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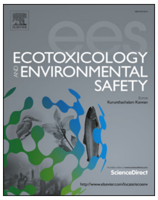

Review

Plant-lead interactions: Transport, toxicity, tolerance, and detoxification mechanisms

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ABSTRACT

Natural and human activities introduced an excess level of toxic lead (Pb) to the environment. Pb has no known biological significance and its interactions with plants lead to the production of reactive oxygen species (ROS). Pb and/or ROS have the potential to cause phytotoxicity by damaging the tissue ultrastructure, cellular components, and biomolecules. These damaging effects may possibly result in the inhibition of normal cellular functioning, physiological reactions, and overall plant performances. ROS play a dual role and act as a signaling molecule in plant defense system. This system encircles enzymatic and non-enzymatic antioxidative mechanisms. Catalase, superoxide dismutase, peroxidase, and enzymes from the ascorbate-glutathione cycle are the major enzymatic antioxidants, while non-enzymatic antioxidants include phenols, flavonoids, ascorbic acid, and glutathione. Pb removal from contaminated sites using plants depend on the plant's Pb accumulation capacity, Pb-induced phytotoxicity, and tolerance and detoxification mechanisms plants adopted to combat against this phytotoxicity. However, the consolidated information discussing Pb-plant interaction including Pb uptake and its translocation within tissues, Pb-mediated phytotoxic symptoms, antioxidative mechanisms, cellular, and protein metabolisms are rather limited. Thus, we aimed to present a consolidated information and critical discussions focusing on the recent studies related to the Pb-induced toxicity and oxidative stress situations in different plants. The important functions of different antioxidants in plants during Pb stress have been reviewed. Additionally, tolerance responses and detoxification mechanisms in the plant through the regulation of gene expression, and glutathione and protein metabolisms to compete against Pb-induced phytotoxicity are also briefly discussed herein.

1. Introduction

Lead ($_{82}Pb^{207.2}$, Latin “plumbum”) is an amphoteric trace metal, naturally occurring element and ranks second among all the hazardous metals (Anonymous-ATSDR, 2011). The natural occurrence of Pb in the environment mainly results from various ongoing happenings and incidents like weathering of rocks, soil erosion, volcanic eruptions, sea and salt lake aerosols, forest fires, and decay products of radioactive elements. Pb has become a major environmental contaminant because of the rapid growth of industrialization and human activities such as mining and smelting of Pb ores (Obiora et al., 2016). The contemporary applications and traditional values of Pb increased its production as well as consumption worldwide. Previous studies indicated that Pb has been mined and used by human being since ancient times (Waldron, 1985). The written documents on Pb toxicity as well as its uses can be found in ancient sculptures (for detail review see Hernberg (2000)). However, in last few decades, Pb pollution and toxicity has gained much scientific attention due to its widespread use in industries, storage batteries (Wang et al., 2016), gasoline, paints and dyes (Kumar and Gottesfeld, 2008), ammunition (Yin et al., 2010), glasses and cosmetic products (Al-Saleh et al., 2009). The extensive use of Pb in a large number of industries is mainly due to its low melting point, high density, ease of casting, acid resistance, ease of fabrication and chemical stability in the environment.

Despite the fact that Pb is present in all three compartments of our environment i.e. soil, water, and air, in different proportions, soil contamination with Pb is considered as one of the most serious threats to Human and other living creatures, and has been studied extensively (Arshad et al., 2008; Ma et al., 2016). A number of in-situ and ex-situ technologies are available for soil remediation of toxic trace metals, including Pb (Kumar et al., 2016; Kuppusamy et al., 2016; Peng et al., 2018). Many of the ex-situ technologies are too expensive for cleanup of contaminated lands. However, phytoremediation, an in-situ plant-based method, gained much scientific attention, as it is a cost-effective and

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eco-friendly technique for the remediation of sites contaminated with Pb and other trace metals (Kuppusamy et al., 2016; Mahdavian et al., 2017; Taiwo et al., 2016). Phytoremediation includes two fundamental processes: i) phytostabilization- plant arrest or stabilizes metals in the rhizosphere and; ii) phytoextraction- metal extraction from the soil by absorbing them in metal accumulating plant tissues (Bhatti et al., 2018; Rajkumar et al., 2012). Furthermore, the phytoremediation potential of a plant depends on its metal accumulation capacity (Gupta et al., 2013a). Based on their potential for metal accumulation, plants are categorized into four major groups, i.e. hyperaccumulator, accumulator, sensitive and excluder (Rascio and Navari-Izzo, 2011). Hyperaccumulator plants can accumulate higher levels of Pb in their tissues without showing significant toxic symptoms (Hesami et al., 2018). On the other hand, accumulator plants express toxic symptoms when they accumulate a large quantity of Pb (Kiran et al., 2017), while sensitive plants are difficult to grow in contaminated media (Fatemitalab et al., 2016).

Tendencies of different plant species to uptake, accumulate, concentrate and stabilize Pb in their tissues have been discussed previously (for review Pourrut et al. (2011b)). However, a number of other plant indexes, tolerance factors, and mechanisms have been developed to understand the plant performance for phytoremediation purposes in the recent past (Buscaroli, 2017; Ferreyroa et al., 2017; Kohli et al., 2018a; Li et al., 2017; Venkatachalam et al., 2017). In this connection, López-Orenes et al. (2018) have characterized *Zygophyllum fabago* plant's performance for metal accumulation by growing it in Pb-contaminated soil and evaluating the plant growth responses, carbon metabolism, and oxidative status. Additionally, sunflower plant has been observed to show dynamic responses when grown in soil contaminated with raised doses of Pb (300, 600, and 900 mg kg^{-1}) (Saleem et al., 2018). Pb treatments gradually interfere with the growth attributes, yield, physiological attributes, antioxidative activities, and Pb uptake in different plant parts (Saleem et al., 2018). In a recent study, Pidatala et al. (2018) have done a comparative metabolic analysis of vetiver grass (a Pb hyperaccumulator) with maize (Pb susceptible) under Pb stress conditions. The study established a clear understanding of the metabolic regulation during hyperaccumulation. However, a consolidated information regarding plant-Pb interactions dealing with Pb translocation within tissues together with its impact on the antioxidative system, DNA damage and protein metabolisms still remains quite limited. Thus, it is highly crucial to have a brief review on the sources and impact of Pb in the plant-based ecosystem, recent advances in Pb-induced phytotoxicity, tolerance responses, and the detoxification mechanism in a variety of plant species under various experimental conditions.

2. Materials and methods

This article attempts to review the existing literature and provides brief and concise information regarding various aspects of plant–Pb–interaction including i) uptake and translocation mechanism of Pb; ii) functions of cell wall or membrane in Pb accumulation; iii) Pb-induced phytotoxicity and; iv) tolerance responses and detoxification mechanisms in plant through the regulation of glutathione metabolisms, gene expression and cellular metabolisms to cope up against Pb-induced phytotoxicity. Last 10 years have seen remarkable progress in the area of plant-based toxicity bioassays of different trace metals, including Pb. From the main literature databases including Web of Science, this review collected 201 previously published articles mainly dealing with plant-Pb interactions. Further, the present review includes two tables and one figure. Table 1 summarizes a number of the published articles from last eight years detailing the Pb accumulation level in, root, stem, and leaves of various plant species grown in different contaminated media. This table mainly explains the relationship between the highest concentration of given Pb treatment and the maximum accumulation level in plant parts. Furthermore, Table 2 encircles the key physiological indexes, biochemical mechanisms, and metabolic responses in a variety of plant species during different Pb concentrations and under different experimental conditions. These two tables stand separately and we tried to cover a wide range of plant species and Pb treatment concentrations. Furthermore, a detailed mechanism of Pb-induced toxicity and tolerance in plant system has been drawn in Fig. 1.

3. Lead availability in plant

3.1. Pb speciation

Pb is non-thermodegradable, non-biodegradable and has no metabolic significance, thus readily accumulates up to the toxic level in soil (Parys et al., 2014; Silva et al., 2016). Generally, Pb can be found as a free metal ion or complex with either organic or inorganic materials. In natural soil, the toxicity of Pb is not only depended on its concentration, but also on its species or chemical form (Kroukamp et al., 2016). Pb takes part in the biogeochemical cycle and is not fixed in the soil forever. It's binding with soil phases can inhibit the mobility of Pb through a series of reaction or various mechanisms such as precipitation, adsorption, ion-exchange, and complexation with inorganic or organic compounds (for review see Cullen Jay and McAlister (2017)). For example, Pb speciation study in soil from Pampa region, Argentina, indicated that season and temperature had a significant influence on Pb solubility in soil (Ferreyroa et al., 2014). In addition, a study also concluded that Pb aging in soil reduces its bioavailability, where most of the stable Pb was detected as mineral complexes (Ferreyroa et al., 2014). Another study has confirmed this phenomenon and suggested that the Pb bioavailability and its toxicity to the plant depend on factors like soil type, Pb aging in soil and migration and distribution of Pb within the soil (Saminathan et al., 2010). The mobility and bioavailability index of Pb in the soil obtained from seven military shooting range area showed that mobility was more than 90% and bioavailability was in a range of 60–90% in all soil samples (Kelebemang et al., 2017). The study also indicated that most of the Pb extracted were bound to carbonate fraction (Kelebemang et al., 2017).

It is well accepted that the determination of the trace metals, including Pb, speciation in soil and plant generally provides a key understanding on its mobility in soil and phytotoxic manifestation when accumulated by plants (Kushwaha et al., 2018). A study showed that Pb particles such as Pb-oxide and Pb-sulfate together with the hexagonal platy crystal of Pb-carbonate were associated on the surface of the leaf of *Lactuca sativa* when exposed to Pb-rich particles, a factory-discharge, through soil or foliar application (Schreck et al., 2014). On the other hand, at similar treatment conditions, the Pb speciation on *Lolium perenne* leaf surface was different and majorly composed of Pb-organic acid complexes (Schreck et al., 2014). Moreover, the organic form of Pb is considered as relatively more toxic than the inorganic complexes. The types of exposure and plant species have also been observed to influence Pb speciation, mobility and degree of toxicity (Shahid et al., 2015; Kroukamp et al., 2016). A number of amendments such as ethylenediaminetetraacetic acid (EDTA), biochar, compost (Chirakkara and Reddy, 2015), citric, oxalic, tartaric and malic acids (Khan et al., 2016b) have shown their potential for altering Pb speciation and reducing its bioavailability to the plants. In a study, *Vicia faba* roots showed a different level of accumulation in its tissue, when treated with Pb in absence and presence of citric acid or EDTA. Presence of EDTA together with Pb treatment inhibits the Pb-induced phytotoxic responses, where citric acid did not influence any of the plant responses induced by Pb stress (Shahid et al., 2015). EDTA is a hexahydric acid and anionic in character. The presence of EDTA together with Pb usually forms Pb-complexes, that is cationic in nature, and chelate it. The Pb-EDTA interaction facilitates the formation of strong bonding between them that leads to the complex stabilization and resulted in a reduced Pb mobility and plant uptake (Shahid et al., 2012). An EDTA-mediated decrease in Pb accumulation was also observed in *Sedum alfredii* (Huang et al., 2008). Furthermore, the addition of glutathione