly demonstrated in Arabidopsis mature embryos. Iron imaging techniques have shown that iron is accumulated in globoids which are embedded in the protein storage vacuoles in endodermal cells of Arabidopsis embryo [17–19]. Iron is also associated to globoids in other species including wheat [21]. AtVIT1, a homolog of yeast CCC1