THE ELEMENTS OF PLANT MICRONUTRIENTS

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Abstract. Amino acid R groups in proteins provide a limited repertoire of functional groups for catalyzing biochemical transformations. The use of inorganic elements, particularly the first row transition metals, expands greatly the range of chemistry that can be catalyzed in a cell. Zinc ions are key for enzymatic catalysis of reactions that require an electrophile, while iron, manganese, copper, nickel, and molybdenum are brokers of redox transformations.
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INTRODUCTION

Each metal has unique chemical properties including ligand preferences, coordination geometries, and redox potentials, which are exploited for diverse, yet highly specific, chemistry. In the photosynthetic electron transfer chain, the midpoint potentials of the metal centers span nearly 1.5 V. The import of metals in biology is evident from the association of approximately 30% to 40% of proteins with a metal (Waldron et al., 2009). Transition metal-protein associations are highly specific, at least in vivo, because mismetallation can block activity or yield undesirable chemistry. In vitro, the associations occur according to thermodynamic preferences described by the Irving-Williams series: For divalent ions, copper and zinc ions bind most tightly relative to manganese and iron ions (Waldron and Robinson, 2009).

MAIN PART

The in vivo specificity is achieved by kinetic control of metal ion assimilation, distribution, and storage and of metalloprotein assembly, or in other words, metal metabolism. For nickel and copper proteins in bacte- ria, specificity can be achieved by direct protein to protein transfer via metallochaperones coupled with structural reorganization and stabilization of the re- sulting holoprotein so that the metal is kinetically trapped. For a periplasmic manganese protein in bac- teria, one study showed that correct metallation is achieved by restricting holoprotein formation to the cytoplasm where the concentration of another com- peting metal ion is reduced by sequestration in bind- ing protein (Tottey et al., 2008). Compartmentation of metal ions is, therefore, a key consideration in metal-loprotein biogenesis pathways.

Nonessential metals like cadmium, mercury, and silver can compete with the essential transition metals for uptake and metalloprotein assembly pathways because protein flexibility can reduce the selectivity of metal-binding sites. A consequence of the redox reactivity and the promiscuous binding of transition metals to thiol, thioether, imidazole, and carboxylate ligands is that inappropriate accumulation of metals is harmful in biology. Therefore, metal metabolism is under homeostatic regulation (plant homeostasis pathways reviewed in Palmer and Guerinot, 2009).

Studies of metalloregulation in bacteria, involving nutrient acquisition pathways as well as metal resis- tance pathways, indicate that regulators for each metal have

coevolved in a single organism as a set of regu- lators with ranked relative affinities for various metals (Waldron and Robinson, 2009). These regulators de- termine the ranges (between deficiency and excess) of the number of atoms of metal available in a bacterial cell to match the number of metal-binding sites. The problem is more complex in a eukaryotic cell where subcellular compartmentation of metals and metallo- proteins is another consideration. In multicellular or- ganisms, there is the question of how regulation at the cellular level is integrated into the context of the whole organism.

The subject of metal-protein interactions in plants needs more attention at all levels of study, from molecular to cellular to whole plant. From a practical perspective, this is important for effective cross-species transfer of metalloenzymes and metal-binding do- mains to ensure that they are populated with the correct metals. Plants are a dietary source of minerals for a large fraction of the human population and zinc and iron deficiency are pressing problems in human nutrition. The understanding of metalloprotein bio- chemistry and plant mineral nutrition, therefore, has global impact. In the coming years, a greater under- standing of human nutrient metabolism will have an impact on the design of micronutrient stores in crop plants.
Decades ago, the focus in studying metals in plants was on establishing micronutrient requirements and describing symptoms of individual deficiencies. One important outcome of these studies was an apprecia- tion for the characteristic phenotype resulting from individual metal deficiencies. These studies under- scored the unique biochemical functions of each metal micronutrient. More recent research, using classical and molecular genetics, has emphasized the discovery of metal transporters and processes that facilitate transport, including mobilization by redox chemistry (particularly important for copper and iron), chelation (relevant for iron and nickel), and extracellular acidi- fication (for review, see Palmer and Guerinot, 2009). Assimilatory pathways are now quite well described, and continued investigation in the near term will distinguish transporters involved in intercellular transport—processes for metal loading into the xylem for root to shoot delivery or for recovery of metal nutrients prior to leaf senescence—and intracellular distribution to the metal utilizing versus storing organelles. Each type of transporter, ZIP, NRAMP, CTR, CDF/ MTP, is found as a family of genes encoding variant proteins (Hanikenne et al., 2009).
Real-time imaging with metal-selective sensors also provides dynamic information for visualizing transient fluxes. Transition metals have not been evaluated for their potential as messengers in signal transduction pathways (analogous to calcium, but with a built-in redox switch). This is completely unexplored in plants, but the path to discovery is now open.

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