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Editorial

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Homeostasis and Response of Plants to Iron and Phosphorus Deficiency: A Brief Overview and Future Spots

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Both iron (Fe) and phosphorus (P) are essential mineral nutrients for all living organisms. In plants, Fe is involved in many key basic redox reactions associated with photosynthesis and respiration and also plays various vital enzymatic reactions such as DNA replication, lipid metabolism, and nitrogen fixation. Although the earth's crust is full of Fe, the amount of bioavailable Fe is always under the demand for plant growth and development in aerobic soils with neutral to basic pH [1-5]. Such alkaline soils are around 30% of the land worldwide, leading to Fe deficiency is a major constraint in crop productivity [6]. Fe deficiency severely compromises chloroplast development and impair chlorophyll biosynthesis, leading to Fe deficiency induced chlorosis, a robust diagnostic symptom of Fe deficiency. Meanwhile, Fe deficiency is the most serious nutritional disorder affecting more than two billions of people in the word (http://www.who.int/nutrition/topics/ida/en). Therefore, engineering Fe-rich plants in edible parts will be of great help to counteract malnutrition when plants are the chief nutrient source in the diet. To achieve this goal, we first must understand how plants maintain cellular Fe homeostasis.

Similarly, Phosphorus, mainly taken up by plants in a form of phosphate (Pi), is required for plant growth and development, associated with signaling, metabolism and photosynthesis, as well as an essential component of macromolecules such as nucleic acids, ATP and phospholipid [7-10]. Due to its chemical properties, Pi tends to form complexes with soil components and to convert into organic P by microbe, which causes up to 90% P inaccessible to most plants. The plant available Pi (~1-2 μM), therefore, is much lower than that of plant's demand, particularly in acid and alkaline soils. In agricultural practice, P shortage thus is a critical limiting factor causing severe yield losses and poor quality in the edible parts. To correct low-Pi stress, a huge amount of P-containing fertilizers are applied in agricultural settings. However, due to less than 20% of the applied P being used by plants during the first growing seasons, the remaining P is sorbed onto soil particles or converted into organic P, or leaches, leading to increasing accumulation of total P in the soil and eutrophication of lakes [7-10]. Therefore, use of P-fertilizers is unsustainable and associated with environmental pollution and economic concerns. Thus, an understanding how plants adapt to P shortage is of great importance to develop P-efficient crops by traditional breeding or biotechnology approaches, and this will eventually reduce the heavy reliance on P-fertilizers.

Plants have developed two strategies to increase Fe acquisition upon Fe deficiency, referred to as strategy I and strategy II [11]. Under Fe deficiency, phtosiderophores are synthesized and secreted by roots in strategy II species including maize, wheat, and other grasses. Followed, Ferric Fe (III) is chelated by phtosiderophores and the complex is taken up into root cells by an ologigopeptide transporter, YELLOW-STRIPE [12] and its homologs [13]. In strategy I plants (non-grass species), upon Fe deficiency, release of Fe (III) is increased by the induction of H-ATPase [14]. Subsequently, Fe (III) is reduced to ferrous Fe (II) by FRO2 (FERRIC- REDUCTION OXIDASE2) [15], and Fe (II) is then transported into root cells by IRT1 (Fe -REGULATED TRANSPORTER1) [16,17]. Expression of both FRO2 and IRT1 is induced by Fe deficiency and controlled by the bHLH family transcription factor FIT [18] and its homologs [1]. Collectively, FRO2 and IRT1 are referred to as main Fe acquisition genes in strategy I plants. FIT itself is induced by Fe deficiency, indicating that some upstream components of FIT must exist and monitor the Fe-status and transmit the signal of Fe deficiency to downstream factors. In the future, searching the sensor for Fe and the upstream components and translating the knowledge on Fe homeostasis to biofortification efforts will be one of the focuses in plant Fe nutrition field.

To cope with Pi deficiency, plants have evolved an array of adaptive mechanisms aimed at to improve both uptake efficiency and use efficiency by triggering a serial of morphological, physiolocal and biochemical, metabolic changes, as well as in gene expression. Under Pi starvation, most plants show reduction in primary root growth and increase in the number and length of lateral roots, and the formation of denser and longer root hairs, which is considered to improve topsoil foraging [7,9]. Meanwhile, root excretion of organic acids and Pi-releasing enzymes including RNases and phosphatases is increased, leading to the rhizospheric Pi pool being available to plants [7,9]. In addition, expression and activity of high-affinity Pi-transporters are induced to facilitate the transport of Pi across the plasma membrane. Moreover, under Pi limitation, lipid is reprogrammed and metabolisms particularly relative to carbohydrate synthesis and assimilation are altered to less depend on the consuming of cellular Pi or ATP. To orchestrate these responses, plants have developed sophisticated mechanisms to sense the Pi-status and activate gene expression to adapt to Pi deficiency. By now, more than 1000 genes have been reported to be regulated by Pi status and some key regulation factors such as PHR1 and SPX3 have been extensively documented [19]. In the future, the sensor for Pi, yet to be uncovered, will be the hot spot in plant P nutrient.

Over the past decade, with the advances of high throughput technologies such as microarray and RNA-seq and proteomics, genome-wide gene expression changes and protein profiling have been extensively explored under either Pi or Fe deficiency in model plants such as Arabidopsis and rice, and hundreds and thousands of genes have been shown induced or repressed by deficiencies of each of them [19,20]. These OMIC studies have identified several novel payers and regulators that subsequently confirmed by genetic study [19,20]. Although suits of the changed genes are functionally annotated, most

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of them remain functional unknown or unclear in the Fe hemostasis or P response. Deciphering the functions of these genes by reverse genetics such as gene editing using CRISPR/CAS9 system [21] will greatly improve our knowledge towards the understanding of how plants respond to mineral deficiency. In addition, with the completion of genome sequencing of more and more plant species including important economic crops will be of great help for us to understand the plant species specific and common responses to Fe and P deficiency.

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