Physiological and Biochemical Changes in Plant Growth and Different Plant Enzymes in Response to Lead Stress

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Abstract Lead (Pb) is one of the most widespread, persistent and toxic heavy metal contaminants in agricultural soil. Though Pb is not an essential metal for plant metabolism, it is taken up primarily by the root system and accumulated in the different plant parts. Because Pb ions accumulate predominantly in roots, root growth is more sensitive to this metal than shoot growth. Growth inhibition due to Pb stress depends on various mechanisms affecting directly (such as reduction of cell division and elongation) or indirectly (such as disorders nutrient uptake, photosynthesis and water uptake) plant growth. After entering the cell, Pb ions can also influence the activity of the key enzymes of different metabolic processes such as antioxidative and photosynthesis. Pb stress might inhibit or induce the activity of these enzymes depending on the plant species, metal type and concentration, and duration of the exposure. The inhibition of enzyme activity by Pb mostly arises from the interaction between the Pb and enzyme sulfhydryl groups. Also, inhibition of metalloenzymes under Pb stress may occur due to the displacement of an essential metal by Pb ion. Furthermore, activities of certain enzymes induced by Pb stress might result from the changes in enzyme synthesis, immobilization of their inhibitors. This chapter reviews from the point of view of physiological and biochemical mechanisms the alterations occurring in growth and the activations of different enzymes in plants due to Pb stress.

Keywords Lead · Growth · Cell division · Cell elongation · Enzyme activity

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1 Introduction

Lead (Pb) is one of the most dangerous heavy metal contaminants of the environment. It is ranked second among all the hazardous substances due to its toxicity, occurrence, and distribution over the globe (ATSDR 2017). Apart from the occurrence of natural, the concentration of Pb is increasing rapidly in the environment with the growth of industrialization and human activities. Mining and smelting activities, automobile exhausts, coal burning, effluents from storage battery industries, lead-containing paints, paper and pulp, pesticides, as well as the disposal of municipal sewage sludge are the main sources of Pb contamination (Khan et al. 2018a). Pb is readily absorbed by plants from the contaminated soil, water and atmosphere cause hazardous health effects on humans and animals via the food chain (Rizwan et al. 2018).

Lead is a non-essential element for plants and has no biological function but several plant species grow on Pb contaminated soils. Pb is mostly absorbed by the plant root system and its small quantity is translocated to the above-ground parts of the plant. Since the majority of Pb absorbed by the plant is accumulated in their roots (approximately 95% or more), Pb mainly affects plants via their root system (Dalyan et al. 2018). Pb stress either directly or indirectly causes severe alteration into various physiological and biochemical processes such as growth, photosynthesis, respiration, mineral nutrition, water uptake, and enzyme activities in plants. Responses of plants to Pb stress include disturbance in mitosis, damage of DNA synthesis (Kumar et al. 2017), inhibition of root and shoot growth (Chen et al. 2017), disruption of mineral nutrition, inhibition of photosynthetic pigments, reduction in photosynthesis, transpiration, and water uptake (Jayasri and Suthindhiran 2016), inhibition or activation of enzymatic activities (Sidhu et al. 2016). However, the effects of Pb stress on the plant can alter depending on the metal type and concentration, exposure time, plant species, the stages of plant development, and different plant organs (Pourrut et al. 2011).

2 Effects of Lead Stress on Growth

Pb stress negatively affects growth and biomass in plants. Pb in growth medium generally causes a decrease in growth parameters such as elongation, fresh and dry biomass in plant root and shoot. For instance, *Medicago sativa* seedlings exposed to $Pb(NO_3)_2$ (0, 10 and 100 μM) for 7 days were gradually decreased in the lengths and fresh weights of root and shoot (Hattab et al. 2016). Also, the different concentrations (0, 100, 200, 300, 400 and 500 mg L^{-1}) of Pb for 12 days in the *Acalypha indica* caused an adverse effect on growth index by reducing the length and fresh and dry biomass of the root and shoot (Venkatachalam et al. 2017). Some other studies reported similar results: root, shoot and leaf growth, fresh and dry biomass were severely decreased by Pb stress in *Triticum aestivum* (Kaur et al. 2012a), *Zea mays* L. (Hussain et al. 2013), cotton (Bharwana et al. 2013), *Sesbania grandiflora*

(Malar et al. 2014a), *Brassica napus* L. (Shakoor et al. 2014), *Brassica juncea* L. (Kohli et al. 2018), and *Ricinus communis* L. and *Brachiaria mutica* (Khan et al. 2018b). Furthermore, the effects of Pb stress on plant growth might show alteration depending on exposure time, metal concentration and plant growth stages. A study with *Zea mays* seedlings exposure to Pb (0, 25, 50, 100, 200 μM) for 1–4–7 days, both root and shoot dry weights did not change at all Pb treatments, with exception after 7 days where shoot dry weight decreased at 200 μM Pb. In addition, shoot fresh weight and root length were not changed in any of Pb treatments (Gupta et al. 2009). Similarly, the different Pb concentrations did not exhibit remarkable effects on the growth parameters in lettuce (Silva et al. 2017).

The growth inhibition due to Pb stress is stronger in the plant roots. Since the most of the Pb taken up by plants is accumulated in the roots (95%) and only a small amount (5%) is transported to the above-ground parts, root growth is more influenced by Pb toxicity (Zhou et al. 2016). In *Triticum aestivum* exposed to different Pb concentrations (500, 1000, 2500 μM) for 7 days, root length reduced in the range of ~23–51% over 500–2500 μM Pb whereas shoot length was decreased by ~17%, 31% and 44% (Kaur et al. 2012a). Similarly, Pb treatment leads to ~67% reduction in root growth of two maize varieties though shoot length remained less affected (Ghani et al. 2010). Furthermore, it was reported that the length and biomass of root decreased due to Pb stress in several plants including *Lathyrus sativus* (Brunet et al. 2008), radish (Gopal and Rizvi 2008), *Zea mays* L. (Kozhevnikova et al. 2009), *Sedum alfredii* (Gupta et al. 2010). This inhibition of root growth might be originated from disturbances in either cell division and/or cell elongation (Rucińska et al. 1999; Kozhevnikova et al. 2009). The decrease of the cell division and elongation rates in the plant roots is associated with various mechanisms including change of cell wall plasticity, inhibition of microtubule development and DNA synthesis, metal-induced chromosomal aberrations, expansion of the mitotic cycle, and reduction of glutathione pool (Seregin and Ivanov 2001).

The antimitotic effect is one of the best-known toxic effects of Pb stress on plants (Shahid et al. 2011). In the first mechanism, Pb ions taken up by roots might bind to cell wall and the cell membranes and thus lead to cell wall mineralization known as calcification and silicification (Wierzbicka 1998). Since cell wall mineralization produces rigidity in the components of the cell wall, the physical and chemical characterization of cell wall change. These alterations in cell wall plasticity cause a reduction in cell division or elongation. In the second mechanism, microtubules that are the main element for mitosis are disrupted. Pb ions negatively affect the G2 and M phases of cell division and lead to the formation of abnormal cells at the colchicine-mitosis stage. This event might be related to direct or indirect interactions between Pb ions and proteins such as cyclins, whose activity is indirectly dependent on glutathione concentration, involved in the cell cycle. The spindle activity disorders due to Pb stress can be temporarily seen and return to the mitotic index initial levels (Shahid et al. 2011).

Pb stress causes a reduction in the number of dividing cells by affecting the normal cell cycle. The decrease of mitotic activity possibly due to blocking of G2 phase prevents the cell from entering the mitosis (Sudhakar and Venu 2001). This effect might be due to the inhibition of microtubule formation and DNA synthesis, degradation of nucleoprotein synthesis and decreased the ATP level to supply energy to microtubule dynamics, spindle elongation, and chromosomal movement (Türkoğlu 2012). Pb stress induced the DNA damage leads to the single and double strand breaks of DNA and irreversible in DNA replication, transcription, and repair. Pb stress was reported to increase the DNA damage in root cells of *Lupinus luteus* (Rucińska et al. 2004), *Nicotiana tabacum* (Gichner et al. 2008), and *Solanum lycopersicum* (Kumar et al. 2017) depending on concentration and exposure time. The disorders of cell division and elongation might occur as a result of direct binding of metal to DNA, disruption of microtubule organization and suppression of cytokines (Seregin and Kozhevnikova 2006).

Although the low concentration of Pb does not have an important effect on mitosis, it induces chromosomal aberrations such as of chromosome bridge formations during the anaphase, chromosome fragmentation, eccentric fragment loss during meiosis, and micronuclei formation (Shahid et al. 2011; Rodriguez et al. 2013). The chromosomal aberrations induced by Pb can be explicated by the negative effects of Pb on the mitotic spindle, microtubule formation and DNA synthesis. Colchicine mitosis and chromosome stickiness are the major chromosomal aberrations. The increased cells with colchicine mitosis are toxic properties of low Pb concentration. Pb behaves in a similar manner to colchicine, a cell division inhibitor. Colchicine inhibits microtubule polymerization, and causes the formation of characteristic colchicine-mitosis by blocking the cells in prometaphase (Checchi et al. 2003). Also, the increment of chromosome stickiness which is another chromosomal aberration is associated with DNA damage depending on Pb stress (Jiang et al. 2014).

In the roots of *Allium cepa* exposed to Pb stress, Pb ions in root cells disorganized the network of microtubules and caused in an important reduction in the chromosomal movement and segregation (Jiang et al. 2014). The possible interplay between Pb and tubulin inhibits the polymerization, damages to the mitotic spindle fibers, and thus leads to increase in colchicine-mitosis stage and chromosomal stickiness, and decrease in mitotic index (Jiang et al. 2014). Similarly, in another study, mitotic index together with the mitotic abnormalities such as metaphase and telophase, vagrant, laggards, and sticky chromosomes were inhibited in onion root tip exposed to Pb (16.6–331 mg L^{-1}) depending on metal concentration (Kaur et al. 2014).

Plant growth inhibition due to Pb stress might be associated with several mechanisms including disrupting nutrient uptake, disturbing photosynthesis, lowering of water potential and increasing oxidative stress (Riffat et al. 2009).

2.1 Mineral Nutrition

Balanced mineral nutrient supply is very important for plant growth. The macro- and micronutrients necessary for the normal growth of plants can alleviate the negative effects of different environmental stresses by developing the physiological and molecular mechanisms of plants (Arshad et al. 2016). These essential nutrients are the main components of many metabolic active compounds that regulate different physiological functions. For instance; nitrogen, phosphorus, potassium, calcium and magnesium are directly or indirectly very important for cell division, cell expansion and differentiation (Alamri et al. 2018).

Pb stress disrupts the plant and nutrient relationship and alters the ratios of internal nutrient between plant tissues (Gopal and Rizvi 2008). The reduction in the growth and biomass of plant due to metal stress originates from alterations in diverse biochemical processes at the cellular level affecting the nutrient uptake and metabolism (Ali et al. 2015). Generally, there is a negative correlation between the contents of mineral nutrient and Pb stress in plants. It was reported that the concentration of some macro- and micronutrients decreased in wheat plants treated with the different concentrations (0, 1.5, 3 and 15 mM) of Pb (Lamhamdi et al. 2013). Similar results were exhibited with the reduction of calcium, magnesium, sodium and potassium concentrations in the shoot and roots of maize plant exposed to Pb stress (Singh et al. 2015). It was also found that Pb treatment led to decrease the concentration of zinc, iron, manganese, copper, calcium, phosphorus and magnesium in *Oryza sativa* (Chatterjee et al. 2004), *Medicago sativa* (Lopez et al. 2007), and *Raphanus sativus* (Gopal and Rizvi 2008).

The reduced uptake of mineral nutrients might occur with two different mechanisms. First mechanism is related to the metal ions size. The competition between the metal ions which has similar size such as potassium ions with Pb might lead to the reduced mineral uptake. Since the interaction between these two metals which are similar radii (Pb^{2+}: 1.29 Å and K^{+}: 1.33 Å) is strong, these ions might compete for entry into the plant through the same potassium channels (Sharma and Dubey 2005). Furthermore, phosphorus shows a negative correlation with Pb amounts in soil (Päivöke 2002). Second metabolism might originate from alterations occurring in cell metabolism in response to metal stress by disturbing cell membrane and inhibiting enzymatic activities. Although Pb stress decreases nitrate uptake from the soil, it does not affect the nitrogen flow of the plant cell. This reduction in nitrogen amounts can be induced by decrease in the activity of nitrate reductase, which acts as rate-limiting in nitrate assimilation (Xiong et al. 2006). Tariq and Rashid (2013) showed a significant reduction in nitrate amount and the activity of nitrate reductase in rice seedlings growing in Pb-contaminated soils. Also, Burzyński and Grabowski (1984) exhibited that decreased nitrate uptake might originate from moisture stress depending on Pb stress.

2.2 Photosynthesis

Pb stress causes membrane content and permeability change, deterioration of the chloroplast ultrastructure organization, disruption of organs including chlorophyll, plastoquinone and carotenoid, and inhibition of enzymes in the Calvin cycle. It also leads to the destruction of photosynthetic pigments such as chlorophyll or the inhibition of the synthesis of these pigments. As a result of these cellular processes, CO_2 deficiency and resulting stomata closure further affect photosynthesis (Khan et al. 2018b).

Pb-induced the reduction of total chlorophyll content might be due to increased chlorophyll degradation, deterioration of chloroplast stromal volume (Stefanov et al. 1995; Hadi and Aziz 2015), or impairment the uptake of main photosynthetic pigment elements, such as magnesium, iron, calcium and potassium (Piotrowska et al. 2009). A reduction in total chlorophyll amount was determined in water hyacinth applied different Pb concentrations (0, 100, 200, 400, 600, 800 and 1000 mg L^{-1}) (Malar et al. 2014b). Similarly, decrease in the level of photosynthetic pigments including chlorophyll a, b and carotenoids was observed in many plant species such as ryegrass, cotton and rice (Bai et al. 2015; Khan et al. 2016; Chen et al. 2017). However, there are also few studies showing that Pb has a positive effect on chlorophyll pigments (Mroczek-Zdyrska et al. 2017). Pb stress generally affects chlorophyll a more than chlorophyll b (Hou et al. 2018). Whereas, Malar et al. (2014b) observed that the most chlorophyll b among photosynthetic pigments was reduced in water hyacinth exposed to Pb. This might be attributed to the change in the photosynthetic pigment composition comprising lower level of light harvesting chlorophyll proteins (LHCPS) (Malar et al. 2014b).

Chloroplast pigments are the main components of photosynthesis, and are responsible for plant biomass production. Pb stress significantly reduces plant growth by decreasing total chlorophyll levels (Aliu et al. 2013). For instance, dry biomass and total chlorophyll amounts showed a reduction in a species of algae under Pb stress. The decrease in dry biomass of the plant might be due to inhibition of cell division which causes growth reduction (Choudhury and Panda 2005). Similarly, it was reported that Pb stress led to a decrease in dry weight and chlorophyll content in lettuce (Đurđević et al. 2008) and wheat (Kaur et al. 2012b). In addition, plant growth and overall biomass production were determined in *Lathyrus sativus* plants exposed to Pb. It has been revealed that Pb can directly affect elongation by inhibiting cell wall enzymes and the plasmalemma ATPase by damaging electron transport in the process of photosynthesis, and thus might cause growth inhibition (Abdelkrim et al. 2018).

2.3 Water Uptake

The growth and physiological mechanisms in plants are directly or indirectly regulated by the water supply. Pb stress leads to decrease in transpiration rate and water content in plants. These negative effects depend on various mechanisms. First, growth retardation occurs with the decreased of leaf area, the most important transpiration organ (Brunet et al. 2009). Second, guard cells are smaller in plants exposed to heavy metals because heavy metals affect leaf growth more than stomata differentiation (Weryszko-Chmielewska and Chwil 2005). Third, Pb ions decrease the water potential by reducing the content of compounds that protect cell turgor and cell wall plasticity such as sugars and amino acids, and this effect is the most important factor of growth inhibition (Barceló and Poschenrieder 1990). For instance, 2 mM Pb treatment was reduced relative water content in wheat plants, and this effect might be due to the growth inhibition or the alterations of cell wall extensibility and cell wall elasticity (Alamri et al. 2018). Fourth, Pb causes the stomata to close by increasing the content of ABA (Atici et al. 2005; Weryszko-Chmielewska and Chwil 2005) and significantly restricts the gas flow between the leaves and the atmosphere. This reduction in incoming CO_2 flow is thought to be the major cause of a significant decrease in CO_2 fixation. With the same interaction mechanisms, Pb might also inhibit some enzymes from Calvin cycle (Romanowska et al. 2002).

3 Effects of Lead Stress on Different Enzyme Activities

Pb stress causes the alteration in many physiological processes by leading to inhibition or induction of some enzymatic activities. Pb has an important effect on enzyme activity, but the mechanism of this interaction has still ambiguous. Generally, Pb ions directly inhibit the enzyme activity due to change the inactivation constant (Ki) of enzymes, and high affinity of –SH and –COOH groups on the enzymes (Seregin and Ivanov 2001; Gupta et al. 2009, 2010). Also, Pb ions can replace the other divalent cations which are necessary for enzyme activation, such as zinc, manganese, and iron or inhibit the absorption of these minerals (Seregin and Ivanov 2001). Furthermore, the indirect effect of Pb on enzymes results from an increase of reactive oxygen species which leads to the oxidative damage on proteins in plants (Kumar and Prasad 2018).

3.1 Reactive Oxygen Species Production and Lipid Peroxidation

Pb stress primarily causes oxidative stress by increasing reactive oxygen species (ROS) production in plants cell (Gill and Tuteja 2010). Many studies reported that Pb caused to the overproduction of ROS such as singlet oxygen ($^1O_2$), superoxide (O^{2-}), hydroxyl radical ($HO^\bullet$), and hydrogen peroxide (H_2O_2) in chloroplast, mitochondria and peroxisomes in various plant species (Liu et al. 2008; Hattab et al. 2016). The excessive accumulation of ROS inhibits normal cell functions such as photosynthetic activity, ATP production, and protein synthesis. In addition, overproduction of ROS damages cell and organelle membrane, photosynthetic pigments and nucleic acid (Gill and Tuteja 2010). Pb also causes the leakage of potassium with the alteration in the composition of the lipid bilayer, and leads to the lipid peroxidation in the cell membrane structure. As a result of lipid peroxidation, the contents of saturated fatty acid reduce, while the contents of unsaturated fatty acid enhance in the cell membrane of many plant species under Pb toxicity (Kumar and Prasad 2018). These change in lipid composition of the membrane cause abnormalities of cellular structures such as cytoskeleton structure and ultrastructure of organelles (Verma and Dubey 2003).

There is been a correlation between lipid peroxidation and ROS production. Lipid peroxidation is commonly known as a biochemical indicator for ROS injury in plants (Gill and Tuteja 2010). However, ROS production does not responsible for the inducement of lipid peroxidation under Pb stress. The metal ions might trigger the free radical production which is originated by apoplastic and enzymatic (Mika et al. 2004). The role of membrane NADPH-oxidases (NOX) in the response to heavy metals such as copper, nickel and cadmium in plants was revealed in many studies (Quartacci et al. 2001; Olmos et al. 2003; Hao et al. 2006). Pourrut (2008) firstly proved that NOX activity was the primary source of oxidative burst under Pb stress. In addition, lipoxygenases (LOX) and phospholipases can enzymatically catalyze the lipid peroxidation (Huang et al. 2012). Pb ions upregulate the gene expression of lipoxygenases and stimulate LOX enzyme activity (Huang et al. 2012). Kaur et al. (2012b) showed that malondialdehyde (MDA) and H_2O_2 content increased in wheat root exposed to 500, 1000, and 2500 μM Pb. Similarly, it was shown that MDA content increased in *Zea mays* L. (Gupta et al. 2009), *Triticum aestivum* (Yang et al. 2011) and *Oryza sativa* (Thakur et al. 2017) under Pb stress. Mroczek-Zdyrska et al. (2017) reported that H_2O_2 and $O_2^{\bullet-}$ accumulation significantly enhanced in 50 mM Pb-treated *Vicia* plants by performing the histochemical analysis of oxidative stress. Another study revealed that the Pb stress increased the free radical (H_2O_2 and $O_2^{\bullet-}$) generation and MDA accumulation in roots and leaves of both *Arachis hypogaea* L. cultivars (Nareshkumar et al. 2015).

3.2 Antioxidative Mechanism

Plants can develop antioxidant enzyme systems for scavenging excessive accumulation of ROS under metal stress. The enzymatic antioxidants includes the key enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidases (POX), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione S-transferases (GST) (Hattab et al. 2016; Alamri et al. 2018; Khan et al. 2018b). When the plant cell produces the excessive ROS as a consequence of Pb toxicity, SOD, a metalloenzyme, is the first defense enzyme that converts $O_2^{\bullet-}$ radicals to form H_2O_2 and O_2 (Hasanuzzaman et al. 2012). H_2O_2 is a very reactive strong oxidant because of being unpaired electrons and is removed by activities of CAT that decomposes H_2O_2 to water and molecular oxygen (Gill and Tuteja 2010). Also, peroxidases are a potential antioxidant for removal of H_2O_2 molecules by turns it into H_2O and O_2 (Singh et al. 2010). Furthermore, the other H_2O_2-scavenging enzyme system occur the Halliwell–Asada pathway including ascorbate–glutathione cycle enzymes such as ascorbate peroxidase, dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR) and glutathione reductase (GR) (Potters et al. 2010). Firstly, APX catalyzes the reduction of H_2O_2 into monodehydroascorbate radical (MDHA) in the presence of ascorbate. MDHA enzymatically is converted to AsA and DHA by the activity of MDHAR (Małecka et al. 2009; Gill and Tuteja 2010). DHAR converts DHA to ascorbate using glutathione as an electron donor, for the glutathione disulfide (GSSG) production. Finally, GR enzyme catalyzes GSSG to glutathione by using NADPH-dependent reduction (Potters et al. 2010). In addition, GST enzymes are also important in ROS and metal detoxification and abiotic stress tolerance (Gill and Tuteja 2010; Hasanuzzaman et al. 2012).

Several studies have determined that Pb stress can inhibit or induce the activity of antioxidant enzymes depending on the duration or concentration of the treatment and plant species (Table 1) (Islam et al. 2008; Singh et al. 2010). It was studied the changes of antioxidant enzyme activities in *Acalypha indica* exposed to lead (100–500 mg L^{-1}) for 1–12 days under hydroponic culture (Venkatachalam et al. 2017). This study revealed that Pb-treated plants significantly enhanced the SOD, CAT, APX and POX activities which diminish the metal-induced phytotoxicity (removal of excess ROS) (Venkatachalam et al. 2017). Gupta et al. (2009) were investigated how maize adapted to the different Pb concentrations (0–200 μM) for 1–7 days. Their results showed that antioxidant enzymes such as SOD and CAT, as well as ascorbic acid level, alleviated Pb stress, which enhanced linearly with increasing Pb concentrations and exposure time (Gupta et al. 2009). In *Arachis hypogaea* L. cultivars, antioxidant enzymes such as SOD, APX, GPX, GR and GST exhibited increase under Pb stress, and also the isozyme band intensities of SOD, APX and GPX were consistent with alterations in the activities of antioxidative enzyme (Nareshkumar et al. 2015). Pb stress led to decrease in ascorbate content by reducing MDHAR and DHAR activities in wheat seedling (Hasanuzzaman et al. 2018). Dalyan et al. (2018) showed that Pb toxicity (2 mM) stimulated the increase of SOD, CAT, POX, APOX, GR and GST enzyme activities in the root of *Brassica juncea* seedlings. In another study, it was revealed that different Pb levels caused more increase in ascorbic acid and H_2O_2 contents, as well as DHA, CAT and APX activities in the roots of metal accumulator *S. alfredii* than non-accumulator (Huang et al. 2012). Although most studies have emphasized important of antioxidant enzymes in response to Pb stress, also it has been reported studies showing changes in the activation of other oxidant enzymes. For instance, the activity of aldo–keto reductase which detoxifies the aldehydes and associated with detoxification of Pb-induced toxicity increased in *T. triangulare* roots under Pb stress (Kumar and Majeti 2014; Ashraf et al. 2015). Additionally, Bali et al. (2019) determined that polyphenol oxidase (PPO) activity increased at 0.25–0.75 mM Pb concentration in tomato seedlings.

3.3 Photosynthesis

Photosynthesis is one of the most important processes that are negatively affected by Pb stress in plants. The Pb toxicity causes to damage in chloroplast membrane and ultrastructure, inhibition of chlorophyll, plastoquinone and carotenoid synthesis and the reduction of enzymatic activities in the Calvin cycle (Stefanov et al. 1995; Liu et al. 2008). It also leads to destruction in the lipid composition of thylakoid membranes in the chloroplasts (Stefanov et al. 1995). Initially, Pb-exposed plants show a

Table 1 List of antioxidant enzymes in various plant species exposed to different concentrations of Pb

Plant species	Pb concentration	Antioxidant enzymes	References
Gossypium spp.	50–100 µM	SOD, GPX, APX, CAT	Bharwana et al. (2013)
Sesbania drummondii	500 mg L^{-1}	SOD, GPX, APX, CAT	Ruley et al. (2004)
Pisum sativum	1 mM	Cu, Zn-SOD, Mn-SOD, CAT	Małecka et al. (2009)
Triticum aestivum	0.5, 1, 2 mM	APX, MDHAR, DHAR, GR, SOD, CAT, GR, GPX, GST	Hasanuzzaman et al. (2018); Alamri et al. (2018)
Brassica juncea	50–500 mg kg^{-1}	SOD, CAT, APX	John et al. (2009)
Raphanus sativus	25–500 ppm, 0.1, 0.5 mM	CAT and POD isoenzymes, APX, GPX, POX, acid phosphatase, ribonuclease	Gopal and Rizvi (2008); El-Beltagi and Mohamed (2010)
Oryza sativa	1 mM	SOD, CAT, POX	Khan et al. (2018a)
Brassica oleracea L. convar. botrytis	0.25, 0.5 mM	SOD, CAT, POD, APX, GR	Chen et al. (2018)
Zea mays	25–200 µM, 1–20 mM	SOD, CAT	Gupta et al. (2009); Chen et al. (2018)
Brassica juncea	0.25, 0.50, 0.75 mM	POD, APOX, GR, DHAR, MDHAR, GST, GPOX, SOD, CAT, PPO	Kohli et al. (2018)
Pogonatherum crinitum	500–2500 mg kg^{-1}	POD, CAT	Hou et al. (2018)
Brachiaria mutica	100–500 µM	SOD, GPOD, CAT	Khan et al. (2018b)
Lathyrus sativus	0.5 mM	GPOX, SOD, APX, CAT	Abdelkrim et al. (2018)
Cassia angustifolia	100–500 µM	SOD, APX, GR, CAT	Qureshi et al. (2007)
Macrotyloma uniflorum *Cicer arietinum*	200–800 ppm	SOD, CAT, POD, GR, GST	Reddy et al. (2005)
Eichhornia crassipes	1000 mg L^{-1}	APX, POX, CAT, SOD	Malar et al. (2014b)
Ceratophyllum demersum	1–100 µM	SOD, GPX, APX, CAT, GR	Mishra et al. (2006)
Lycopersicon lycopersicum	0.25–0.75 mM	SOD, POD, CAT, GPOX, GST, GR, PPO	Bali et al. (2019)
Ricinus communis	100–500 µM	SOD, GPOD, CAT	Khan et al. (2018b)

dramatic decrease in pigment content due to increased chlorophyll degradation. The degradation process of chlorophyll pigments can be explained by increasing chlorophyllase, protochlorophyllide reductase, pheophorbide oxygenase, Mg-dechelatase, and red chlorophyll catabolite reductase activities (Drazkiewicz 1994; Harpaz-Saad et al. 2007; Liu et al. 2008). Moreover, Pb ions accelerate chlorophyll degradation by reduced uptake of the essential components of chlorophyll structure such as Mg and Fe (Burzynski 1987). In addition, Pb disturbs the structure of metalloenzymes such as δ-aminolevulinic acid dehydratase (ALAD) which is an essential metalloenzyme in chlorophyll biosynthesis by replacing with the divalent ions (Cenkci et al. 2010). Under Pb toxicity, Zn^{2+} ion of ALAD enzyme is replaced by Pb^{2+} (Cenkci et al. 2010). Cenkci et al. (2010) determined that 0.5–5 mM concentrations of lead nitrate decreased photosynthetic pigment content due to inhibit ALAD activity in 20-day-old seedlings of *Brassica rapa*. On the other hand, Pb ions led to reduction in the activities of ferredoxin NADP+ reductase (Gupta et al. 2009); inhibition activities of Calvin cycle enzymes (Xiong et al. 2006; Singh et al. 2010); decrease the activity of phosphoenolpyruvate carboxylase (PEPC) (Sharma and Dubey 2005); decline of the rubisco activity (Alamri et al. 2018) in plant photosynthetic process. Alamri et al. (2018) revealed that 2 mM Pb treatment significantly reduced the Rubisco activity in wheat leaves. Many researchers reported that Pb stress led to loss of the photosynthetic pigments including chlorophyll a, chlorophyll b and total carotenoids in radish (El-Beltagi and Mohamed 2010), *Brassica rapa* (Cenkci et al. 2010), wheat and spinach (Lamhamdi et al. 2013), *Jatropha curcas* (Shu et al. 2012), maize (Zhang et al. 2018), *Pogonatherum crinitum* (Hou et al. 2018).

3.4 Respiration

The excessive accumulation of Pb has a detrimental effect on plant physiology and biochemistry. Especially, lead toxicity has harmful effect on mitochondrial membranes and respiratory enzymes in plants. Lead stress causes a decrease in respiration rate via inhibiting flow the electrons in the electron transport system (Bazzaz et al. 1975; Ashraf et al. 2015). Mostly, Pb ions damage the electron transport chain reaction in result binding to mitochondrial membranes. It was exhibited that Pb stress inhibited ATP synthetase/ATPase activity in maize (Tu and Brouillette 1987). However, Romanowska et al. (2002) determined that 5 mM lead nitrate increased ATP content and the ATP/ADP ratio in detached leaves of pea and maize in respiration for 24 h.

3.5 Nitrate Assimilation

Pb toxicity disturbs the balance of inorganic compounds by blocking of nitrate uptake or inhibiting activity of nitrate reductase (NR) in the plants (Sengar et al. 2009). NR, a metalloprotein, is the first enzyme in the nitrogen assimilation pathway that converts nitrate to nitrite in the cytosol (Ashraf et al. 2015). Also, NR catalyzes nitric oxide synthesis which is a signal molecule in plants (Khan et al. 2017; Alamri et al. 2018). Many studies reported that lead toxicity caused a reduction in the activity of nitrate reductase and limit the nitrate assimilation in plants (Xiong et al. 2006; Sengar et al. 2009). Pb stress led to the significant decrement of nitrate reductase activity in rice seedlings (Tariq and Rashid 2013; Sharma and Dubey 2005). Furthermore, Xiong et al. (2006)

showed that NR activity significantly decreased in *B. pekinensis* treated with lead (4 and 8 mmol kg^{-1}). In addition, NR activity negatively affected under Pb treatment in *Pisum sativum*, *Medicago sativa*, *Picea rubens* and *Triticum aestivum* (Porter and Sheridan 1981; Päivöke 1983; Yandow and Klein 1986; Alamri et al. 2018).

3.6 Soluble Protein

High concentration of Pb not only changes the activity of enzyme but also it alters the soluble protein content in plants (Mishra et al. 2006; Singh et al. 2010). Shu et al. (2012) determined that high concentration of Pb ions reduced the protein content in *Jatropha curcas* L. Although the low concentrations of Pb increase protein content by stimulating stress proteins, the high concentrations of Pb trigger to catabolism of protein synthesis. This reduction can be explained by proteins oxidation (Wang et al. 2008), the increase of ribonuclease activity, and the decrease of protease activity (Gopal and Rizvi 2008). Excessive Pb treatment increased the ribonuclease activity in radish (Gopal and Rizvi 2008), rice (Mukherji and Maitra 1976) and maize (Maier 1978).

3.7 Proline Synthesis

One of the important defense strategies against Pb is biosynthesis of low molecular weight proteins such as proline (Rucińska-Sobkowiak et al. 2013). Proline, is known as an organic osmolyte, plays an important role for scavenging ROS and protecting the protein structure in plants under stress conditions (Parys et al. 2014). Pb stress controls proline accumulation by activating ornithine-δ-aminotransferase and r-glutamyl kinase enzymes in ornithine and glutamate biosynthesis pathways (Yang et al. 2011; Kumar and Prasad 2018). A study with wheat cultivar showed that short term Pb stress (1–4 mM) led to increased accumulation of proline by induction of ornithine-δ-aminotransferase and r-glutamyl kinase enzymes (Yang et al. 2011).

3.8 Seed Germination

Lead has an inhibitory effect in the seed germination process of many plant species (Pandey et al. 2007). The major effect of Pb is seen on the inhibition of germination enzymes such as protease and amylase which is synthesized during the germination. Pandey et al. (2007) reported that amylase and protease activities decreased seed germination of *Catharanthus roseus* under high concentration of Pb. Lamhamdi et al. (2011) observed that amylase activity in wheat seeds was reduced with increasing level of Pb. This inhibition might show that lead ions replace the calcium ions which are essential for the activities of these enzymes (Lamhamdi et al. 2011).

3.9 Phytochelatins

Pb ions induce the synthesis of phytochelatins (PCs) that has an important role in the detoxification and accumulation of the metals in plants (Piechalak et al. 2002). PCs can constitute metal-PC complexes and transport Pb to vacuoles and chloroplasts (Piechalak et al. 2002; Estrella-Gómez et al. 2009). The biosynthesis of PCs is catalyzed by phytochelatin synthase enzyme (PCS) that connect of γ-Glu-Cys to substrate glutathione molecules (Estrella-Gómez et al. 2009; Fischer et al. 2014). Thus, PCs biosynthesis depends on glutathione level which can correlate with phytochelatin content and metal sequestration (Thangavel et al. 2007). Estrella-Gómez et al. (2009) revealed that excessive lead accumulation increased both phytochelatin synthase (PCS) activity and phytochelatins content in the root of *Salvinia minima* as known the Pb^{2+} hyperaccumulator aquatic fern.

4 Concluding Remarks

Lead is a non-essential nutrient for plants, but it is easily taken up by the plant roots and transported to aboveground parts at its very small amount. Because the majority of Pb accumulates in the roots, Pb mainly affects the plants through root systems. In this review, the effects of Pb stress on growth and different enzymes in the plant are explained, and the following points are illuminated based on the studies so far: (1) Pb stress inhibits plant growth through directly or indirectly by various mechanisms. Lead-induced growth inhibition depends on directly the alterations in cell division and elongation by decreasing cell wall plasticity or by inhibiting microtubule development. In addition, lead can inhibit growth indirectly by various mechanisms such as disturbing of mineral nutrition, disrupting of photosynthesis, reduction of water potential. (2) Lead might inhibit or induce the activity of key enzymes in physiological and biochemical processes such as antioxidative mechanism, photosynthesis, respiration, seed germination, protein synthesis, nitrogen assimilation, proline synthesis, and phytochelatin synthesis. However, the effects of Pb on all these processes in the plant might show alteration depending to concentration, duration of exposure, plant species and different plant organs.

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