

# Regulation of ion homeostasis in plants

## Current approaches and future challenges

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The dependency of plants on essential macro- and micro-elements to complete their life cycle serves as a major entry point of these elements into the global food web. However, plants often face depletion of one or more essential elements limiting their growth. Thus, in modern agriculture, improving plant mineral nutrition has gained fundamental importance in order to address the issue of sustainable food resources for the growing world population. Heavy fertilization of soil was, for long time, chosen as a strategy to cope with the deficiency of these elements. Yet, this strategy is neither economically nor ecologically conceivable at long-term. As an alternative, genetic and breeding approaches that provide plants new characteristics enabling them to grow in nutrient-depleted soils, has become a major focal interest. The research emphasis so far has been on elucidating the molecular physiology of individual nutritive elements. However, in practice, application of such knowledge is hindered by complex cross-talks, which are emerging in the face of new data, between these elements. Developing integrative approaches, combining genetic, comparative genomics and 'omics' platforms, is crucial to untangle the interconnected signaling networks regulating ion homeostasis in plants.

It is well established that growth of higher plants depends on the availability of various minerals in the soil, which have been assigned as macro- and micro-nutrients depending on their concentrations in planta. In most agricultural ecosystems, availability of these elements is often inadequately low, and thus, is a major limiting factor for plant growth and development a situation, which significantly contributes worldwide to the pressing problem of food security and malnutrition. For long time in modern agriculture, fertilization of soil was chosen as a strategy to cope with deficiency of elements in agricultural systems, which is neither economically nor ecologically sustainable at long-term. Facing this alarming situation, many ambitious scientific projects have been initiated with a long-term goal of improving the ability of crops to use available nutrients more efficiently, enabling such

crops to grow on nutrient-depleted soils. To date, results of such research programs have often provided us a comprehensive view on the adaptive strategies employed by plants to cope with deficiency or excess of individual macro- or micro-elements in their growth media. These efforts have, thus, resulted in characterization of detailed phenotypic responses triggered by changes in the availability of single elements, production of lists of genes that are differentially expressed in such stress conditions and proposals of signaling pathways involved in maintaining the homeostasis of individual elements. One can believe that based on such remarkable progress, genetic approaches are feasible, and current knowledge is sufficient to modify the transport system and/or signaling pathways to provide plants new characteristics to improve their mineral nutrition. However, accumulating data proved the situation to be more complex than previously anticipated surfacing the existence of complex connections between the various regulatory layers of the homeostasis of these elements. Such interconnections manifest themselves at both physiological and molecular levels and can account for shortcomings of current agronomic models that are typically focused to improve the assimilation of individual elements.

The interconnectivity between the homeostasis of mineral nutrients in plants is, perhaps, best illustrated by the case of phosphate (Pi; macro-nutrient) or iron (Fe) and zinc (Zn) (essential micro-nutrients). The connection between these elements starts at the level of bioavailability, where the already low availability of Pi, Fe and Zn is further aggravated by their weak solubility in soil due to their high tendency to interact with each other and form insoluble complexes at the root surface. At physiological level, it is striking to observe the similarity between the phenotypic response of plants to Pi deficiency, or Fe or Zn toxicity, which all lead to a significant reduction in primary root growth. Now we are learning that the connection between the homeostasis of these elements is not restricted to the phenotypic similarities in the response of plants to the deficiency or over-accumulation of these elements. Several studies have reported that under Pi starvation plants over-accumulate Fe and Zn, and vice versa.<sup>1-4</sup> Whether this phenomenon is a genetically programmed response of the plant or it reflects a situation that the plant can not avoid due to the enhanced availability of one ion in the absence of others, remains largely unknown. Nevertheless, importance of such interconnectivity between the homeostasis of different nutritional elements started to surface in the recent years. It is crucial not to neglect

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this yet-to-be-characterized cross-talk for developing fundamental and applied research programs aiming at understanding the regulation of plant mineral nutrition. A noteworthy example in this context is the effect of the over-accumulation of Fe on root growth phenotype, in conditions where Pi is deficient. It has been reported that the striking aspect of the root architecture, the inhibition of primary root elongation when plants are grown in Pi-deficient medium, is most likely a result of iron toxicity.<sup>2,3</sup> The reduction of Fe concentration in the medium, in spite of low concentrations of Pi, leads to the recovery of not only the primary root growth, but also the ability of plant to uptake phosphate. Clearly, phenotypic response of plants to nutritional stress is an outcome of complex interactions between homeostasis of different ions, and therefore does not provide a decisive basis for the status of individual ions in plants.

The interconnectivity between the homeostasis of different elements is also apparent at molecular level, where common signaling networks take part in the regulation of homeostasis of different macro- and micro-nutrients. Such regulatory pathways have been shown to include phytohormones and photo-assimilates (e.g., sugar). Global transcriptional profiling revealed that deficiency or excess of one element often involves modification of the expression of genes coding for proteins specific for the homeostasis of others elements, ranging from uptake transporters, internal distribution transporters, to proteins that function in assimilation of or tolerance against (in case of toxicity) these elements.<sup>4,5</sup> Sticking to the case of Pi and Zn, for example, it is well described that Zn deficiency causes an upregulation of the expression of high affinity phosphate transporters in plants, resulting in accumulation of Pi.<sup>1</sup> Noteworthy, this molecular interconnectivity operates beyond conditions in which plants are subjected to external limitation of one element. For example, induction of the expression of phosphate transporters AtPT2/AtPHT4 is observed in plants that naturally overaccumulate Zn.<sup>5-7</sup> This observation strongly suggests a molecular link between the mechanisms that regulate ion homeostasis, likely to provide flexibility for adapting to fluctuating environmental conditions and to increase the chances of plants to complete their life cycles. Deciphering the precise mechanisms and the nature of the cross-talk between nutrient signaling networks is required to fully appreciate the regulation of ion homeostasis in plants. Recently, a molecular mechanism employing regulatory molecule microRNA has been uncovered as a common strategy for plants to cope with nutrient

limitation and shown to mediate the cross-talk between different macro-nutrient limitation signaling pathways.<sup>8</sup> Now we have lines of evidence for the genetic basis of the regulatory cross-talk that mediates adaptation of plants to availability of mineral nutrients. Next task will be to develop a comprehensive understanding of the coordination of the ion homeostasis by discovering new signaling and regulatory networks.

The current view clearly indicates that the phenotype could not be our sole “placemark” to define status of single ions in plants, and states the obvious that future work aiming at manipulating one element should first consider the existence of a cross-talk with other nutrients. One way to tackle such a complex situation is to undertake an integrative approach promoting a global view, which has, fortunately, become possible in light of recent technical advances. Development of the technique of ionomics (ICP-MS phenotyping platform; <http://www.ionomicshub.org/home/PiiMS>), high-throughput profiling of elemental composition, in combination with already well established technique of genome-wide analysis of transcriptome offers us a unique opportunity to get closer to uncover the common signaling pathways between different ions, and to identify genes which can be used as good molecular markers for monitoring the integrative ionic status of plants.<sup>9</sup>

In conclusion, it has become clear that the regulation of plant mineral nutrition is more complex than previously anticipated in light of emerging data showing interconnections between the homeostasis of different nutrients, which manifest themselves at physiological and molecular levels. Despite the indispensable importance of such interconnections for amelioration of plant nutrition, currently, their molecular bases and biological significance are still poorly studied. Thus, understanding the plant ionome and deciphering the mechanisms that regulate it become critical in order to enable biotechnological and agronomic strategies aimed at improving crop yield in nutrient-depleted soils, and bio-fortification. A large part of the solution will be building an integrative model that is necessary to understand the nature of ion homeostasis networks. Such an approach, integrating different levels of “omics”, will be a powerful tool to meet future challenges for plant scientists.

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