



Review

Plant chromium uptake and transport, physiological effects and recent advances in molecular investigations



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ABSTRACT

Increasingly, anthropogenic perturbations of the biosphere manifest in a broad array of global phenomena, causing widespread contamination of most ecosystems, with high dispersion rates of many contaminants throughout different environmental compartments, including metals. Chromium (Cr) contamination in particular, is, increasingly, posing a serious threat to the environment, emerging as a major health hazard to the biota. However, although the molecular and physiological mechanisms of plant responses to many heavy metals, especially lead (Pb) and cadmium (Cd), have been focused upon in recent years, chromium has attracted significantly less attention. In this context, this review discusses aspects of Cr uptake and transport, some physiological and biochemical effects of Cr exposure in plants, and molecular defense mechanisms against this metal. Recent advances in determining these responses, in fields of knowledge such as genomics, proteomics and metalloomics, are discussed herein.

1. Introduction

Increasingly, anthropogenic perturbations of the biosphere manifest in a broad array of global phenomena, including accelerated industrialization, intensive agricultural activities, extensive mining accompanied by significant increases in the human population and, consequently, rapid urbanization (Emamveridian et al., 2015). This has, in turn, caused widespread contamination of most ecosystems, with high dispersion rates of many contaminants throughout different environmental compartments, including metals.

Chromium (Cr) is the seventh most abundant element in the earth's crust and the sixth most abundant transition metal (Mohan and Pittman, 2006; Panda and Choudhury, 2005). It is present in the ecosystem as a result of the weathering of the earth's crust and deposition of waste from anthropogenic activities, such as the metallurgical (mainly steel and metal) and chemical (pigments, electroplating, leather, among others) industries (Kotaš and Stasicka, 2000; Tchounwou et al., 2012). This element is detected in most of the environmental matrices (air, water, soil) and has, in recent decades, increased exponentially in aquatic and terrestrial ecosystems (Velma et al., 2009). This metal can be detected in several oxidation states (Cr⁰, Cr¹⁺, Cr²⁺, Cr³⁺, Cr⁴⁺, Cr⁵⁺, Cr⁶⁺). Cr⁰, Cr⁴⁺ and Cr⁵⁺ do not occur

naturally. While Cr⁰ is mainly found in metal alloys, such as stainless steel, and is an additives which gives metallic material properties, such as corrosion resistance wear, high temperature and higher color durability (Gomez and Callao, 2006; Zayed et al., 1998), the latter Cr species are unstable intermediate forms in oxidizing and reduction reactions of Cr³⁺ and Cr⁶⁺ (Kotaš and Stasicka, 2000; Zayed and Terry, 2003). Cr⁺¹ is rarely seen except when stabilized in complexes (Lay and Levina, 2012) and Cr²⁺ is relatively unstable and is readily oxidised to the trivalent state which occurs naturally in ores (Zayed and Terry, 2003).

Among all Cr oxidation states, Cr³⁺ and Cr⁶⁺ are the most stable in aquatic and terrestrial environments (Augustynowicz et al., 2010; Santos et al., 2009; Zayed et al., 1998), although they differ in terms of mobility, bioavailability and toxicity (Panda and Choudhury, 2005). Generally, the oxidation of Cr(III) to Cr(VI) is a very slow process at pH above 5 (Eary and Rai, 1987), and alkaline conditions favor the oxidation of Cr(III) to Cr(VI) (Pantsar-Kallio et al., 2001; Seaman et al., 2001). The reduction of Cr is influenced primarily by the decomposition of organic matter, dissolved reduced sulphates and industrial effluents that may alter the physical-chemical parameters of the environment (Stanin and Pirnie, 2004). As oxygen concentrations are usually low in polluted environments, the reduction of Cr⁶⁺ to Cr³⁺

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is favored (Stanin and Pirnie, 2004), this reduction can indirectly influence and change environmental pH to both alkalinity or acidity extremes (Hawley et al., 2004). In soil, this phenomenon might in turn disturb nutrient bioavailability and their sorption by plants (Emamverdian et al., 2015).

Although Cr^{3+} has been shown to be less toxic than Cr^{6+} and is a necessary nutrient for maintenance of metabolic activities in animals (Mohan and Pittman, 2006; Urrutia et al., 2008), both Cr species, when present in high concentrations, can show highly toxic effects on the biota (Dazy et al., 2008; Sreeram et al., 2004). Particularly, the range between Cr^{3+} toxicity and the need for this element is very narrow (Chang et al., 1996). Regarding plants, there is no conclusive evidence of the essentiality of the role of Cr in plant metabolism, and literature results are discrepant in this regard; while some studies indicate that Cr is not essential in plants (Hayat et al., 2012), others have shown that small additions of Cr have stimulating effects on plant growth and productivity (Ghosh and Singh, 2005; Zayed and Terry, 2003).

Common physicochemical treatment technologies that remove Cr pollution are based on reduction–oxidation, precipitation, accumulation, and sorption (Hawley et al., 2004). Plants pose mechanisms of contaminant remediation related to all of the mentioned strategies, however, the details of these mechanisms are not clear (Augustynowicz et al., 2013). Thus, knowledge on the biological processes that affect the mobility, chemical distribution and speciation of Cr in the physical and chemical environment is essential in order to develop effective preventive and/or remediation strategies to counteract the toxic effects of this metal (Zayed and Terry, 2003).

Plants employ several different types of strategies for metal tolerance or detoxification, as described previously (Emamverdian et al., 2015). Briefly, as a first step, plants adopt avoidance strategies, such as restricting or excluding metal uptake from the soil, thus preventing metal entry into the roots (Viehweger, 2014), by either immobilizing the metal ions by mycorrhizal association or complexing the metals through organic compounds produced and exuded from the roots (Dalvi and Bhalerao, 2013). If this fails and the metal enters the plant, tolerance mechanisms for detoxification are activated, such as metal sequestration and compartmentalization in different intracellular compartments (Patra et al., 2004), metal transport or binding to the cell wall and biosynthesis and accumulation of several compounds aimed at metal complexation and protection against metal toxicity, such as prolines and metallothioneins (Dalvi and Bhalerao, 2013; John et al., 2009). If all these measures prove unsuccessful and plants begin suffering effects of metal toxicity, activation of antioxidant defense mechanisms is then pursued (Manara, 2012).

2. Cr absorption, transport and distribution in plants

Many factors influence metal absorption in plants such as environment, temperature, pH, aeration, electrical conductivity, competition between species, type of plant, plant size, root system, element availability, type of leaf, and soil and plant moisture content (Yamamoto and Kozłowski, 1987). The phytotoxic effects of Cr are primarily dependent on the speciation of the metal, which determines its uptake, translocation and accumulation (Shanker et al., 2005). Cr absorption and distribution mechanisms in the vegetative and reproductive organs of plants, however, are still not fully understood (Hayat et al., 2012). It has been reported that Cr is transported and accumulated in plants via carrier ions, such as sulfate or iron, and is not directly absorbed by plants (Gajalakshmi et al., 2012; Singh et al., 2013). It is also known that Cr can be absorbed both as Cr^{3+} and Cr^{6+} , but no specific mechanism for Cr absorption has yet been postulated (Oliveira, 2012; Singh et al., 2013).

Most studies have demonstrated excessive accumulation of Cr in roots, and the immobilization of this metal in the vacuoles of plant root cells is suggested as the main reason for this bioaccumulation (Nematshahi et al., 2012; Oliveira, 2012), and is proposed as a means

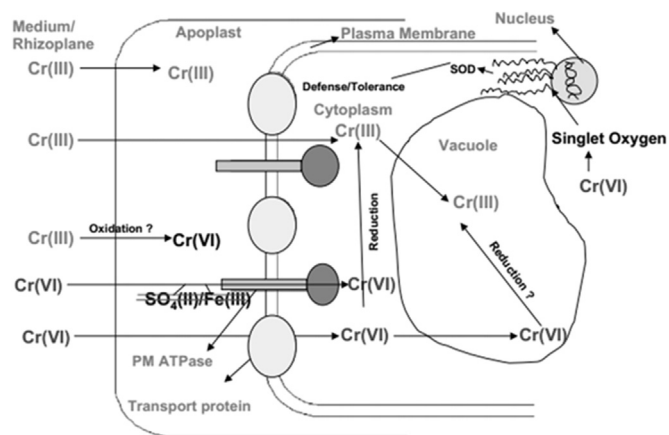


Fig. 1. Hypothetical Model of Cr transport and toxicity in plant roots (adapted from Shanker et al. (2005)).

of protecting the photosynthetic apparatus in leaves (Brune et al., 1995). In roots, Cr^{6+} absorption occurs actively, while Cr^{3+} absorption occurs by osmosis (Barros et al., 2006). The plasma membranes of roots are the first functional structure to come into contact with metals (Fig. 1), and play a crucial role in metal tolerance (Hayat et al., 2012). It is possible that the entry of this element in root cells occurs through entry channels of essential ions (Liu et al., 2011).

In a study with *L. hexandra*, the absorption of Cr^{3+} was shown to be dependent on metabolic energy, with no relation to Ca^{2+} and K^{+} uptake channels. However, higher amounts Cr^{3+} in plants that received Fe^{3+} were observed (Liu et al., 2011). This suggests that Cr^{3+} absorption by plant roots may be mediated in part through Fe^{3+} complex carriers (Liu et al., 2011). Moreover, other studies indicate that, in addition to Fe, S and P also compete with Cr for the binding site in the carrier complex (Fig. 1) (Cervantes et al., 2001; Shanker et al., 2005). This was also corroborated by the fact that, in maize, chromate inhibited sulfate absorption when supplied for a short period of time (López-Bucio et al., 2014).

Following Cr entry through the roots, transport by translocation to the shoots occurs very slowly, another reason why Cr is retained preferentially in roots (Paiva et al., 2009; Singh et al., 2013; Sundaramoorthy et al., 2010). Cr in roots also inhibits cell division and shortens the overall length of roots, which may lead to severely restricted water and nutrient absorption processes, in turn leading to decreased shoot growth (Shanker et al., 2005). Metal ions can also be actively absorbed by root cells through the plasmalemma and adsorbed on cell walls by passive diffusion and delivered via acropetal transport in aquatic plants (Mishra and Tripathi, 2009).

In order to study Cr bioaccumulation, a study was conducted with *Brassica chinensis* L., investigating effects of increases in the concentrations of CrCl_3 medium (0, 2.5, 5 and 10 mg L^{-1}). Results showed that, after increasing exposure, Cr concentrations in the cell wall, plastids, nuclei and mitochondria also increased. The authors deemed it noteworthy that Cr in roots increased two-fold (5.43, 1.44, 2.35, 3.79 and 4.43 mg L^{-1}) compared to shoots (2.55, 1.63, 3.01 and 3.43 mg L^{-1}) (Wu et al., 2013). In several macrophytes (*Alternanthera philoxeroides*, *Borreria scabiosoides*, *Polygonum ferrugineum* and *Eichhornia crassipes*) exposed to 25 and 50 mg L^{-1} of $\text{CrCl}_3 \cdot 6\text{H}_2\text{O}$, higher Cr concentrations in roots were also observed when compared to the stem, and with the exception of *E. crassipes* ($9.02 \text{ mg Cr kg}^{-1}$ dry weight (d.w.)), almost negligible amounts of Cr were found in leaves ($0.15 \text{ A. philoxeroides}$; $0.13 \text{ B. scabiosoides}$; $0.04 \text{ P. ferrugineum mg Cr kg}^{-1}$ d.w.) of Cr in the leaves (Mangabeira et al., 2011). In a previous study, Mangabeira et al. (2004), observed, by ion microscopy, large amounts of Cr in the vascular cylinder of *E. crassipes* roots and leaves exposed to 25 and 50 mg L^{-1} for 30 days. Cr was mainly located in the cell wall of roots, as well as in the parenchyma of the roots. Furthermore, the

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