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SHORT COMMUNICATION

Root developmental adaptation to Fe toxicity: Mechanisms and management

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ABSTRACT

Iron (Fe) is an essential microelement but is highly toxic when in excess. To cope with Fe excess, plants have evolved complex adaptive responses that include morphological and physiological modifications. The highly dynamic adjustments in overall root system architecture (RSA) determine root plasticity and allow plants to efficiently adapt to environmental constraints. However, the effects of Fe excess on RSA are poorly understood. Recently, we showed that excess Fe treatment in Arabidopsis not only directly impairs primary root (PR) growth but also arrests lateral root (LR) formation by acting at the tip of the growing primary root. Such a change is believed to help RSA adjust and restrict excessive Fe absorption in the part of the rhizosphere subject to acute toxicity while maintaining the absorption of other nutrients in the less stressed components of the root system. We further showed that the suppression of PR growth and LR formation under excess Fe is alleviated by K^+ addition, providing useful insight into the effectiveness of nutrient management to improve RSA and alleviate Fe toxicity symptoms in the field.

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Iron (Fe) is an essential microelement but is highly toxic when in excess. Classic symptoms of Fe toxicity are leaf discoloration (bronzing) and a stunted root system.[1] To cope with, and survive, adverse iron-toxic soil conditions and excessive iron accumulation in tissue, plants have evolved morphological and physiological avoidance and/or tolerance strategies. These include restricting excessive Fe absorption at the root level,[2] immobilization of active iron that entered the tissues in "dumping sites," e.g., old leaves or leaf-sheath tissue,[3] and inclusion and tolerance *via* increased thresholds to elevated levels of Fe^{2+} within cells, such as through enzymatic detoxification.[4] Among these strategies, restricting excessive Fe absorption is one of the most important, by "engaging the enemy outside the gates." Highly dynamic changes in the overall root system architecture (RSA) determine root plasticity and allow plants to efficiently acclimate to environmental constraints and restrict the excessive accumulation of nutrients and toxicants. In fact, plants can respond to the heterogeneous availability of nutrient resources by flexibly, and relatively rapidly, allocating carbon flow to facilitate directional root growth to patches where the most favorable conditions are found.[5-7] Excess Fe has been shown to inhibit LR initiation but not subsequent LR development,[8,9] and these inhibitory effects are only seen in newly grown roots that are engaged in the elongation process for the duration of exposure to excess Fe and are not seen in the proximal root portions.[8,9] Moreover, physical contact of the PR tip with excess Fe is necessary, and indeed sufficient, for LR formation inhibition in the newly grown roots.[8] Excess Fe also arrests PR growth by decreasing both cell elongation and division,[1,9,10] and principally results from direct contact of the root tip with external Fe.[10,11] Concentrations of the main toxic (ferrous) form, Fe^{2+}, tend to increase in vertically lower soil strata, where low pH and/or anoxic conditions prevail.[12] Thus, we propose the purpose of the observed RSA adjustment to be the restriction of excessive Fe absorption, which also occurs predominantly in the Fe^{2+} form, and prevent serious Fe toxicity. Meanwhile, the relatively stable LR number and length in the proximal root portions may permit the maintenance of the absorption of other nutrients in the less stressed areas.

Additional to the above, a significant shift in plant tissue cation homeostasis, especially that of potassium (K), has been noted under Fe toxicity.[1,13] Although the previous reports by our group and others laboratory had shown that potassium plays a critical role in regulating root development under Fe toxicity,[10,14] the detailed

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morphological and physiological targets were not identified. Here, our data show that the suppression of PR growth and LR formation in the newly developed roots (the distal portion of the root system) under excess Fe is significantly alleviated by K^+ addition (Fig. 1). This rescue effect from Fe toxicity is strongly reminiscent of K^+'s alleviatory effects under the cation stress brought about by the NH_4^+ ion,[15,16] an ion whose toxicity is also sensed at the root tip,[17] and K^+ amendment, thus, offers itself as a practical agricultural strategy to reduce the manifestation of cation toxicity in the field.[18] Although the mechanism of alleviation remains as yet poorly understood, there are several plausible hypotheses, 1) K^+ may reduce the activity and availability of Fe^{2+} in the root medium, thus facilitating maintenance of root development; 2) K^+ may reduce the transport of Fe^{2+} into root cells to limit toxicity; 3) K^+ may act on the target of Fe-mediated root development or the enzymatic systems that control Fe^{2+} immobilization and detoxification. These hypotheses require testing to identify the precise targets of K^+ action, but the positive effects on RSA, and the alleviation of Fe toxicity symptoms in general by K^+, may constitute a reasonable nutrient management approach to combating Fe toxicity in real-life agricultural settings.

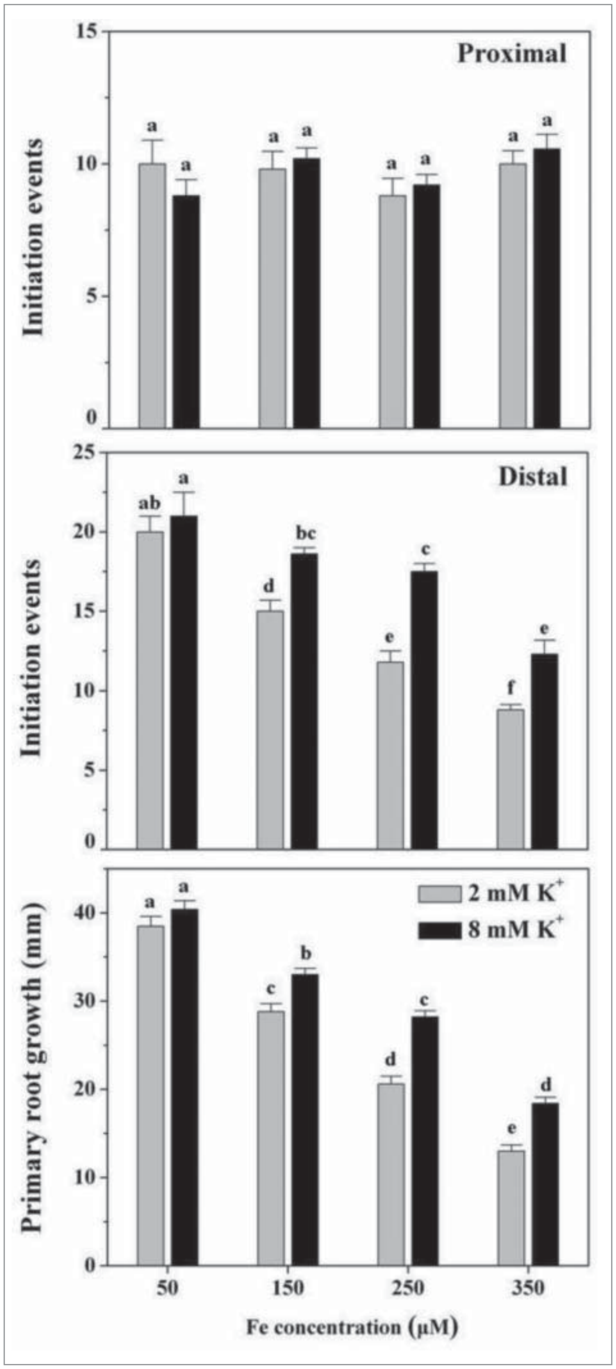

Figure 1. The effect of exogenous K^+ on primary root growth and lateral root formation in *Arabidopsis* under excess Fe. Five-day-old *Arabidopsis* (Col-0) seedlings were transferred to medium supplemented with various concentrations of Fe (provided as Fe-EDTA; $FeSO_4.7H_2O$ plus EDTA) plus various concentrations of K^+ (provided as K_2SO_4) for an additional 5 days. Values are the means ± SE, $n \geq 4$. Different letters represent means statistically different at the 0.05 level (one-way ANOVA with Duncan post-hoc test). Distal: distal root portion; Proximal: proximal root portion.

Disclosure of potential conflicts of interest

No potential conflict of interest were disclosed

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