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AtbHLH38 and AtbHLH39 interact with FIT, functioning in control of iron uptake in Arabidopsis

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Introduction

Iron is an essential nutrition element for all organisms. It functions as a component of many important enzymes and proteins involved in fundamental biochemical processes. Iron deficiency causes anaemia afflicting more than one billion people worldwide. In plants, iron is one of the most common elements limiting plant growth because it exists predominantly in an oxidized ferric form [Fe(III)] in aerobic environments. The ferric iron has an extremely low solubility at neutral or basic pH and is not readily available to plants. To meet iron demand for growth and development, two effective iron acquisition systems known as strategy I and strategy II (Roemheld and Marschner, 1986) have evolved in higher plants. All plants except grasses use the strategy I mechanism to effectively acquire iron from soil. Under iron deficiency, strategy I plants show typical iron deficiency responses, including (1) acidification of the rhizosphere by enhanced proton extrusion to increase solubility of ferric iron, (2) activation of ferric-chelate reductase reducing Fe^{3+} to Fe^{2+} on the root surface in the subapical region, (3) induction of the high-affinity Fe^{2+}-transporter system to absorb ferrous iron from soil into roots, as well as morphological changes of the roots, such as thickening of the subapical root zone, increased formation of root hairs and so on. These responses are carefully regulated at molecular level because excess iron is toxic for plants.

FIT interacts either with AtbHLH38 or AtbHLH39, directly functioning in controlling the transcription of iron uptake genes

Arabidopsis is a model plant for studying the molecular mechanism of iron uptake in strategy I plants. Several key genes involved in iron uptake and its regulation were isolated and characterized during the last decade. The Fe(III)-chelate reductase *AtFRO2* and the high affinity Fe(II)-transporter *AtIRT1* are two major functional genes for iron uptake in Arabidopsis. *FIT* (*AtbHLH29*), a homolog of tomato *FER* in Arabidopsis, encodes a bHLH protein. It is a central transcription factor regulating the iron deficiency responses and iron uptake in roots of Arabidopsis because the insertion mutant of *FIT* (*fit1-1*), same as *FER* mutant T3238*fer* of tomato (Ling et al., 2002), lacks such responses and suffers strongly from iron deficiency under iron limiting conditions (Bauer et al., 2007; Colangelo and Guerinot, 2004; Yuan et al., 2005). Recently, we identified two new iron-regulated bHLH proteins (AtbHLH38 and AtbHLH39) in Arabidopsis. Yeast two-hybrid analysis and transient expression in Arabidopsis protoplasts showed that AtbHLH38 and AtbHLH39 interacted with FIT. Expression of *FIT/AtbHLH38* or *FIT/AtbHLH39* in yeast cells was able to activate *GUS* expression driven by ferric chelate reductase (*AtFRO2*) and ferrous transporter (*AtIRT1*) promoters. Overexpression of both *FIT* and either *AtbHLH38* or *AtbHLH39* converted the expression of the iron uptake genes *AtFRO2* and *AtIRT1* from induced to constitutively, and the overexpression plants accumulated more iron in their shoots than the wild type and exhibited more tolerance against iron deficiency (Yuan et al., 2008).

In conclusion, we demonstrated that transcription of the iron uptake genes *AtFRO2* and *AtIRT1* in Arabidopsis was directly regulated by a complex of FIT/AtbHLH38 or FIT/AtbHLH39. These results give a new insight to understand the molecular regulation mechanisms of iron uptake in strategy I plants and is very useful for design and breeding of iron-efficient crops for improving human iron nutrition.

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