CHAPTER 8
HEAVY METAL STRESS

KSENJIA GASIC AND SCHUYLER S. KORBAN

Department of Natural resources and Environmental Sciences, University of Illinois, Urbana, Illinois, 61801, USA
(e-mail: kgasic@uiuc.edu; korban@uiuc.edu)

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1. INTRODUCTION

Heavy metals are defined as those having densities higher than 5 g cm\(^{-3}\). Ions of heavy metals such as iron, copper, zinc, cobalt, or nickel are essential micronutrients that are critically involved in functional activities of large numbers of proteins involved in sustaining growth and development of living organisms. However, at excess concentrations, these metal ions can become detrimental to living organisms. Furthermore, these organisms can be also exposed to highly toxic ions of cadmium, lead, mercury, and other metals that are generally considered non-essential.

It is apparent that complex network of transport, chelation, and sequestration processes has evolved over time that functions in maintaining concentrations of essential metal ions in different cellular compartments within a narrow physiological range, thus minimizing the damage caused by entry of non-essential metal ions into the cytosol (Halloran and Cullota, 2000; Clemens, 2001).

At the cellular level, plants have a wide range of potential mechanisms that are likely involved in the detoxification, and thus tolerance to heavy metal stress. Important components of heavy metal homeostasis and detoxification systems are membrane-based heavy metal transporters (reviewed by Williams et al., 2000), intracellular metal chaperones for efficient distribution of scarce essential metals, chelation (reviewed by Cobbett and Goldsbrugh, 2002), and sequestration processes. Loss of any one of these critical processes will lead to hypersensitivity to heavy metal ions.

Depending on their oxidation states, heavy metals can be highly reactive, resulting in toxicity in most organisms. The ability of plants to increase antioxidative protection to combat negative consequences of heavy metal stress appears to be lim-
ited, as it has been shown that exposure to elevated concentrations of redox reactive metals results in decreased rather than increased activities of antioxidative enzymes. The toxic effects of heavy metals on plants can be characterized by the following: (a) production of reactive oxygen species by autoxidation and the Fenton reaction, which is typical for transition metals such as iron and copper, (b) blocking of essential functional groups in biomolecules, which has been mainly reported for non-redox-reactive heavy metals such as cadmium and mercury, and (c) displacement of essential metal ions from biomolecules, which occurs with different kind of heavy metals (Schützendübel and Polle, 2002).

2. METAL ACQUISITION

Understanding the processes involved in the movement of essential and non-essential metal ions into plant cells at the molecular level has vastly advanced in recent years. Associations between elevated steady-state transcript levels of metal transporter genes of the Zn-regulated transporter (ZRT), Fe-regulated transporter (IRT)-like protein (ZIP), and cation diffusion facilitator protein (CDF) families and metal hyperaccumulation (Pence et al., 2000; Lombi et al., 2002) or metal tolerance (Van der Zaal et al., 1999; Assunção et al., 2001; Persans et al., 2001) have been observed.

All heavy metal pumps, heavy metal ATPases (HMA), from bacteria, plants, and humans share significant sequence similarities, and cluster together as the \( P_{1B} \) subfamily (Palmgren and Axelsen, 1998). Ion pumps belonging to the P-type ATPase superfamily share a common enzymatic mechanism in which ATP hydrolysis is used to transport ions across a membrane. The “P-type” designation is attributed to a phosphorylated intermediate characteristic of the enzyme’s catalytic cycle (Pedersen and Carafoli, 1987). Comparing rice (Oryza sativa) and Arabidopsis genome sequences has revealed similar numbers of P-type ATPase genes in both plant species, 43 and 46, respectively, despite the fact that the size of the rice genome is three times larger than that of Arabidopsis (Baxter et al., 2003). Both rice and Arabidopsis have representatives in all five major subfamilies of P-type ATPases. These include heavy-metal ATPases (\( P_{1B} \)), \( \text{Ca}^{2+} \)-ATPases (endoplasmic reticulum-type \( \text{Ca}^{2+} \)-ATPase and autoinhibited \( \text{Ca}^{2+} \)-ATPase, \( P_{5B} \) and \( P_{28} \)), \( \text{H}^{+} \)-ATPases (autoinhibited \( \text{H}^{+} \)-ATPase, \( P_{3A} \)), putative aminophospholipid ATPases (ALA, \( P_{1} \)), and a branch with an unknown specificity (\( P_{5} \)). Genome sequence analysis of Arabidopsis has also revealed eight members of a \( I_{R} \) ATPase subfamily of which four members are related to known Cu (I) transporters and contain N-terminal metal-binding site (MBS) motifs similar to those identified in other organisms. The remaining four members are more closely related to known divalent cation transporters in prokaryotes, three of which form a closely related group and are believed to be Zn (II) transporters (Cobbett et al., 2003).

Members of the ZIP gene family of metal transporters are capable of transporting a variety of cations, including cadmium, iron, manganese and zinc. The ZIP name is derived from the first identified members that include “ZRT (zinc-regulated trans-