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Iron dynamics in the soil and its importance for plant health

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Abstract
Iron (Fe) in the soil mostly present in the form of insoluble Fe (III) oxides and hydroxides. The total iron in soil is much higher than most crops require. However, the concentration of free Fe (III) in most agricultural soils is below that required for optimal plant growth. Generally, chelation of Fe (III) is the most successful mechanism by which plants roots can acquire Fe. Production of chelating compounds by microorganisms increases Fe solubility in the rhizosphere and hence increases plant Fe acquisition. Bacterial siderophores, fungal siderophores and other chelating metabolites are assumed to serve as major sources of plant-available Fe in the rhizosphere. In cultivated soils iron is oxidized to form ferric oxide and oxy hydroxides results in low availability of iron for living organisms. To face the demand of Fe (III) in the rhizosphere leads to strong competition for this nutrient among living organisms, plants and microorganisms have developed active strategies of iron uptake. Efficient siderophores of microbial populations from the rhizosphere do not compete with the plant harboring them and even seems to contribute to the plant iron nutrition. The complex interaction between soil chemical properties, plants, and microbes affects the iron dynamics in the rhizosphere and later on affect the plant health and nutrition.

Keywords: dynamics, rhizosphere, siderophores, oxidation, nutrition, uptake

Introduction
Iron is essential for major metabolic processes in most organisms such as reduction of ribonucleotides and molecular nitrogen and the energy-yielding electron transfer reactions of respiration and photosynthesis. Because of its electronic structure, iron is capable of reversible changes in oxidation state over a wide range of redox potential. In cultivated soils which are mainly oxic environments, iron is mostly in the Fe (III) redox state. The iron speciation in soil solution includes inorganic hydrolysis species and a range of inorganic and organic complexes. Iron is the fourth most abundant element of the earth crust. However in cultivated soils at pH values compatible with plant growth, the solubility of iron is controlled at extremely low levels by stable hydroxides, oxyhydroxides and oxides (Marschner 1995) [8]. Iron is essential for plants and microorganisms due to its involvement in major metabolic processes such as reduction of ribonucleotides and molecular nitrogen, and the energy-yielding electron transfer reactions of respiration and photosynthesis (Guerinot and Yi 1994) [3]. Iron is a central element of the photosynthetic electron transfer chain, and therefore plays an essential role in plant growth and ultimately in crop yield. Beside the yield, the plant iron uptake and homeostasis impact also the plant iron content, and therefore the quality of edible parts of plants. Increase of this content in order to enrich the amount of bioavailable iron in the diet is a major challenge of world agriculture because diet of humans the most affected by iron deficiency is mainly composed of plant products, poor in iron (Briat and Gaymard 2007) [1].

The absolute biological requirement for iron contrasts with the concentrations of Fe(III) species generally far below those required for optimal growth of plants. In the rhizosphere, its concentration is even lower due to the iron uptake by both roots and microbes, and the concentrations of Fe(III) species are generally far below those required for optimal growth of microbes and plants. The combined low concentration of Fe (III) in soil solution (low supply) together with the requirements of aerobic organisms (plants and microorganisms) creates high demand lead to a considerable level of competition for Fe (III) in the rhizosphere. To acquire this essential element in spite of its low availability, plants and microbes have evolved active strategies of uptake which are based on a range of chemical processes (Loper and Buyer, 1991) [6]. Iron (Fe) in the soil is present mostly in the form of insoluble Fe (III) oxides and hydroxides (e.g. haematite, goethite, ferrihydrite). The total iron in soil is much higher than most crops require. Nevertheless, the concentration of free Fe (III) in most agricultural soils is far below that required for optimal plant growth. Iron dynamics in the rhizosphere are under the control of the combined effects of soil properties, uptake and activities of plants and microorganisms and interactions between them. In this review, the status of iron in soils rhizospheres will be examined. In this context, it is a major challenge for microorganisms and plants to acquire Fe(III) which is essential for their metabolism and growth. To meet this challenge, plants and microbes have evolved active strategies of uptake which are based on a range of chemical processes.

Iron status in soils: Iron is the 4th most abundant element in the earth's crust after O, Si and Al (Ma, 2005) [7]. And it ranges in soil from 1- 5 % total Fe in plough layer and in plants more than 50 ppm. It occurs in two oxidation states as Ferric (III) and Ferrous (II). Availability of Fe is more in acidic pH predominantly included in the crystal lattice of a range of primary and secondary ferromagnesium silicates and in high pH Fe (III) precipitate as hydroxides, oxyhydroxides and oxides so concentration of Fe^{3+} in the soil solution is extremely low.

Chemical reactions of iron
Under aerobic condition
Oxidation - Fe^{2+} to Fe^{3+}
$Fe(OH)_3 \leftrightarrows Fe^3 + 3OH$
$FeOOH + 3H^+ \leftrightarrows Fe^3 + 2H_2O$
Solubility: Less soluble
Under anaerobic condition
Reduction- Fe^{3+} to Fe^{2+}
$Fe(OH)_3 \leftrightarrows Fe^{2+} + H2O$
Solubility: More soluble.

Role of iron: Iron plays critical role in metabolic processes such as DNA synthesis, respiration and photosynthesis. It is necessary for the synthesis and maintenance of Chlorophyll. It is a structural component of the molecules like Cytochromes, Peroxidase, Haematins Catalase etc. It activates a number of enzymes like Pxygenase, Dioxygenases, Ferredoxin hydrogenase, Glutamate synthase (Rout *et al*., 2011) [10].

Iron deficiency symptoms: Symptoms of iron deficiency appear on the youngest, newest leaves. The area between the leaf veins becomes pale yellow or white. Under severe deficiency condition tissues show necrotic symptom. Necrosis spreads from tip and margin into interveinal zones. In barley, maize and sorghum leaves, reddish spots may be formed.

Study of iron in soils: Considering the different iron mobilization strategies used by plants and microorganisms and the range of intensities with which they are employed, the difficulty to define measures of iron availability as a soil property becomes apparent. Nevertheless, methods of determining soil iron availability have been developed. The most common methods use as extractants to mobilize iron from soil material during a specified time and under defined conditions. Extractants include chelating agents such as DTPA, ammonium oxalate, citrate/ascorbate or reducing agents such as dydroxylamine. While these extractions targeted only an available iron pool, other methods attempt to detect and quantify several distinct soil iron pools using sequential extractions. These sequential extraction procedures were developed not only for the investigation of solid state iron pools but also for the speciation of other nutrients or pollutants (Gleyzes *et al*. 2002) [2]. A fundamental problem of single or sequential extraction procedures is the operational definition of the iron pools. In contrast, spectroscopic methods promise to detect soil iron species directly. Mössbauer spectroscopy has been successfully used to identify a range of iron bearing phases in soils and has been compared to iron pools as determined to sequential extractions. An advantage of Mössbauer spectroscopy is that it can identify x-ray amorphous phases such as ferrihydrite at low ions. The most common methods report iron availability defined in terms of content (mol kg^{-1}) (Harmsen 2007) [5]. To our knowledge, few studies exist where kinetics of metal release from soils has been compared to root uptake. The use of organisms as reporters of iron availability integrates the thermodynamic and kinetic factors influencing iron availability. Moreover, the use of microorganisms as biosensors introduces a high level of spatial resolution.

Iron uptake by plants: Iron enters the plant via the root from where it is distributed inside the plant. Generally, iron is present in concentrations of about 10 - 500 µg Fe/g dry weight in plant tissues. Iron homeostasis is a tightly controlled process whereby control of the iron transporters is crucial. Due to its easier handling, most of our knowledge has been gained on the soil iron uptake processes taking place after germination. As a strategy for restricting excessive uptake of Fe, wetland species have evolved mechanisms for oxidizing ferrous Fe (Fe^{2+}) in the rhizosphere. Plants, living under aerobic soil conditions, have developed two phylogenetically distinct strategies to cope with the extremely low availability of soluble Fe compounds. Dicots and nongraminaceous monocots employ a Fe acquisition mechanism termed Strategy I based on the reduction of Fe in the rhizosphere. Under Fe-deficient conditions, such plants exhibit enhanced proton extrusion in the rhizosphere, increased Fe^{3+} reduction capacity at the root surface, followed by an uptake of Fe^{2+} via a ferrous transporter on the root plasma membrane. As a result, plants elevate the Fe availability in the rhizosphere and enhance its uptake. In response to Fe deficiency, graminaceous monocots release high-affinity Fe-chelating substances from the mugineic acid family, called phytosiderophores. These substances solubilize Fe^{3+} and the resulting Fe^{3+} hytosiderophore complexes are taken up by the root cells via a specific plasma membrane transport system without reduction of the ferric ion. This mechanism is termed Strategy II (Römheld and Marschner 1986) [9] and it might resemble the microbial siderophore strategy. Among the achievements of the past years is the identification of strategy I and strategy II genes that now serve as a skeleton for studying Fe uptake responses (Fig. 1).

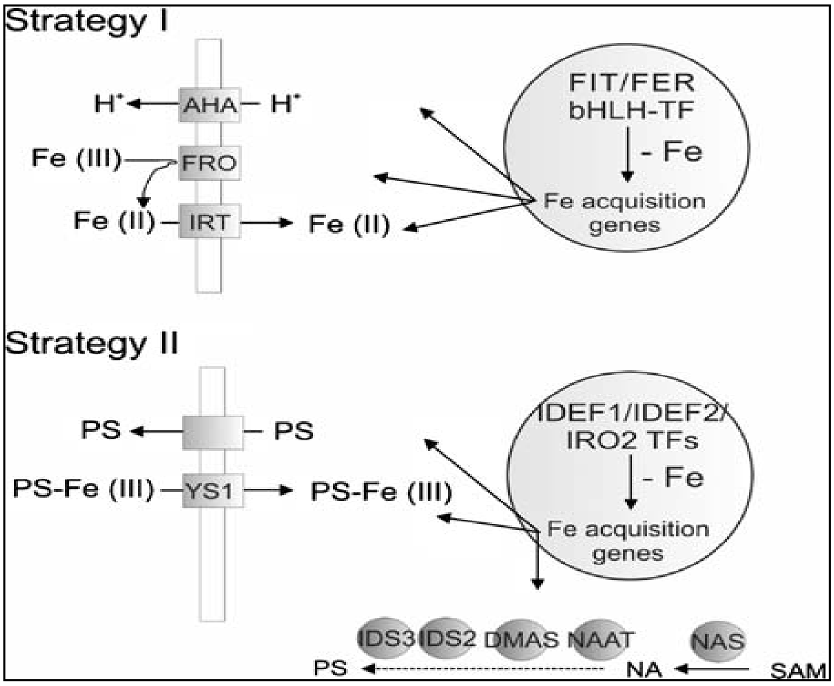

Fig 1: Schematic representation of Fe acquisition mechanisms followed by dicot and nongraminaceous monocot (strategy I) and gramineceous monocot (strategy II) plants

Iron uptake by microorganism: Microbes (bacteria and fungi) have evolved active strategies of iron uptake. Among them, the major one relies on the synthesis of low-molecular weight (generally less than 1,000 Daltons) molecules called siderophores ('iron carrier' in Greek) showing a high affinity for ferric iron (Guerinot 1994) [3]. Ferric siderophores are transported into cells via specific Fe siderophore membrane receptors. Bacterial siderophores and membranes receptors are only synthesized under iron stress conditions and are down-regulated by a dimeric protein, the ferric uptake regulator (Fur), which acts as transcriptional repressor of iron-regulated promoters through its Fe^{2+}-dependent DNA binding activity, as first described in coli. Despite the high diversity among siderophores, with more than 500 so far characterized. Fungal siderophores belong to the hydroxamate group (Winkelmann 2001) [11].

Conclusion: Iron is an essential element for organisms which densities are high in the rhizosphere. However, in cultivated soils, iron is mostly complexed as hydroxides, oxyhydroxides and oxides and its solubility is low. Therefore, plants and microorganisms have evolved active strategies of iron uptake. These strategies interact together and result in complex relations between plants and microorganisms in the rhizosphere. These relations are under the control of the soil physico-chemical properties. They may either involve competition or mutualism and are driven by co-evolution processes. This competition induces a decrease of the pathogen growth in the rhizosphere and leads to the health promotion of the host-plant which supports these bacteria via the root exudates. Significant progresses have been made in the methodologies to characterize the iron status in soil, the iron-uptake mechanisms by plants and microbes. Further studies are now required for analyzing the different types of interactions in soil, plant and micro-organisms. These progresses are expected to provide information and tools enabling us to develop strategies to improve plant iron nutrition and health with decreases in the application of chemical inputs in farming.

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