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Morphological and Physiological Responses of Plants to Cadmium Toxicity: A Review

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ABSTRACT

Cadmium (Cd) contamination has posed an increasing challenge to environmental quality and food security. In recent years, phytoremediation has been particularly scrutinized because it is cost-effective and environmentally friendly, especially the use of metal-hyperaccumulating plants to extract or mine heavy metals from polluted soils. Under Cd stress, responses of hyperaccumulator and non-hyperaccumulator plants differ in morphological responses and physiological processes such as photosynthesis and respiration, uptake, transport, and assimilation of minerals and nitrogen, and water uptake and transport, which contribute to their ability to accumulate and detoxify Cd. This review aims to provide a brief overview of the recent progresses in the differential responses of hyperaccumulator and non-accumulator plants to Cd toxicity in terms of growth and physiological processes. Such information might be useful in developing phytoremediation technology for contaminated soils.

Key Words: heavy metal, hyperaccumulator, metal accumulation, mineral elements, photosynthesis, phytoremediation, water transport, water uptake

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INTRODUCTION

In general, when the total cadmium (Cd) concentration in soil exceeds 8 mg kg^{-1}, or the bioavailable Cd concentration becomes > 0.001 mg kg^{-1}, or the Cd concentration in plant tissue reaches 3–30 mg kg^{-1} (Solís-Domínguez *et al.*, 2007; Chen *et al.*, 2011), most plants exhibit visible Cd toxicity symptoms such as stunted growth, chlorosis, necrosis, root browning, and even death (Gratão *et al.*, 2009; Chang *et al.*, 2013). Excess Cd accumulation in plants can profoundly interfere with a series of physiological processes such as photosynthesis (Feng *et al.*, 2010) and respiration (Smiri *et al.*, 2009; Andosch *et al.*, 2012; Volland *et al.*, 2014), uptake, transport, and assimilation of mineral nutrients (Wang *et al.*, 2007; Nedjimi and Daoud, 2009), and uptake of water (Polle *et al.*, 2013). In addition, Cd stress alters gene (Qian *et al.*, 2010; Irfan *et al.*, 2013) and protein expression, induces or inhibits enzymes, enhances reactive oxygen species (ROS) accumulation and lipid peroxidation, and disturbs metabolisms (López-Millán *et al.*, 2009; Semane *et al.*, 2010).

However, the threshold of phytotoxic concentration of Cd varies across plant species, ecotypes, cultivars, and even plant tissues (He *et al.*, 2015). Cadmium hyperaccumulators accumulate > 100 mg Cd kg^{-1} in the shoot dry biomass (McGrath and Zhao, 2003). For correlations of plant Cd concentrations with growth or morphological parameters, contrasting results have often been obtained in the hyperaccumulating ecotype (HE) of *Sedum alfredii* and its non-hyperaccumulating ecotype (NHE) (Li *et al.*, 2009). Cadmium-containing enzymes or Cd-binding proteins possibly exist in plants, play a vital role in photosynthesis and growth stimulation, and facilitate Cd tolerance in Cd-hyperaccumulating plants such as *Thlaspi caerulescens* and *Thalassiosira weissflogii* (Lane *et al.*, 2005; Liu M Q *et al.*, 2008; Qiu *et al.*, 2008). Although Cd inhibits photosynthesis in most

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plants, increased chlorophyll contents were observed in some Cd hyperaccumulators such as *S. alfredii* (Zhou and Qiu, 2005). The Cd-induced activities of antioxidative enzymes were higher in Cd-accumulating species and genotypes such as *Arabidopsis halleri* (Chiang *et al.*, 2006), black oats (*Avena strigosa*) (Uraguchi *et al.*, 2006), yellow fleabane (*Dittrichia viscosa* (L.) Greuter) (Uraguchi *et al.*, 2009), *T. caerulescens* (Boominathan and Doran, 2003), Indian mustard (*Brassica juncea*) (Wang *et al.*, 2008), and *Solanum nigrum* L. (Sun *et al.*, 2007) than in the non-accumulating plants. Cadmium competes with other elements, especially divalent metal ions, but Cd uptake is not inhibited by zinc (Zn) in Cd hyperaccumulator *T. caerulescens* (Lombi *et al.*, 2001) or is even enhanced by Zn addition in the HE of *S. alfredii* (Li *et al.*, 2009). These different effects of Cd on growth, chloroplasts, and antioxidative enzymes and its interactions with divalent metal ions in accumulators and non-accumulators can probably be attributed to the differences in their abilities in sequestering and detoxifying Cd. Clarification of the differential morphological responses and physiological characteristics of hyperaccumulator and non-hyperaccumulator plants to Cd is vital for understanding the mechanisms of metal hyperaccumulation and detoxification. The primary objective of this review is to compare hyperaccumulator plants with non-hyperaccumulator plants in their responses to Cd stress and the related morphological and physiological mechanisms in order to facilitate genetic engineering in hyperaccumulator plants and optimize management practices such as chemical enhancement in the field application of phytoremediation.

HYPERACCUMULATOR AND NON-HYPERACCUMULATOR PLANTS

Phytoremediation is a technology of using metal-hyperaccumulating plants to extract or mine heavy metals from contaminated soils. In theory, the use of hyperaccumulator plants could substantially enhance remediation efficiency since these plants are able to tolerate and accumulate Cd more than 100 mg kg^{-1} dry weight (DW) (0.01%) in shoots, which is more than 100 times higher than that accumulated by non-hyperaccumulator plants (Krämer, 2010). Furthermore, a Cd hyperaccumulator can be distinguished from related non-hyperaccumulating taxa because of its bioconcentration factor (BCF) and translocation factor (TF) values of >1 (BCF is the ratio of metal concentration in the shoot to that in the soil; TF is the ratio of metal concentration in the shoot to that in the root) and its tolerance property (the plants tested should not have toxic symptoms such as necrosis, chlorosis, and significant decrease in shoot biomass) (Rascio and Navari-Izzo, 2011; Wei *et al.*, 2012). To date, few plant species have been identified as Cd hyperaccumulators, and their Cd-accumulating ability and related BCF and TF values have been listed by He *et al.* (2015). However, most of these Cd hyperaccumulator plants have a slow growth rate and short life cycle with a low biomass yield. Kabata-Pendias and Pendias (2001) stated that metal-hyperaccumulating plants have lower biomass production because they use a great part of their metabolism energy in adapting themselves to the high-metal concentration environment.

Recently, increased interest has been directed to the non-hyperaccumulator plant species with rapid growth habit, high biomass yields, and desired Cd-accumulating capacity. Many plant species were identified to have the potential for Cd accumulation, such as Bermuda grass (*Cynodon dactylon*), vetiver grass (*Vetiveria Zizanioides*), red fescue (*Festuca rubra*), bulrush (*Typha latifolia*), and rape (*B. juncea*). Some economic plant species such as *indica* × *japonica* hybrids (biofuel crop) and safflower (*Carthamus tinctorius* L.) have been tested for their application in phytoremediation (Baker *et al.*, 1994, 2000; Oh *et al.*, 2014). Table I lists non-hyperaccumulator plant species that are promising for application in the phytoremediation of Cd-contaminated soils.

MORPHOLOGICAL CHANGES

Roots

Root browning has been observed in many plants subjected to Cd exposure (Lux *et al.*, 2011; Chang *et al.*, 2013). Cadmium toxicity is often described as decreased root length and dry mass, as well as enlarged root diameter (Gratão *et al.*, 2009). Lunáčková *et al.* (2003) reported that the roots of willow (*Salix alba*) and poplar (*Populus* × *euramericana* cv. Robusta) became shorter and thicker after treatment with 10 μmol L^{-1} Cd(NO$_3$)$_2$. Inhibition of root elongation has been shown to be one of the earliest and distinct symptoms of Cd toxicity (Lux *et al.*, 2011). Cadmium-induced inhibition of root elongation might be attributed to the depolymerization of microtubules of cell cytoskeleton and the formation of chromosome aberrations, which result in lower mitotic activities of meristematic cells (Seth *et al.*, 2008). Cadmium stress results in greater root diameter owing to increased parenchyma cell size and enlarged cortical tissues, which have a functional role in increasing plant resistance to radial flows of wa-