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Heavy metal accumulation and signal transduction in herbaceous and woody plants: Paving the way for enhancing phytoremediation efficiency

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ABSTRACT

Heavy metal (HM)-accumulating herbaceous and woody plants are employed for phytoremediation. To develop improved strategies for enhancing phytoremediation efficiency, knowledge of the microstructural, physiological and molecular responses underlying HM-accumulation is required. Here we review the progress in understanding the structural, physiological and molecular mechanisms underlying HM uptake, transport, sequestration and detoxification, as well as the regulation of these processes by signal transduction in response to HM exposure. The significance of genetic engineering for enhancing phytoremediation efficiency is also discussed. In herbaceous plants, HMs are taken up by roots and transported into the root cells via transmembrane carriers for nutritional ions. The HMs absorbed by root cells can be further translocated to the xylem vessels and unloaded into the xylem sap, thereby reaching the aerial parts of plants. HMs can be sequestered in the cell walls, vacuoles and the Golgi apparatuses. Plant roots initially perceive HM stress and trigger the signal transduction, thereby mediating changes at the molecular, physiological, and microstructural level. Signaling molecules such as phytohormones, reactive oxygen species (ROS) and nitric oxide (NO), modulate plant responses to HMs via differentially expressed genes, activation of the antioxidative system and coordinated cross talk among different signaling molecules. A number of genes participated in HM uptake, transport, sequestration and detoxification have been functionally characterized and transformed to target plants for enhancing phytoremediation efficiency. Fast growing woody plants hold an advantage over herbaceous plants for phytoremediation in terms of accumulation of high HM-amounts in their large biomass. Presumably, woody plants accumulate HMs using similar mechanisms as herbaceous counterparts, but the processes of HM accumulation and signal transduction can be more complex in woody plants.

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1. Introduction

1.1. HM contamination in soil

Generally, heavy metals (HMs) are referred to as elements with a density more than 5 g cm^{-3}, and most transition elements, such as Zn, Cu, Mn, Ni, Cd, Pb, Hg and As (a metalloid, but it is included as a HM hereafter), belong to HMs (Clemens et al., 2002). The natural distribution of these elements in the earth crust varies significantly from site to site and these metals cause no serious problems to the health of natural ecosystems and human beings. However, anthropogenic activities, such as mining, smelting, combustion of fossil fuels, application of phosphate fertilizers, and sewage sludges, have led to the activation and release of HMs in the crust to the soil, water and atmosphere (Clemens, 2006). It is estimated that, for example, about 30,000 tons of Cd are emitted into the atmosphere each year worldwide due to anthropogenic activities (Gallego et al., 2012). As a consequence of anthropogenic activities, large areas on the earth have been contaminated by HMs. For instance, about 2.88×10^6 ha of land have been destroyed by contamination with HMs due to mining in China alone (Clemens, 2006).

Some HMs, such as Zn, Cu, Mn and Ni, are biologically important because they are micronutrients for most organisms, although higher levels of these metals are detrimental to organisms (Ducic et al., 2006; Luo et al., 2014; Mizuno et al., 2005; Shi et al., 2015b). Other HMs including Cd, Pb, Hg and As have no known biological functions and are toxic to most organisms (Kramer, 2010; Schutzendubel and Polle, 2002; Verbruggen et al., 2009a). HM contamination has posed a serious threat to the health of natural ecosystems and humans because HMs eventually enter the food chain and are accumulated in organisms, leading to biodiversity losses and productivity decreases of ecosystems (Mayor et al., 2013), and causing serious damage to human beings (Bertin and Averbeck, 2006).

Many physical and chemical approaches have been applied to remediate HM contaminated soils. These approaches include excavation, transport, soil washing, extraction, and addition of chemicals, such as ethylenediaminetetraacetic acid (EDTA) and limestone, into the soils to complex the toxic HMs (Barrutia et al., 2010; Bolan et al., 2014; Suthar et al., 2014). Application of physical and chemical methods to remediate HM-polluted sites is extremely expensive. About 6–8 billion US dollars are spent annually in remediation efforts in the USA alone and on a global scale, annual costs of ca. 25–50 billion US dollars are estimated (Tsao, 2003). Moreover, these physical and chemical remediation approaches are generally labor intensive, prone to cause secondary pollution, and inappropriate to remediate large land areas with HM contamination (Ali et al., 2013; Doty, 2008). Alternatively, phytoremediation is proposed to clean up HM-polluted soils.

1.2. Phytoremediation

Phytoremediation is referred to using plants and associated soil microbes to reduce concentrations of HMs in soils (Kramer, 2005). Obviously, phytoremediation is an environmental friendly and cost effective method in comparison with physical and chemical remediation approaches. It has been estimated that phytoremediation costs about 25–100 US dollars per ton of soil (Movahed and Maeiyat, 2009). The annual revenue of the phytoremedation market is estimated to be 235–400 million US dollars (Yadav et al., 2010). The success of phytoremediation mainly depends on the ability of plants to absorb and translocate HMs to the aerial parts (Kramer, 2010; Milner and Kochian, 2008), and the activity of soil microbes (such as mycorrhizal fungi and growth-promoting bacteria) which can promote HM enrichment in aerial parts of host plants (Luo et al., 2014; Ma et al., 2014; Rajkumar et al., 2012). The significance of the associations between plants and soil microbes in remediating HM-polluted soils has recently been reviewed (Luo et al., 2014; Ma et al., 2011; Miransari, 2011; Rajkumar et al., 2012). Therefore, we focus in the present review on HM accumulation and signal transduction in herbaceous and woody plants.

Previous studies on phytoremediation mainly concentrated on the identification of plants whose aerial parts can accumulate HMs at high concentrations (hyperaccumulators) and the understanding of the underlying physiological and molecular mechanisms. Many hyperaccumulating herbaceous plants have been identified and the mechanisms for HM uptake, transport, sequestration and detoxification have been elucidated in these plants (Clemens, 2006; Clemens et al., 2013; Kramer, 2010; Maestri et al., 2010; Milner and Kochian, 2008; Verbruggen et al., 2009b). Due to the limitations of herbaceous plants in phytoremediation (see below), fast growing woody plants have been proposed in recent years (Capuana, 2011; Peuke and Rennenberg, 2005a, 2015b; Robinson et al., 2000; Yadav et al., 2010). In this review, we first report the progress in understanding the physiological and molecular mechanisms underlying HM uptake, transport, sequestration and detoxification in herbaceous and woody plants. Subsequently, we discuss signal transduction and the significance of genetic engineering to enhance the phytoremediation efficiency in herbaceous and woody plants.

1.3. Using herbaceous versus woody plants for phytoremediation

Some plants are able to accumulate HMs at extraordinarily high levels in their aerial parts. Leaves accumulating HMs (μg g^{-1}) above 10,000 for Zn and Mn, 1000 for Cu, Pb, Ni and As, and 100 for Cd are regarded as hyperaccumulating plants (hyperaccumulators) for the respective element (Kramer, 2010). With the potential application for phytoremediation, hyperaccumulating plants are extensively exploited. Currently, about 500 plant species with HM hyperaccumulation traits have been found and most of them belong to the families of Asteraceace, Brassicaceae, Caryophyllaceae, Poaceae, Violaceae and Fabaceae (Cappa and Pilon-Smits, 2014; Gallego et al., 2012; Milner and Kochian, 2008).

Most hyperaccumulators are herbaceous plants with limited biomass. Although these hyperaccumulators can accumulate HMs at high concentrations in their aerial parts, the amount of HMs in aboveground parts of plants is limited due to the low biomass production (van der Ent et al., 2013). Thus, it was proposed that plants for phytoremediation are desired to possess the following characteristics: high growth rate, high aboveground biomass, deep and highly branched root system, and efficient uptake of HMs and translocation to the aerial parts (Ali et al., 2013). As a result, fast growing woody plants, such as *Populus* and *Salix* species, are proposed for potential application in phytoremediation (Capuana, 2011; Doty, 2008; Migeon et al., 2009; Peuke and Rennenberg, 2005a, 2015b; Robinson et al., 2000; Tognetti et al., 2013; Yadav et al., 2010). Moreover, these woody plants can be

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