Addendum

The iron deficiency-induced phenolics secretion plays multiple important roles in plant iron acquisition underground

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In non-graminaceous monocots and dicots, phenolic compounds are frequently reported to be the main components of root exudates in response to Fe deficiency. We show that the phenolics secretion is an important part of a plant's adaptive strategy to Fe deficiency stress that encourages a reutilization of the considerable amounts of Fe normally stored and unavailable in the root apoplast. Besides, we also found that the secreted phenolics can selectively alter the soil microbial community, and the altered soil microbial community may in turn favor plant Fe acquisition by producing siderophores and auxins.

Generally, when grown in Fe-limited conditions, the Fe-efficient plants undertake both morphological and physiological responses, including Fe-solubilising root exudations.¹ In non-graminaceous monocots and dicots (Strategy I plants), phenolic compounds are the most frequently reported to be the root exudates in response to Fe deficiency.²⁻⁴ Compared with other compounds in root exudates, phenolics are particularly interesting because of their multiple chemical and biological functions. These functions include chelating, reducing, radical scavenging, antimicrobial activity, and carbon source for microbial growth.⁵⁻⁷ However, the role of the phenolics in plant Fe acquisition is poorly understood.

In the past decades, the phenolics were suggested to enhance Fe availability in the rhizosphere soil as an alternative or supplement to the membrane-bound reductase through chelating and reducing insoluble Fe.⁷ Recently, we showed that removal of secreted phenolics from the growth medium significantly inhibited the utilization of root apoplast Fe of red clover (*Trifolium pratense* L.),

and thereby intensified Fe deficiency and promoted leaf chlorosis.⁸ In vitro studies with the extracted root cell walls further demonstrate that excreted phenolics efficiently desorb Fe from extracted cell walls, suggesting that the secreted phenolics per se have the ability to remove cell-wall-bound Fe.⁸ These results suggest that the Fe-deficient-induced secretion of phenolics is an important part of a plant's adaptive strategy that encourages a reutilization of the considerable amounts of Fe normally stored and unavailable in the root apoplast. The reutilization of Fe previously accumulated in plant tissues is very important for Fe nutrition due to the limited availability in soils. Recently, Kim et al. (2006) demonstrated that the vacuolar iron uptake transporter (VIT1) play a critical role in reutilization of seed Fe storage during the germination.⁹ In wheat, the NAC transcription factor (NAM-B1) was demonstrated to accelerate leaves senescence and increased zinc and iron remobilization to the grains.¹⁰

Besides, the soil microorganisms have been demonstrated to play an important role in plant iron acquisition from the soil.¹¹⁻¹³ We found that when soil solution extracted from the calcareous soil was incubated with phenolics collected from the root exudates of Fe-deficient red clover, only a few microbial species thrived while growth of the rest was inhibited, suggesting that the Fe-deficient root exudates can selectively influence the rhizosphere's microbial community.¹³ Further test showed that 86% of the phenolics-tolerant microbes could produce siderophores and 71% could secrete auxin-like compounds.¹³ Generally, the siderophores production by soil microorganisms is seen as the microbial activity most supportive of Fe acquisition by plants, because siderophores are chelators with a high affinity for Fe(III).¹⁴ Many Fe(III)-siderophore chelates have been proven to be a source of available iron for plants.^{15,16} In addition, the ferric reduction system indicated by Fe-EDTA reduction and ferricyanide reduction, were greatly enhanced by microbial auxins,¹³ suggesting that microbial auxins, in addition to siderophores, are important to plant Fe uptake. These results suggest that the Fe-deficient-induced secretion of phenolics to the rhizosphere soil may be also an important part of a plant's adaptive strategy that altered microbial community which in turn favors plant Fe acquisition by producing siderophores and auxins.

Taken all these findings together, we believe that the iron-deficiency-induced phenolics secretion by Strategy I plants should have multiple important functions in plant iron acquisition underground. These functions can be summarized as following and Figure 1:

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and

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Figure 1. Possible mechanisms of Fe-deficiency-induced secretion of phenolics in plant Fe acquisition from the Fe-deficient soil. The roots of Fe-deficient plants secrete phenolics which in turn facilitate Fe acquisition through following approaches. (1) phenolics aid the reutilization of root apoplast Fe by the plant. (2) phenolics selectively influence microbial community in the rhizosphere, and the altered microbial community in turn favors plant iron uptake through siderophores and auxins production. (3) phenolics itself directly solubilize the insoluble Fe in the rhizosphere soil by its reducing and chelating ability.

(1) During slow growth stages of plant, the Fe requirement is low and its concentration in rhizosphere soil should be relatively higher. Thus, the Fe in plant tissues is also usually sufficient. However, when plant growth rate is accelerated, along with the slow diffusion of Fe^{3+} in the soil, Fe in the rhizosphere soil solution can be easily exhausted. Hence, the Fe accumulated in the roots apoplast during slow stages of growth could be reutilized with the help of the secreted phenolics.

(2) Secreted phenolics induced by Fe deficiency accumulate in the rhizosphere, and selectively alter the microbial community through its functions of antimicrobial activity and carbon source. The altered microbial community in turn favors plant iron uptake through siderophores production to increase Fe bioavailability in the rhizosphere, and auxins production to increase root Fe(III) reduction capability.

(3) Secreted phenolics induced by Fe deficiency accumulate in the rhizosphere, and solubilize the insoluble Fe bound to the soil particle through its functions of chelating and reducing ability.

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