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**Title**

Mechanisms of iron homeostasis in plants and their regulations

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## **Introduction**

Plants are an essential component of the food chain because they are responsible for mineral acquisition from the soil and for carbon, sulfur and nitrogen assimilation leading to amino-acids and vitamins synthesis. They bring, therefore, essential nutrients to the animal and human diets. In this context, iron is concerned twice. As an essential metal, iron acquisition from the soil by plant roots, enables its entry into the food chain. Furthermore, biochemical reactions required for mineral C, N, and S assimilation into organic molecules take place in plant specific sub-cellular organelles, the plastids, and involve an important number of proteins containing iron as heme or Fe-S clusters (1).

## **Iron uptake and distribution within the plant**

Plants are botanically sub-divided into the graminaceous and non-graminaceous families. These two groups use different pathways to mine iron from the soil. The non-graminaceous plants use a Fe(III) reduction / Fe (II) uptake strategy (2). In the model plant *Arabidopsis* iron deficiency leads to induction of the *FRO2* gene, encoding a ferric chelate reductase. The produced Fe (II) is then transported inside the root by the *IRT1* gene product, a metal transporter located at the plasmalemma of root epidermal cells (3). The IRT1 / FRO2 system is subjected to complex transcriptional and post-transcriptional regulations (4, 5), involving iron itself as a local inducer, and also uncharacterized systemic signals (6, 7). In graminaceous plants iron is taken up by the soil following a chelation-based strategy. In maize, iron deficiency induces root secretion of deoxymugineic acid (DMA), which is synthesized from nicotianamine, a secondary amino-acid derived from methionine (8). DMA has a strong affinity for Fe(III), and the Fe(III)-DMA chelate is transported inside the roots by a specific transporter, named YS1 (9). Iron is then transported from roots to leaves, chelated as Fe (III)-citrate, through xylem vessels. More generally, small organic molecules and various transporters (YSLs, NRAMPs, VIT1) are responsible for iron distribution between the various organs of a plant and between the various subcellular compartments (10).

## **Iron utilization**

In leaves most of the iron is found within the chloroplasts where photosynthesis takes place to assimilate C and produce O<sub>2</sub>. In addition to the general mitochondrial Fe-S cluster synthesis pathway, chloroplasts are autonomous for their Fe-S cluster synthesis (1,11). In addition, it is within this plant specific subcellular compartment that ferritins store and buffer iron, therefore participating to protect against oxidative stress (12). In contrast to animals, regulation of ferritin gene expression in response to iron excess occurs mainly at the transcriptional level. Cytosolic aconitase is not involved in this regulation (13) which requires a DNA *cis*-regulatory element named IDRS (for Iron Dependent Regulatory Sequence), necessary to repress *AtFer1* ferritin gene expression under low iron conditions (14). The signal transduction pathway leading to the increase of *AtFer1* transcript level after iron treatment requires nitric oxide, produced in the plastids after iron treatment, and which acts downstream of iron and upstream of a PP2A-type phosphatase. The repressor down-regulating plant ferritin gene expression under low iron conditions is unlikely a transcription factor directly bound to the IDRS. This repressor is ubiquitinated upon iron treatment and subsequently degraded through a proteasome-dependent pathway (15).

## **Conclusion**

This last decade, a wealth of information describing iron transporters in plants has been obtained. It has enabled to characterize the high affinity root iron uptake systems, both in grass and non-grass plants. These systems are very efficient under iron starvation conditions.

They could also play a role in the uptake of iron under Fe-sufficient conditions. However, most of these molecular data have been obtained using hydroponic or *in vitro* culture systems. Very little is known about iron uptake mechanisms under conditions prevailing within the rhizosphere. There is clearly a need of research in that direction.

Although putative transporters involved in iron allocation within the plant have been described, we are still far from a complete knowledge of their respective roles in major physiological functions such as leaf metabolism and photosynthesis, nodule biology and nitrogen fixation or iron storage in seeds.

Iron is a limiting factor for plant productivity and biomass production. Heme and iron-sulfur proteins play a key role in these aspects and our knowledge of the biosynthesis of these co-factors has recently made huge progress. However, the beneficial effect of iron on plant biomass and seed production appears dependent on the presence of ferritins (12, 16). Indeed, growing a ferritin-less mutant under elevated iron conditions revealed major developmental defects associated with iron homeostasis perturbations and oxidative stress. In nature, ferritin gene expression is modulated by many environmental factors. Throughout their life cycle, plants often experience these stresses, which are variable in intensity, location, duration, and which can transiently raise intracellular free iron pools, leading to an increased reactivity with oxygen. Thus, the regulation of ferritin gene expression is indicative of the importance of these proteins for the adaptive response of plants to environmental changes.

The new challenge we are facing now will be to understand how these activities are integrated at the whole plant level, and what are the signaling networks and regulatory molecules responsible for the control of iron dynamics in plants.

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