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The plant ionome coming into focus

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92 elements have been identified on earth and 17 of these are known to be essential to all plants. The essential elements required in relatively large amounts (>0.1% of dry mass) are called macronutrients and include C, H, O, N, S, P, Ca, K, Mg. Those required in much smaller amounts (<0.01% of dry mass) are referred to as micronutrients or trace elements and include Ni, Mo, Cu, Zn, Mn, B, Fe, and Cl. Plant growth and development depends on a balanced supply of these essential elements and thus the plant has a range of homeostatic mechanisms operating to ensure that this is maintained. Beneficial elements which promote growth and may be essential to some taxa, include Na, Co, Al, Se and Si. Elements such as the heavy metal Cd and the metalloid As have no demonstrated biological function in plants, but are nevertheless taken up and cause severe toxicity in most plant species. The concept for this special issue is the plant ionome, a word coined to encompass all these elements and allow focussed discussion and investigations on the mechanisms that co-ordinately regulate these elements in response to genetic and environmental factors (reviewed in Salt et al., 2008).

To fulfil their requirements for metabolic processes and to minimize deleterious effects of excesses and deficits of mineral nutrients in the environment, plants have developed flexible and adaptive strategies to a) achieve sufficient quantities of essential elements, b) avoid excessive accumulation which could be toxic, and c) deal with deleterious effects of non-essential elements. To sense and respond appropriately, complex mechanisms have evolved. To address these topics and to give a more integrated view of the complicated tasks faced by plants, elements in this issue have been discussed in particular groups. We asked scientists at the forefront in the field of plant nutrition to report on the most recent developments in this rapidly advancing field. The authors have embraced this challenge and have succeeded in shedding light on the sophisticated and finely tuned mechanisms operating in the multi-tasking plant that are required to balance mineral supply with demand. The major physiological roles of essential and beneficial elements are highlighted in our three introductory articles by Maathuis, Hansch and Mendel, and Pilon-Smits et al. These range from structural roles in proteins, osmotic balance, maintaining electrochemical potential, signalling and enzyme activation. The elements are required in varying amounts depending on developmental stage and different environmental and stress conditions.

Excesses and deficiencies of macro and micronutrients can have serious effects on plant metabolism, affecting the type and amounts of metabolites. In crops this has an impact on yield,

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nutritional quality, taste, processing and storage, and pathogen resistance. Therefore, we need to understand how different nutritional inputs determine the metabolic output of plants. New insight into how plants experiencing nutrient shortage re-prioritise different metabolic pathways and integrate metabolism with growth are covered by Amtmann and Armengaud. They discuss the enormous challenge in predicting the outputs of the metabolic network in response to varying inputs, and how this relies on measuring pool sizes for all metabolites, metabolic fluxes, *in-vivo* reaction rate constants, gene expression regulation and protein modification, compartmentalization and transport kinetics. Multi-level approaches which are combining transcriptional regulation, metabolite profiling and enzyme activity measurements are proving promising in relation to understanding the exact relationship between nutrient supply and metabolic adjustment.

Fundamental to the processes of element homeostasis are transport proteins mediating transport of essential and non-essential elements. They often exist as part of large families which confers the flexibility required for membrane transport in particular tissues, cells and organelles, and under different environmental conditions. Some are very specific for particular solutes whereas others are less specific and can potentially transport a range of related solutes. As pointed out by Karley and White, the distinctive patterns of mineral element accumulation in tissues, cells and subcellular compartments are products of transport processes catalysing both short and long-distance distribution. Long distance transport of macro and micronutrients, their intra and intercellular distribution, and the forms they are transported in are discussed in detail by Miller et al. (N, P, S), Karley and White (Ca, K, Mg), Puig and Penarrubia (Cu, Zn, Mn, Fe), Tejada-Jimenez et al. (Ni, Mo, Cl) and Miwa et al. (B). Some of these same transporters are responsible for the uptake and distribution of toxic metals/metalloids, discussed by Verbruggen et al. and Zhao and McGrath. For example, work carried out in rice has revealed that arsenite, which has a molecular size and structure similar to silicic acid is taken up by the silicon transporter OsNIP2;1/Lsi1 (Ma et al. 2008).

Proteins involved in trafficking and compartmentalization are also highlighted in this issue. Puig and Penarrubia discuss the role of metallochaperones in delivering metal micronutrients such as Cu to specific proteins and transporters such as RAN1 and HMA5, and also highlight potential roles in activating transcription factors or indeed acting themselves as transcriptional regulators. Compartmentation within the vacuole is now a well established mechanism for storing metal micronutrients and macronutrients, and sequestering toxic elements. We are also starting to understand how metal micronutrients are transported and compartmentalised in the chloroplast. This is vital given the transition metal requirement of proteins in this organelle. In the case of Cu, P_{1B}-ATPases, PAA1 and HMA1, have been implicated in transport across the plastid envelope into the stroma while PAA2 mediates import into the thylakoid lumen.

Regulation of element homeostasis is a fascinating area and further insight into this is provided in the articles by Gojon et al. (N, P, S), Luan, (Ca, K, Na), Pilon et al. (Cu, Zn, Mn, Fe), and Tejada-Jiménez et al. (Ni, Mo, B, Cl). For micronutrients most is known for Fe and regulation is at several different levels with transcriptional and post-transcriptional responses playing important roles (discussed in Pilon et al.). In response to Fe deficiency in *Arabidopsis* ferric-chelate reductase FRO2 and the Fe transporter IRT1 are upregulated in a process involving bHLH transcription factors (eg. AtFIT1, AtbHLH38 and AtbHLH39). Nitric oxide is a component of Fe signalling and seems to act upstream of these transcription factors in Fe deficiency signalling and also as an upstream signal in response to excess Fe (see Giel et al. for discussion). In addition, lysine residues in an intracellular loop of AtIRT1 are important in AtIRT1 turnover, thus adding a further level of control.

microRNAs are involved in the regulation of a number of nutrient responses including Cu (see Pilon et al), P and S (see Gojon et al). The transcription factor AtSPL7 seems to be a master

regulator under low Cu availability, activating transcription of a number of genes involved in copper uptake and assimilation as well as several Cu-microRNAs. The latter target non-essential Cu-dependent proteins and so there is the intriguing possibility that this would allow preferential allocation of Cu to essential Cu-requiring proteins such as plastocyanin in low Cu conditions (see Pilon et al. for discussion).

We are starting to uncover links at the molecular level between various elements. Luan discusses the calcineurin B-like proteins (CBL) and CBL-interacting protein kinases (CIPKs) which provide the molecular link between K^+ transport, Na^{2+} toxicity, and Ca^{2+} . In response to changing cytosolic Ca levels, triggered by high salt levels, CBL4 (also known as SOS3) and CIPK24 (also known as SOS2) are thought to enhance the Na^+ detoxification process by regulating SOS1, a Na^+/H^+ antiporter. In addition, a mechanism is discussed whereby changes in cytosolic Ca are triggered in response to low K^+ levels; this leads to CBL1/CBL9-CIPK23 regulation of AKT1, a voltage gated K^+ -channel thus providing a connection between Ca and K^+ -uptake in plants. Transporters may not only be targets but also components of signalling pathways as has been observed for NRT1.1, which has been shown to function as a nitrate sensor (see review by Gojon et al.).

We are starting to learn much more about the multiple levels of regulation of transporters, which is a fundamental process in micronutrient and macronutrient homeostasis. Pilon et al. highlight the transcriptional control in relation to Zn, Fe and Cu homeostasis and discusses advances made using genome wide transcript profiling. Several examples of post-transcriptional and post-translational control mechanisms are discussed throughout this issue. Sumoylation has been discussed in relation to P homeostasis (Gojon et al.). Allosteric regulation has been proposed for the ammonium transporters, AMT1, which form trimers. They are modulated probably by phosphorylation of residues in the C-terminus and it is thought that a single phosphorylation event can lead to inactivation of several transporters, providing a mechanism for fast modulation of transport activity (see review by Gojon et al.).

Communication between roots and shoots is vital to match nutrient demand with acquisition, and to respond appropriately to environmental fluctuations. Two of the articles in this issue focus on long distance signalling mechanisms for the mineral macronutrients, (N, P, S K, Mg, Ca (Chiou et al.) and mineral micronutrients Fe, Cu, Zn, Mn, (Giehl et al.). We are starting to elucidate the nutrient-specific signalling and sensing pathways, and the various signalling molecules that have been implicated include hormones, sugars, nutrients themselves or their metabolites. More recently, microRNAs have been shown to play an important role in long distance signalling in response to phosphorus stress and it is possible that this systemic signalling mechanism operates more widely in controlling other elements.

In adjusting nutrient acquisition to the needs of the plant there must be mechanisms for sensing and signal transduction to ensure the appropriate response. We still do not know the mechanism and sites of sensing of many of the macro and micronutrients. In relation to mechanisms controlling root architecture, Gojon et al. discusses the role of microRNA167a/b and the Auxin Response Factor gene ARF8 in controlling lateral root emergence in response to N signalling. We need to know much more about coordination of regulatory networks and cross-talk between homeostatic pathways regulating different nutrients and more broadly with hormone and sugar signalling pathways.

The exciting applied aspects are considered in the article by Zhao and McGrath who discussed “the global and challenging problems of micronutrient malnutrition in humans and environmental contamination with heavy metals or metalloids”. We now need to consider how to produce nutritious food as well as concentrating on crop yields. Micronutrients are deficient in many cereal crops and this in turn leads to human malnutrition. Important goals are to

increase the bioavailability of micronutrients such as Fe, Zn and Se in the food we produce to help alleviate deficiencies in these essential micronutrients in much of the world's population. Zhao and McGrath highlight work showing that a NAC transcription factor (*NAM-B1*) accelerates senescence and increases remobilization of nutrients (N, Fe and Zn) from leaves to developing grains in certain varieties of wheat (Uauy et al. 2006). As modern bread wheat varieties carry a non-functional *NAM-B1* allele, introgression of the locus encoding a functional transcription factor into these varieties may improve the nutrient content. With biofortification strategies involving manipulation of transporters we have to be careful that in increasing levels of useful nutrients we also run the risk of increasing levels of toxic elements that hijack particular transport processes. Strategies for altering the substrate specificities of particular transporters may prove useful. High levels of certain metals can be toxic and the process of phytoremediation where plants are used to cleanse or stabilize contaminated soil is of great interest. Much research has focussed on identifying potential metal hyperaccumulating plants and understanding the mechanisms they use to accumulate metals to high levels. Future goals will be to use this knowledge to produce high biomass plants that can economically, effectively and safely be deployed for environmental restoration applications.

In the final article, Baxter discusses the advantages of an ionic approach which involves studying the ionome (the total mineral nutrient and trace element content of the plant). Linking this approach to high-throughput genotyping technology will help to efficiently identify genes and gene networks that co-ordinately control elemental accumulation in plants. This will also provide a greater understanding of the relationships between different elements, and the responses of the plant to environmental conditions at different stages of growth and development. An interesting example was discussed which demonstrated that a single physiological change in the plant (increase in root suberin probably in casparian strip) can alter the concentrations of multiple elements which do not share the same transporters.

We still have much to learn about the plant ionome and the mechanisms that regulate it. However, from the topics highlighted in this issue we are making substantial progress towards this goal. By combining the powerful tools currently used to determine gene function with genetics, comparative genomics, high-density "omics" platforms and advanced modelling approaches in the future we will certainly make even more rapid progress in understanding the integrated mechanisms that underlie the coordinate regulation of the ionome at the cellular, tissue and whole organism levels. Though not covered in this issue, studies also need to focus on the important interactions between rhizosphere micro-organisms and plant roots, and its role in element homeostasis.

Biographies

Lorraine Williams' lab is focused on membrane transport processes in plants particularly in relation to mineral nutrition. Plants require certain heavy metals such as copper, zinc and manganese as essential nutrients for growth and development. Without these metal micronutrients, deficiency symptoms arise and in crop species this can lead to losses in yield. When present in excess these, and non-essential metals such as cadmium, can become extremely toxic. Thus mechanisms must exist to satisfy the requirements of cellular metabolism but also to protect cells from toxic effects. Lorraine's group is investigating the role of key membrane transport proteins in heavy metal uptake, distribution and detoxification. These processes are studied in *Arabidopsis* using molecular, genetic and biochemical approaches. More recently this has been extended to barley where she is studying membrane transporters that function in delivering metals to the grain. A long term goal of the lab is to identify key genes involved in heavy metal transport and to determine how these can be manipulated to enhance the nutritional quality of crops. Lorraine also has a long-standing interest in the role

of membrane proteins in the developing seedling, particularly in relation to sugar and amino acid transport and also in nutrient allocation during pathogen infection.

David E Salt's long term research interest is to understand the function of the genes and gene networks that regulate the plant ionome (elemental composition), along with the evolutionary forces that shape this regulation. To achieve this his laboratory couples high-throughput elemental profiling, with bioinformatics, genomics and genetics, biochemistry and physiology in both genetic model species (yeast, *Arabidopsis thaliana* and rice) and "wild" plants that hyperaccumulate various metals (Cd, Ni & Zn), metalloids (As) and non-metals (Se) in their native habitat, including various *Thlaspi*, *Pteris* and *Astragalus* species. David E Salt has been involved in such work since his Ph.D (Liverpool University, UK, 1985 – 1988) working on the mechanisms of copper tolerance in *Mimulus guttatus* (yellow monkey flower). He also has a B.Sc in Biochemistry (University of North Wales, Bangor, UK, 1981 – 1984) and an M.Sc in Computer Science (Hallam University, UK, 1984 – 1985), and has held faculty positions at Rutgers University (1993 – 1997), Northern Arizona University (1998 – 2001), and is currently a Full Professor at Purdue University, where he has been since 2001. David E Salt has published over 80 peer reviewed papers since 1989 with currently approximately 4000 citations.

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