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REGULAR ARTICLE

Iron nutrition in plants: an overview

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Abstract
Background Plants require iron for a large number of metabolic processes. Due to its low availability in high pH soils, and the impaired acquisition by roots, iron chlorosis is one of the most important limiting factors on plant development in many countries.
Scope This editorial paper gives an overview of the latest aspects related to iron nutrition presented at the 18th International Symposium on Iron Nutrition and Interaction in Plants: (i) Iron chemistry and dynamics in soils; (ii) Agronomic practices to correct Fe deficiency, from diagnosis to fertilizer development and genetic approaches; (iii) Physiology of the Fe acquisition, transport and distribution in plants, including microorganism-rhizosphere interactions; (iv) Molecular regulation of Fe homeostasis; (v) Iron and plant metabolism; (vi) Iron interaction with other elements and (vii) Iron fortification of crops for a better human nutrition.
Conclusions The outcomes of the meeting will allow a step forward on the understanding of iron nutrition and open new approaches to cope the iron deficiency problem.

Keywords Fe deficiency · 18th ISINIP

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Introduction

Iron (Fe) chlorosis is a major nutritional disorder in crops growing on calcareous soils, manifested as yellowing of the upper leaves, interveinal chlorosis, and stunted growth (Jeong and Connolly 2009). Fe deficiency affects the plant development and decreases the yield and quality of many sensitive crops, thereby causing important economic losses (Briat et al. 2015). This nutritional disorder is consequence of the low Fe availability in alkaline soils, defective Fe uptake mechanism and/or impairment in the iron transport and utilization in plant, altering plant metabolism. As consequence of the Fe shortage in some plants, human Fe nutrition can be also severely affected.

The International Symposium on Iron Nutrition and Interaction in Plants (ISINIP) is a scientific conference where prestigious researchers present the latest knowledge on iron nutrition in plants and is an excellent forum for scientific discussions and the exchange of ideas among young and leading researchers. The Symposium is organized every two years in different countries, being the latest one (18th ISINIP) organized in Madrid (Spain) by the group of Micronutrients in Agriculture (http://www.micronutrientsinplants.com/) of the University Autónoma of Madrid (UAM) (May, 30th till June 3rd, 2016). Previous symposia information is gathered in http://www.stressphysiology.com/isinip/. Next meeting is scheduled for 2018 in Taipei (Taiwan). More than 150 delegates from 22 countries attended at the 18th ISINIP that also had 5 Plenary and 10 Keynote speakers. In total there were 50 oral presentations and 73 posters.

Communications were authored by 370 researches. The main topics dealt with: (i) Iron chemistry and dynamics in soils; (ii) Agronomic practices to correct Fe deficiency, from diagnosis to fertilizer development and genetic approaches; (iii) Physiology of the Fe acquisition, transport and distribution in plants, including microorganism-rhizosphere interactions; (iv) Molecular regulation of Fe homeostasis; (v) Iron and plant metabolism; (vi) Iron interaction with other elements and (vii) Iron fortification of crops for a better human nutrition.

Overview of the main topics

In general, a soil pH in the range of 7.4–8.5 caused a low solubility and slow dissolution kinetics of iron-bearing minerals. Also elevated bicarbonate concentrations, typical of calcareous soils, reduce the iron acquisition by plants grown on alkaline soils. These are found to be the most critical factors inducing Fe chlorosis owing to both, the limited bioavailability of Fe in soils and the impaired acquisition and translocation of Fe in plants under these conditions. Iron oxides typically control Fe solubility in the soil solution, which is limited to around 10^{-10} M in the case of calcareous soils. This concentration is not enough for a plant optimal growth, therefore deficiency symptoms appear, such as interveinal leaf yellowing or necrosis (Fig. 1) moreover, crop yield and quality could be severely reduced (Lucena 2000).

To overcome Fe deficiency, efficient plants develop different strategies. Dicots and non gramineaceous plants increase the root Fe(III) reduction power through an Fe(III)-chelate reductase coupled with an increase on the biosynthesis of a Fe(II) transporter and rhizosphere acidification. Gramineaceous plants (strategy II) release to the rhizosphere specific Fe-chelating agents, called phytosiderophores, to solubilize Fe from the soils (Hindt and Guerinot 2012). Moreover, under Fe deficiency, plants exuded several compounds, mainly (i) carboxylates, such as citrate and malate, which originate from the primary metabolism, and (ii) phenolics and flavins, which originate from the secondary metabolism. The release of phenolic compounds, was ascribed as a tool to increase the available Fe in the rhizosphere (Curie and Mari 2017), as well as to contribute to the iron apoplastic pools remobilization. At the 18th ISINIP, the role and production of coumarins as extractants of the apoplastic iron were thoroughly discussed. Also phytosiderophore chemistry in the soil and rizhosphere was studied in order to have a better understanding of their role on the Fe^{3+} mobilization. Walter et al. (2017) describes in this Special Issue, through kinetic experiments with 2′-deoxymugineic acid in a calcareous clay soil, that rhizosphere pH, electrolyte type and concentration and temperature could have a pronounced effect on Strategy II Fe acquisition by affecting the time and concentration 'window of Fe uptake' in which plants can benefit from phytosiderophore-mediated Fe uptake.

In plants from both strategies, insoluble Fe pools might be detected in the apoplast as well as in the root surface, the so-called iron plaque. The formation of the iron plaque is a consequence of the oxidation of ferrous ion to ferric ion, followed by the precipitation of iron oxide or hydroxide on the root surface, according to the oxidizing capacity of the roots. The iron plaque may act as Fe source on Fe deficient plants and also as Fe sink in plants grown under Fe surplus such as in reduced conditions. Fuente et al. (2017), studying the distribution and localization of iron and other metals in the Fe hypertolerant, *Imperata cylindrica*, observed that Fe accumulation was found both in the cell walls and intercellular spaces of most of the tissues, excluding sclerenchyma cells, of every plant vegetative organ and endodermis of root cells. Besides Fe-oxides, jarosite ($KFe_3(OH)_6(SO_4)_2$) was also observed in all samples.

Plant strategies to cope Fe deficiency problem (Strategy I and II) provide the key factors to geneticists to improve plants to overcome this nutritional problem; and to stablish the bases, along with the use of fertilizers, for a better agronomic practices to alleviate Fe deficiency. While traditional variety selection is still valid, several studies highlight the importance of iron homeostasis genes, DNA replication and defences in protecting plants against Fe deficiency. Looking at gene expression at the early time points allows the characterization of early signalling events between shoots and roots, controlled by novel suites of transcription factors briefly activated within these time points (Moran Lauter et al. 2014). As example, improving soybean tolerance to iron deficiency was examined at the 18th ISINIP. In their minireview, Aksoy et al. (2017), taking into consideration that efforts to understand the molecular mechanisms behind iron deficiency tolerance and their use to develop tolerant soybeans via molecular breeding and transgenic approaches, concluded that soybean should be used as a new model plant in understanding the Fe-deficiency tolerance mechanisms especially because of its high potential to be used as a bio-fortified crop to treat the iron deficiency in humans in the future.

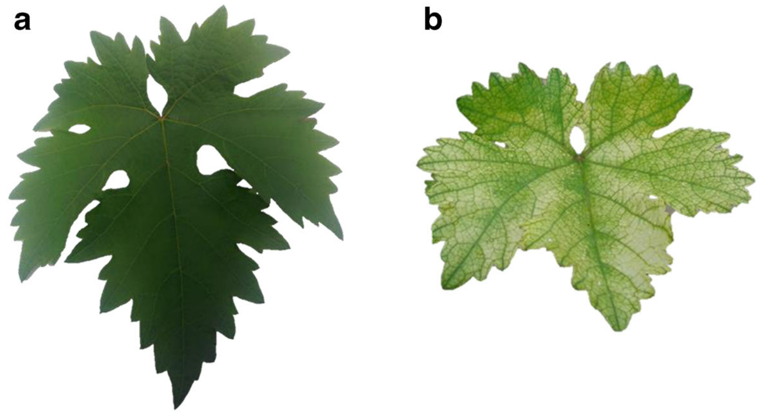

Fig. 1 Grapevine leaves from a Spanish vineyard located in La Rioja, with normal iron nutrition (**a**) and under iron deficiency (**b**)

The final step in Fe uptake in strategy I plants involves Fe^{2+} import through transporters, e.g. AtIRT1, of the ZIP family. Considering that most of the green organisms and plants presents this basic process, but some green organisms, like *Chlamydomona*s and rice, possess alternative iron-acquisition mechanisms, Ivanov and Bauer (2016) studied the potential interactions between Strategy I and alternative iron acquisition mechanisms. They investigated gene-coexpression networks in *Chlamydomonas*, rice and *Arabidopsis*, and used the sequences of the variable regions of the selected IRT proteins to identify the conservation of key amino acids, and suggested that the regulation of Strategy I is closely connected to those existing iron-acquisition strategies.

Iron transport can be also a limiting step in Fe nutrition. After the root uptake, Fe should suffer radial transport across the root and then to be uploaded on the xylem. Xylem loading can be a main regulative step for an adequate nutritional status of plants for some nutrients. In the xylem, it can be transported in chelated form, being citrate the main complexing agent involve in this transport. Remobilization and retranslation via phloem to youngest leaves and reproductive organs can reduce the chlorosis severity, although Fe is known to have low mobility within the plant organs. Nicotianamine (NA) is one of the Fe chelator in plants which is involved in metal translocation in the plant body. Increasing the NA content in crops is an attractive technique to improve agricultural productivity and crop qualities at the same time. Nozoye et al. (2016) studied the sweet potato plants overexpression of the barley NA synthase 1 (HvNAS1) gene. The NA content of transgenic sweet potato leaves were up to 8-fold greater than that of non-transgenic sweet potato. This was related with a higher Fe concentration in transgenic than in non-transgenic sweet potato leaves. Furthermore, the transgenic sweet potato showed tolerance to low Fe availability in calcareous soil. As consequence the authors suggest that increasing the NA content in crops by the overexpression of HvNAS1 offers potential benefits for agricultural productivity.

Once the crops are stablished, the use of fertilizers by soil application is the main solution to cope with iron deficiency. Among them Fe chelates are the most efficient, and profusely studied (i.e. Álvarez-Fernández et al. 2005; Martín-Fernández et al. 2016). The basis for their efficacy have been well stablished in the past. In brief, a high stability in solution, determined after chemical speciation in the soils or growing media conditions, and the ability of the root ferric chelate reductase enzyme to interact with the chelates and to reduce Fe, are determinant aspects. Also the degradation kinetic is important, mainly in the new chelating agents that has recently being developed, which are based on biodegradable amino-acid derived compounds. Among them IDHA (N-(1,2-dicarboxyethyl)-D,L-aspartic acid) and [S,S´]EDDS (ethylenediaminedisuccinic acid, S,S isomer) are the most recently studied, but due to their relatively low stability in soil, they are mainly recommended for soilless cultures and foliar applications, as was exposed during the meeting. Also, other fertilisers such as complexes or other Fe containing byproducts, and novel management techniques were presented. Specially intercropping was reviewed as a methodology to reduce iron chlorosis occurrence.

To optimize Fe acquisition, distribution and use efficiency, plants react to change its availability in their environment by tightly regulating Fe homeostasis, but also by adapting their metabolism (Vigani and Briat 2016). A low Fe content implies a high energy request and affects the functionality of respiratory and photosynthetic electron transport chains, which are Fe-dependent processes. Moreover, a low Fe availability affects the content of a wide number of metabolites in the plant. These metabolites may have a role in some signalling pathways. In the meeting it was pointed that despite many of the genes involved in the regulation process have been isolated and their functions have been illustrated, there is still a great need to identify novel genes/pathways for effectively improving plant tolerance to Fe deficiency.

It has been also recognized that iron homeostasis and immunity may be connected. Hosts and pathogens often compete for iron acquisition but also other complex interactions may occur. The role of phenolic compounds accumulated during plant iron deficiency, as well as the role of the siderophores secreted by phathogens on the iron scavenging capacity, were discussed. Some genes involved in plant defence signalling are also involved in plant response to Fe deficiency. Similarly, heavy metals in excess can cause Fe deficiency-like chlorosis in plants, indicating that they negatively affect Fe homeostasis. It was shown that metal-induced Fe deficiency responses at physiological and morphological levels are uncoupled from transcriptional regulation (Yang et al. 2011).

Finally Fe is by itself a nutrient for human beings. Micronutrient deficiency affects more than 2000 million people, mainly on developing countries. Both scientific evidence and predictive cost-benefit analyses show that biofortification of staple food crops is one of the most reliable strategies for providing elevated micronutrients to vulnerable populations (Nestel et al. 2006). But not only is Fe presence in the foodstuff important but also its bioavailability. It is our duty to provide the scientific basis to obtain enough, healthy and Fe-enriched food for the whole world population, and this is the main goal of the ISINIP.

The organizing committee of the 18th ISINIP thanks the large number of private companies and public organisms that participate and sponsored the meeting as well as "Plant and Soil" for publishing this Iron Nutrition Special Issue.

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