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Potential Enhancement of Plant Iron Assimilation by Microbial-Induced Root Exudation of Phenolic Compounds

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ABSTRACT

Iron (Fe) deficiency in crop plants is a modern agricultural problem worldwide. Although multiple strategies have been evolved to improve Fe assimilation, some plant species, especially dicots and nongraminaceous monocots (strategy I plants), cannot avoid Fe deficiency in low Fe-availability soils. It is well documented that graminaceous plants (strategy II plants) employ the chelation-based Fe acquisition, and the strategy I plants use the reduction-based strategy to take up Fe. Intriguingly, under Fe deficiency the strategy I plants have recently been found to acquire Fe via exudation of phenolic compounds to mobilize Fe, which is much similar to the chelation-based mechanism of strategy II plants. Hitherto, increasing evidence has shown that soil microbes play a cooperative role in plant Fe acquisition. Several beneficial rhizobacteria have been found to increase plant Fe accumulation via activation of the reduction-based strategy. Moreover, microbial-induced root exudation of phenolic compounds can also promote plant Fe absorption by efficient mobilization of Fe, which increases Fe bioavailability in calcareous soils. Here, we briefly review the recent progress on the Fe assimilation strategies of strategy I and II plants, and further discuss the possible mechanisms underlying soil microbes enhance plant Fe acquisition.

INTRODUCTION

Iron (Fe) is an essential micronutrient for all living organisms such as plants and animals. Fe deficiency is the most widespread micronutrient deficiency in human diet, which results in 0.8 million death annually and affects about 2 billion people health [1]. Moreover, Fe deficiency becomes the most ranging agriculture problem that severely constrains plant growth, biomass and product quality. Despite high abundance of Fe in the earth's crust, Fe is extremely insoluble in calcareous soils. Fe is found to form Fe^{3+} oxy-hydroxides, which is not easily utilized by plants [2,3]. Many plant species, such as *Arabidopsis*, soybean (*Glycine max*) and potato (*Solanum tuberosum*) grown in calcareous soils, often displayed Fe-deficiency symptoms (such as growth inhibition and chlorotic leaves) and yield loss [4,5]. Therefore, improving plant Fe absorption is a major issue in the development of modern agriculture.

The Reduction-Based Fe Acquisition Mechanism of strategy I Plants

Until now, many endeavors have been made to advance our understanding of the regulatory mechanisms of plant Fe acquisition at the molecular level. Different plant species have evolved complicated mechanism to take up Fe from the rhizospheric soils. To acquire Fe, dicots and nongraminaceous plants (strategy I plants) have been shown to primarily employ a reduction-based strategy [6]. The mechanism includes Fe-deficiency induced release of protons into the vicinity of plant roots (i.e. rhizosphere), the process that is mainly controlled by the plasma membrane H^+-ATPase (AHA_2; Santi and Schmidt) [7]. Root-secreted protons decrease the pH of rhizosphere, thereby increasing the solubility of Fe3+ oxy-hydroxides. The form of Fe^{3+} is subsequently reduced to the form of Fe^{2+} by the ferric chelate reductase (FRO2; Connolly et al.,) [8]. Lastly, Fe^{2+} is transported into epidemic cells of plant roots via the Fe-regulated membrane protein [9]. These individual components of the strategy I are tightly regulated by some key transcription factors such as *FIT1, bHLH38* and *bHLH39* [10,11].

However, the strategy I plants with the reduction-base Fe acquisition often exhibited poor growth and Fe-deficiency-induced leaf chlorosis in calcareous soils. Indeed, the protons secreted by Fe-deficient plants were largely buffered by bicarbonate, and the activity of the ferric chelate reductase was also severely inhibited (Ohwaki and Sugahara), indicating that the strategy of reduction-based Fe acquisition was impeded under calcareous soil conditions [12].

The Fe-Chelation Mechanism of Strategy II plants

Graminaceous plants (strategy II plants) base their Fe acquisition strategy on small molecules called phytosiderophores (PS) that are synthesized and released by Fe-deficient plants to chelate Fe (strategy II) [13]. Thanks to this mechanism, strategy II plants displayed better growth performance than the strategy I plants grown in calcareous soils [14]. The PS-Fe^{3+} complexes can be directly absorbed by plant roots without requiring a reduction step of the strategy I plants. Differing from the mechanism of the reduction-based Fe acquisition, the chelation-based strategy is very insensitive to high pH or calcareous soil conditions.

The Fe-Mobilizing Mechanism of Strategy I Plants

Parallel to the reduction mechanism, strategy I plants have recently been found to employ also a chelation-based strategy for coping with low Fe bioavailability in calcareous soils. It has been reported that Fe deficiency can stimulate the biosynthesis and secretion of organic compounds such as phenolics and flavins [15]. The phenolic compounds can facilitate plants to mobilize Fe from the rhizosphere. For instance, Jin et al., have shown that phenolic compounds released by roots of red clover play a pivotal role in the regulation of Fe absorption via increased Fe accumulation in the root apoplast, indicating that these phenolic compounds could enhance the utilization of apoplastic Fe. Recent reports have shown that Arabidopsis plants can also produce and release a large amount of fluorescent phenolic compounds such as coumarins under Fe deficiency [16,17]. Some of these compounds possessed the ability to mobilize Fe, and improved plant adaption to low Fe-availability conditions. These researches clearly demonstrate that the strategy I plants employ a chelation-based strategy to take up Fe under calcareous soil conditions rather than the reduction-based strategy.

Root-Secreted Phenolic Compounds Tightly Relate to the Adaptive Ability of Strategy I Plants to Low Fe-availability Conditions

Why did most graminaceous plants grown in calcareous soils own the strong ability to take up Fe compared with dicots and nongraminaceous plants? One assumption is that the ability of dicots and nongraminaceous plants to acquire Fe likely relates to the levels of root-secreted phenolic compounds under calcareous soil conditions. As reported previously, *Parietaria judaica L*., a kind of perennial dicot, is the most universal flora grown in highly calcareous soils, and have not exhibited Fe-deficiency-induced chlorosis. Although the reduction-based Fe acquisition machinery had been found to activate, the extent of its activation cannot contribute to the adaption of this plant species to low Fe-availability conditions [18]. Further studies have shown that a significant increase of phenolic compounds is observed in root exudates of *P. judaica* plants under Fe deficiency, indicating that these phenolic compounds plays a cardinal role in assisting plants take up Fe form low Fe-availability soils [19]. In contrast with *P. judaica* species, Arabidopsis plants exhibited growth interruption and typical symptoms of Fe deficiency in calcareous soils, although these plants had the ability to produce and secrete phenolic compounds for mobilizing Fe [5]. Hence, there exist large differences among strategy I species in their tolerance to low Fe-availability conditions. To a certain extent, the differences may rely on the ability of different strategy I species to produce and secrete phenolic compounds. It allows us to infer that elevating ability of the strategy I plants to produce and secrete phenolic compounds could improve plant Fe assimilation under calcareous soil conditions. However, such mechanisms still need to be further elucidated since complex genetic regulation mechanisms could underlay plants response to Fe starvation. In fact, recent pieces of evidence have revealed that Fe deficiency condition can affect the DNA methylation, suggesting that epigenetic control of gene expression might have a role in the response to Fe stress [20].

Soil Microbes can Enhance Plant Fe Absorption in Low-Fe Availability Soils via Exudation of Phenolic Compounds

With the increasing recognition of the potential roles of soil microbes in promoting plant growth and enhancing plant mineral nutrition, literature about microbial improvement of plant Fe absorption have gradually flourished in recent years [21-25]. Recent findings have highlighted that Fe deficient monocot and dicot plants are able to shape the rhizosphere microbial community in order favor the growth and the colonization of those bacterial strain exhibiting plant growth-promoting traits, and thus positively affect their growth and development [26]. The growth-promoting-bacteria (PGPB) *Bacillus subtilis* GB03 remarkably increases Fe content in Arabidopsis plants via activated expression of *FRO2* and *IRT1,* and increased acidification of the rhizosphere, implying that GB03-induced Fe absorption attributes to activate the reduction-based Fe acquisition mechanism [22]. Moreover, *B. subtilis* GB03 has been found to augment Fe accumulation in cassava (*Manihot esculenta*) [25]. However, it is still unclear whether *B. subtilis* GB03 could improve plant Fe absorption in calcareous soils because the reduction-based strategy is largely suppressed under these conditions. On the other hand, Fe deficient cucumber plants grown on calcareous soils inoculated with the PGPB *Azospirillum brasilense* showed a fast increase in the chlorophyll content as compared to untreated plants, suggested that the bacterium might enhance the Fe bioavailable fraction of the soil, either directly via siderophores secretion or indirectly by influencing the root exudation profile [21].

Recently, Zamioudis et al. have reported that the rhizobacteria *Pseudomonas fluorescens* WCS417 can regulate the biosynthesis and exudation of Fe-mobilizing phenolic compounds via up-regulation of the Arabidopsis *MYB72* [23]. It has previously been indicated that MYB72 is an early activator that regulates rhizobacteria-induced systemic responses (ISR) in Arabidopsis plants, implying that *MYB72* functions as a key linker protein between rhizobacteria-induced ISR and Fe deficiency responses in host plants [27]. Interestingly, several strains of beneficial rhizobacteria such as *Bacillus amyloliquefaciens* IN937a and *Paenibacillus polymyxa* E681 can improve plant growth, and concurrently stimulate ISR in plants [28,29]. It has previously been shown that the beneficial rhizobacteria *Serratia marcescens* NBRI1213 induces plant defense responses with increased accumulation of phenolic compounds [30]. Inoculation of *P. fluorescens* has also been reported to promote the accumulation of phenolic compounds in chickpea plants [31]. More recently, the rhizobacteria *Streptomyces spp* remarkably elevates the content of phenolic compounds in roots of Eucalyptus plants for inducing systemic responses [32]. These pieces of research suggest that some beneficial rhizobacteria may have great potential to increase plant Fe absorption by regulating metabolic pathways of phenolic compounds. Therefore, it will be a potential approach that utilization of beneficial rhizobacteria enhances plant Fe acquisition under low Fe-availability conditions via induced exudation of phenolic compounds to mobilize Fe.

CONCLUSION AND OUTLOOK

Recent pieces of research have made great advances in elucidating molecular regulatory mechanisms of plant Fe acquisition. However, exploring the mechanisms of microbially improved Fe absorption remains a difficult task considering the complexity of microbial-plant interaction. It has recently been indicated that the activities of soil microbes play a pivotal role in plant Fe uptake. Several strains of rhizobacteria can stimulate root-secreted phenolic compounds to mobilize Fe from low Fe-availability conditions, but the mechanisms underlying the process is still quiet elusive. It is likely to involve certain metabolites released by rhizobacteria directly or indirectly activate the biosynthesis and exudation of phenolic compounds to induce systematic responses, and concomitantly theses phenolic compounds can be utilized to chelate Fe. Thus, future challenges will be to identify rhizobacteria-secreted metabolites and analyze their effects on plant Fe absorption, which may help to improve Fe uptake of some strategy I crop species grown in low Fe-availability soils.

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