

Chapter 10

Effect and Responses of Lead Toxicity in Plants



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Abstract Heavy metal toxicity is becoming a great concern to living organism due to exponential population growth and futile race of development. As one of the latent contaminants, lead (Pb) contributes about 10% of the trace metal(oids) pollution. It can easily absorb and accumulate in different plants parts but have not any beneficial role in cell metabolism. Increase in Pb content in environment is caused by natural as well as human activities such as industrial waste, mining, and irrigation by sewage water, sewage sludge application, chemical fertilizer, and pesticides. Plants such as crops, vegetables, and fruits grown on highly Pb contaminated soil show some toxic symptoms that may retard their growth (vegetative and reproductive), reduction in photosynthetic rate, seed germination rate blackening of roots, decline in quality, and yield of the plants. Lead also affects the activity of various enzymes that play a significant role in metabolic pathways, i.e., catalase, peroxidase, superoxide dismutase, ATP synthase, RuBP carboxylase/oxygenase, APX, AsA, GPX, and ABA. When the contaminated produce consumed by living being, it causes many life-threatening diseases. In this chapter, the uptake and noxious effects of Pb on photosynthetic rate, germination rate, yield, nutrient uptake, accumulation, ultrastructural and oxidative damage, carbon metabolism, and alteration in enzymes activities were reported.

Keywords Lead (Pb) · Heavy metal · Crops · Soil · Human health

10.1 Introduction

Lead is recalcitrant, highly pernicious, and non-degradable heavy metal after arsenic which contributes 0.002% of Earth's crust (Zulfiqar et al. 2019). Anthropogenic activities including smelting and mining of Pb ores, automobiles, activities, etc.,

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released excessive amounts of Pb into the environment that causes harmful effects on environment and human health and also known as protoplasmic poison (Hadi and Aziz 2015; Lathwal et al. 2023). Pb intake in human should not exceed $25 \mu\text{g kg}^{-1}$ of human body per week. In soil, Pb content may occur up to 10 ppm, but for human being, acceptable permissible range is 0.003 and 0.005 mg/l (Agrawal 2009; WHO 2017; Gaur et al. 2021).

The various forms of lead are present in soil which can be differentiated by their bioavailability, mobility, and toxicity. Bioavailability can be defined as the concentration available for absorption by living organisms such as plants, humans, and animals which is strictly related to the metal chemical form. However, in soil, the chemical forms of lead is affected by various processes such as ion exchange; precipitation and dissolution; complexation; absorption and desorption; immobilization and biological mobilization by plants. Lead accumulation contaminates the food by interfering with soil and roots. Absorption of Pb may vary from species to species, but absorbed Pb is mainly accumulated in roots, and only a small fraction is transported to the aerial tissue (Collin et al. 2022). As a result, root vegetables like potato, carrot, radish, and sweet potatoes may contain highest level of Pb (Collin et al. 2022) and leafy vegetables like lettuce and Swiss chard absorbed least Pb content (Aponte et al. 2020). Pb contamination had stimulatory effect on soil enzymatic activities and microbial biomass at low concentration but inhibitory effect at higher level. High Pb content causes increase in membrane permeability, changes in the catalytic activities of various enzymes, decline in content of photosynthetic pigments, disruption of nutrition mineral balance, inhibition on biomass production and plant growth, and alters the genes. In a study, Liu et al. (2009) reported more than 1310 genes were altered in response to Pb treatment in *Arabidopsis*. Moreover, in plants, Pb-induced excess reactive oxygen species (ROS) have been detected (Reddy et al. 2005). Some plants have tolerance to the high level of Pb contamination; they complete their life cycle without showing any stress symptoms and accumulate > 1000 ppm of Pb content in their plant biomass which are known as hyper-accumulators. Over 400 hyper-accumulating plant species from all over the world can accumulate high concentrations of metals from contaminated soils.

10.2 Sources of Lead (Pb)

Pb have various sources as natural processes such as rock weathering, volcanic eruptions, forest fires, and soil-forming or can be originated from anthropogenic processes such as fertilizer applications, industrial waste, smelting, and sewage disposal (Fig. 10.1). Pb is persistent and non-biodegradable in nature and found in ionic form such as Pb (II) in soil at low pH, but at higher pH, it is found in more stable form.

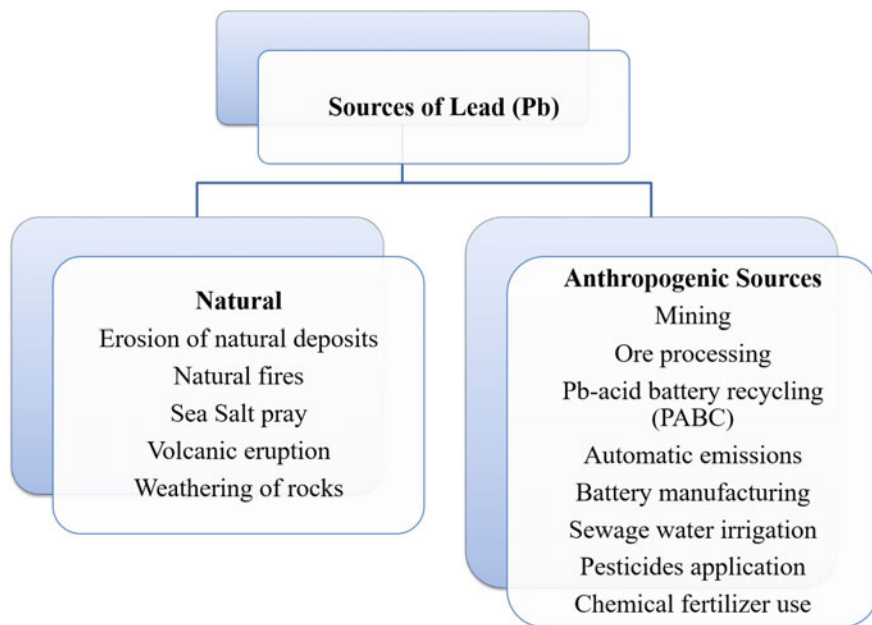


Fig. 10.1 Sources of Pb in environment

10.3 Absorption and Accumulation of Pb in Plants

Absorption of Pb depends upon many factor such as forms of Pb in soil, water and air, soil pH, organic matter, chelating agents, plant type, and concentration of Pb in soil. In soil, Pb acts as a weak Lewis acid which imparts an intense covalent character to majority of ionic bonds it forms. Owing to this intense chemical binding with colloidal and organic materials, it is suggested that only a tiny portion of the lead in soil is soluble, and consecutively available for plant uptake (Kopittke et al. 2008a, b; Punamiya et al. 2010). Solubility of Pb in soils having pH ranged from 5.5 to 7.5 is regulated by carbonate and phosphate precipitates. Pb may exist as free metal ion, organic ligands (e.g., amino acids, humic acids, and fulvic acids) and complexed with inorganic constituents (e.g., HCO_3^- , CO_3^{2-} , SO_4^{2-} , and Cl^-). Anthropogenic sourced lead generally accumulates primarily in the surface layer of soil, and its concentration decreases with depth which makes it challenging to calculate the bioavailable amount of Pb (Cecchi et al. 2008). Availability of Pb to plants primarily depends on soil conditions. The Pb in soil is adsorbed according to Langmuir adsorption isotherm and pegged to soil pH in the range of 3.0–8.5 (Lee et al. 1998). Soil pH significantly helps in retention and uptake of lead from soil. At acidic pH, lead is present as free ionic species while lead is principally found as lead carbonates and phosphates at high pH which are insoluble in nature. When soil pH was below 5.2 ± 0.2 , solubility of lead increases and significantly increased its

availability to plants (Martinez and Motto 2000). Kushwaha et al. (2018) reported negative correlations between the pH and total lead concentration in all the horizons of soil except horizon deficit of Fe and Al oxides and clay. The alteration of pH may be the indirect consequence of microbiological activity which in turn controls the reduction and oxidation of iron, and manganese. Sauve et al. (1998) found that at highly acidic pH, 30–50% of soluble lead exists in ionic (Pb^{2+}) and in ion pairs form (e.g., PbSO_4), but increasing the pH from 3 to 6.5 leads to decrease in solubility of Pb, and when pH increase from acidic to alkaline (6.5–8), formation of organo-Pb complexes was increased, and finally at neutral pH, 80–99% of lead predominantly occurs in the form of organic complexes. Thus, it can be concluded that at acidic pH, the mobility and bioavailability of lead are increased which ultimately enhance its uptake by plants and further cause toxic effects on living beings after consumption.

In another study when plants grown in Pb contaminated soil, plants absorbed more Pb content at low pH compared to high pH or alkaline soil, but the effect was not accurately measured somewhat due to differing amounts of organic matter (Kushwaha et al. 2018). In soil, 80–90% humic substances are present which contributed as total organic carbon. Degradation of plant residue generated three-dimensional interlinked, aromatic polymers known as humic acids. These units have functional groups like carbonyl which have free electron pair and are available for the coordinative binding with Pb which completes the coordinative sphere of Pb. Thus, it is the most significant reaction for Pb adsorption by humus. Binding of Pb is found to be directly proportional to pH and inversely proportional to ionic strength (Xiong et al. 2013). Similar notion was observed by Ahmed et al. (2019) that atmospheric lead remains in the upper 2–5 cm of undisturbed soils with 5% organic matter at $\text{pH} \geq 5$ while insoluble organic lead complexes are formed in having organic content at pH 6–8. When the amount of organic matter is low in soil and pH is 6–8, it leads to precipitation of Pb with carbonate and phosphate ions or form complexes with hydrous oxide. These organic lead complexes are solubilized and become available for plant uptake at pH 4–6. Pb was mainly accumulated in vascular bundles and humic acid transport the Pb content vascular bundles to shoot and in young stem (Xu et al. 2018).

Ethylenediaminetetraacetic acid (EDTA) as chelating agent is introduced to achieve the remarkable improvement in Pb concentration in shoot. It has great ability to form complex with Pb (Kroschwitz 1995). The large size of Pb particles renders their passage through casparian strip of root endodermis tissue. Formation of complex with EDTA simultaneously reduced their size and increased its solubility (Vassil et al. 1998). Chelation of Pb provides it an escape route from the precipitation with phosphates and carbonates and aids to avoid binding to cell wall in cation exchange process (Jarvis and Leung 2002). Moreover, the transport of solutes from parenchyma cells and vascular cylinder to vessels and tracheids of xylem is intensively selective active-carrier based and thus prevents the transport of charged Pb particles (Raven et al. 1999). However, Pb chelate complex has better chances to get transported through this route.

Labile forms (Pb^{2+} , PbOH^+ and PbCO_3) constituted a major portion of lead input from the washout of the atmospheric deposits, whereas particulate or bound forms

of lead were dominant in urban runoff and ore mining. The abundant forms of Pb in sediments are lead sulfates, lead carbonates, and lead sulfides, and in surface waters, the concentrations of dissolved lead are low. In air, the main Pb compounds present are tetra methyl lead and tetra ethyl lead, which are used as gasoline antiknock additives. These are only present in immediate proximity of anthropogenic sources (Pattee and Pain 2003).

Type of plant or plant species plays very crucial role for the uptake of Pb from air, water, and soil. Plant should have tolerance to Pb contamination, strong and vast root system, and large biomass production. Rani et al. (2023) reported that bamboo has the potential to remediate the heavy metal contaminated soil due to their special characteristics such as large biomass production, ability to uptake large amount of heavy metal, resistant to abiotic and biotic stresses, large CO₂ sequestration, and worldwide distribution. The plants which absorbed Pb from atmosphere have different plant morphology and plant physiology. Barber et al. (2004) opined that plant factors such as leaf surface area, leaf longevity, functional type, and cuticular structure may affect the air-vegetation transfer. Little (1978) and Madany et al. (1990) demonstrated that leaves having rough and hairy surface tend to accumulate remarkably more lead (up to 10 times) compared to smooth leaves. Rao and Dubey (1992) also stressed the role of leaf morphological factors such as trichome density and length, and stomatal index on the efficiency of dust collection by plants. Downey leaves have high affinity for heavy metal from atmosphere (Godzik 1993). Lead particles from atmosphere in the form of lead sulfide (PbS) are caught in tiny folds of leaf and get deposited on the leaf surface and undergo oxidation resulting in the formation of secondary Pb-containing compounds such as PbO, PbSO₄, and PbCO₃. These secondary Pb particles penetrate inside the leaf through two possible routes. Firstly, Pb-containing nanoparticles noticed in the stomata may enter in the apoplasm as solid compounds and particles were identified beneath the cuticle membrane (Uzu et al. 2010). Secondly, lead formed from the dissolution of primary particles may diffuse through aqueous pores of stomata and cuticles along the hydrophilic pathway, causing necrosis augmented with lead.

10.3.1 Translocation of Lead: Soil to Root

Adsorption/Absorption by plant roots is the major mechanism of transfer of lead from soil to plant system. Roots of plants are actively engaged in the absorption of lead present in solution (Sharma and Dubey 2005; Uzu et al. 2009). The process of lead uptake by plants may occur in two steps. In the first step, lead present in soil is chemically adsorbed on the outer layers of radicular cortex which consists of rhizoderm and collenchyma/parenchyma tissues. This is achieved by binding of lead to polysaccharides of the rhizoderm cell surface and carboxyl groups of mucilage uronic acid as demonstrated by Kushwaha et al. (2018). Kopittke et al. (2007), Ginn et al. (2008), Meyers et al. (2008), Uzu et al. (2009), and Krzesłowska et al. (2009, 2010) also observed the same trend in *Vigna unguiculata*, *Festuca rubra*, *Brassica*

juncea, *Lactuca sativa*, *Funaria hygrometrica*, respectively, under Pb which was adsorbed on the surface of root. After being adsorbed to roots surface, lead gains entry into root system through passive absorption along with water.

At molecular level, the determination of exact mechanism of lead migration from soil to plant root system demands further exploration. There is limited detail in literature regarding the mechanisms of Pb transport into root cells; however, a number of possible pathways have been purposed by several scientists. It is well established that lead is non-selectively absorbed (Hirsch et al. 1998). Transportation of adsorbed lead on the root surface has to pass through plasma membrane of root-cell. This can be achieved by the assistance of ionic channels/transporters. The most well-known transport pathway of these cationic channel is Ca-channels which is widely documented and reported by several researchers such as Marshall et al. (1994) and Huang et al. (1996) who isolated right-side-out plasma membrane vesicles from the roots of corn and wheat plants and identified a voltage gated Ca-channel in the plasma membrane of their root cells. Activity of these voltage gated Ca-channels was substantially suppressed by Pb in the plasma membrane of wheat crop either by blocking them or by migrating preferentially with respect to Ca^{2+} through them as established by Monferrán and Wunderlin (2013). This conclusion was concredited with the findings of Wang et al. (2007) which observed a surge in Pb accumulation with depleting Ca content in roots of maize and accredited it to stronger interaction with the transporting proteins such as calmodulin where it can compete with Ca^{2+} and bind to Ca^{2+} binding sites on the transmembrane transporting proteins.

10.4 Accumulated Pb Distribution in Plant Parts

Pb content in different plant organs tend to accumulate in the following order: seeds < inflorescence < leaves < root. The application of Pb to the foliar in *Phaseolus vulgaris* resulted higher content of Pb in roots than the control, indicating that the Pb was absorbed by leaves and translocated within to roots of the plant (Feleafel and Mirdad 2013). In another study, Nicklow et al. (1983) observed that vegetable crops show different Pb concentration in different parts such as root peel of beets accumulate highest (90 ppm) and lowest in the root (23 ppm) while turnip had the highest Pb concentration in leaf and lowest in root peel. Burzynski (1984) reported that Pb was accumulated in roots (93–96%) predominantly and partially in hypocotyle (4–7%) in cucumber seedlings. Spinach, coriander, cabbage, lettuce, and cauliflower had Pb concentration in the following order: leaves > stem > roots, but in reddish, the lead content followed the different trend, i.e., roots > stem > leaves (Farooq et al. 2008). Root had a significant ability for lead accumulation as compared to stem and shoot. In contrast with the control, Pb accumulation increased by 10.15–40.04, 30.21–185.16, 30.61–97.62 times in shoot, stem, and root (Yongsheng et al. 2011). In *Brassica napus*, Pb was mainly accumulated in roots at flowering and physiological maturity stage (Ferreiroa et al. 2018).

10.4.1 Intracellular Localization of Pb (in Cell Wall, Vacuole, and Cell Membrane)

It has been deduced from the ultrastructural investigations that Pb is mainly amassed in intercellular space, vacuole, and cell wall, while minor deposits have been observed in other cell organelles such as dictyosome, dictyosome derived vesicles, and endoplasmic reticulum. About 90% of the adsorbed Pb is deposited in cell wall and vacuole (Wierzbicka and Antosiewicz 1993). Plants take up free Pb ion either by capillary action or from atmospheric air through cellular respiration. A well-developed root system of the plants takes up divalent Pb ions with the nutrients from the soil and also get absorbed passively and transported through xylems and unloads in the endoderm (Engwa et al. 2019).

The atmospheric Pb was absorbed via cuticle and stomata present in the surface of leaves. Absorbed Pb causes the chlorosis in leaves reaching to the endodermis region and bound to the cell wall and plasma membrane. Endodermal cells act as a barrier for the transport of Pb such as apoplastic and symplastic pathway. Casparian strip block the apoplastic pathway and then Pb can only translocate through symplast pathway. And the role of this barrier in leaf cell vacuole is only to restrict the transport of Pb (Collin et al. 2022).

10.4.1.1 Within Cell Walls

Cell wall serves as a site of Pb accumulation in the form of insoluble lead complexes such as lead phosphate complex (Lane and Martin 1982; Zegers et al. 1976) and prevents the entry of Pb into cytoplasm. The mechanisms employed in restricting the movement of high levels of lead in the cells of the tolerant clone demands further exploration (Qureshi et al. 1986). Plant cell walls contains abundance of divalent and trivalent cation binding compounds which contain functional groups like $-OH$, $-COOH$, and $-SH$. Phenolics, proteins, amino acids, and polysaccharides are the most significant compounds. The ability of these compounds to bind trace metal ions such as Pb is highly dependent on the number of these functional groups present in them (Pelloux et al. 2007). The amount of polysaccharides presents in cell wall which are abundant in carboxyl groups principally determines the binding capacity of cell wall. Homogalacturonan is one of the four major polysaccharide domains which constitute pectin. Those fractions of homogalacturonan which have low degree of methyl esterification contain free carboxyl which binds the Pb^{2+} (Dronnet et al. 1996; Fritz 2007). Binding of Pb^{2+} to pectin in cell wall renders it metabolically inactive. Gall et al. (2015) said that cell wall form the first barrier for the entry of heavy metal for the cell which plays significant role in detoxification mechanism. Under transmission electron microscopy, Islam et al. (2007) reported that in *Elsholtzia argyi* main organ of the Pb accumulation was cell wall.

Another mechanism by which cell wall protects internal cell organelles from Pb^{2+} ion exposure is by separating sequestered Pb deposits in it from plasma membrane

through a callose layer which metal ions are unable to penetrate; thus, it essentially acts as a barrier against intrusion of Pb^{2+} into the protoplasm (Hall 2002; Patra et al. 2004). Thus, endocytosis of sequestered Pb returning into cell wall with compounds of cell wall provides a robust safeguard to plant cells (Krzyszowska et al. 2010). Thickening of cell walls occurs to aid in restricting the trace metal ion uptake into the plants (Probst et al. 2009). This change in cell wall morphology is induced by raise peroxidase activity and lignification of cell wall (Liu 2012). The amount of trace metals entering the protoplast is reduced chemically by thickened cell walls by binding trace metals to the negatively charged substances, synthesizing lipid compounds and callose to introduce physical barrier against immigration of ions and function as a compartment as well for the accumulation of trace metals. Xu et al. (2018) showed that *Typha orientalis* when grown under hydroponic Pb stress resisted the Pb-induced damage by the isolating the Pb content in the cell wall.

10.4.1.2 Inside Vacuoles

Vacuole is an important membrane-bound cell organelle which plays a key role in detoxification of cytoplasm by sequestering the metal ion, thus imparting the tolerance to plant against lead (Seregin and Ivanov 2001). Sahi et al. (2002) has established the existence of this mechanism in leguminous shrub *Sesbania drummondii* which procures the globular deposits of Pb in vacuoles. First, Pb ions from the external solution may enter endoplasm reticulum closely linked to the apoplast. The Pb particles which had entered the cytoplasm is firstly gathered into membrane-bounded vesicles followed by their subsequent sequestration within the vacuole, evidently through exocytosis (Koppitke et al. 2008). Inside the vacuole, two types of compounds are present (i) Compounds of organic acids such as malate and oxalate which have high affinity for Pb ions, and (ii) the compounds that interact with heavy metals to form low-soluble complexes which causes predominate localization of Pb in this organelle (Krotz et al. 1989; Mazen and El Maghraby 1997). Moreover, the introduction of heavy metal ions inside cytoplasm triggers the synthesis of metal binding peptides through the induced expression of the gsh1, gsh2, and MT genes which forms metal peptide complex and transported to vacuole (Vögeli-Lange and Wagner 1990, 1996; Seregin and Ivanov 2001). These vacuoles are called Pb-sequestering vacuoles which specifically function to entrap cytosolic Pb which is transported to them via specific intracellular mechanisms (Meyers et al. 2008). Pb-sequestering and non-sequestering vacuoles can lie side by side. Exposure to heavy metal prompts the production of additional vacuoles particularly to store toxic metals. This is evident from the observations made by Sridhar et al. (2005) in a conventional transmission electron microscopy (TEM) study of *B. juncea* root which indicated a rise in the number of vacuoles in the cortical and epidermal cells of roots following exposure to Cd and suggested the existence of a similar mechanism active in the root tips of *B. juncea* against Pb exposure. The sequestration of Pb and Cd in vacuoles is an energy-requiring process (Salt and Rauser 1995). Jiang et al. (2019) studied the effect of lead on cell and found that Pb is strategically translocated from cell wall to

vacuole to avoid the damage caused to sensitive parts of cell such as mitochondria and protoplast and provide extra space to cell wall under tolerance strategy.

10.4.1.3 Within Cell Membrane

The plasma membrane functions as a living barrier of the cell to uninterrupted influx of Pb ions across the cell membrane through diffusion (Jiang and Liu 2010). Membrane transport systems located in cell membrane are an integral component of mechanisms which involves uptake, accumulation and removal of heavy metals from the cell. These mechanisms ensure protection against heavy metal toxicity by maintaining the optimum concentration of heavy metals inside cell required to perform its normal functions (Malecka et al. 2008). Strange and Macnair (1991) suggested that cell membrane is the site of primary tolerance mechanism against toxicity of heavy metal. Transmission electron microscopy and X-ray microanalysis of root sections of hyper-accumulator shrub *Sesbania drummondii* by Sahi et al. (2002) established the localization of Pb granules in plasma membrane. This can be attributed to the large number of functional groups present in cell membrane (Gardea-Torresdey et al. 2001). Accumulation of Cu in root apoplast at cell membrane deters its entry into cytosol (Ernst et al. 1992). Wojcik and Tukiendorf (2003) observed this mechanism in *Arabidopsis thaliana* plants. Root ultrastructural studies conducted by Islam et al. (2007) detected the dispersion of fine Pb particles across cell membrane. On being exposed to high concentration of heavy metal ions, there is induction of constitutive alterations in the structure of plasma membrane (Ernst et al. 1990). The enfolding's of plasmalemma produce certain vesicles which accumulate Pb inside them and deter the dissemination of free Pb ions in cytoplasm, thereby confining them to minimal space (Jiang and Liu 2010; Clemens 2006).

10.5 Effects and Responses of Plants Under Pb Stress

Metal phytotoxicity occurs when metals take up by plants from roots and transported to various parts of shoot. Excessive Pb concentration causes deleterious effects in plants such as decline in photosynthetic rate, chlorophyll synthesis, affects the Calvin cycle, closing of stomata by creating deficiency of CO₂, growth inhibition which is connected with cell division, let down mineral nutrition and water balance and enzyme activities (Fig. 10.2). It also brings the changes in lipid composition and chlorophyll b content (Kumar and Rai 2007; Collin et al. 2022). There is some unexpected possible mechanism such as changes in the permeability of the cell membrane, reaction to sulfhydryl groups with cations, possible attraction for phosphate groups and active groups of ATP and ADP (Hadi and Aziz 2015). Spraying of various rates of Pb on tomato plant causes the leaves margins burning, bending of branches and sudden decrease in flowers (El-Shebiny 1989). Apart from these, Pb toxicity

enhanced the production of reactive oxygen species (ROS) which cause the oxidative stress in the plant cell. Plants activate their antioxidant system to prevent the oxidative damage by ROS enzymatically and non-enzymatically. These antioxidants (superoxide dismutase, peroxidase, catalase, glutathione reductase, and ascorbate peroxidase) appears to play a pivotal role in combating oxidative stress. Ashraf et al. (2017) reported that under Pb conditions photosynthetic pigment destructions, induction of oxidative stress with increased production of H_2O_2 , MDA, protein production, and soluble sugar. Fazeli et al. (1991) study found that the Pb only affects the growth of tomatoes, and the content of Vitamin C remains constant. Mishra et al. (2006) found decreased level of sucrose in vegetables due to inhibition of carbohydrate synthesis. Pb reduced the plant height, number of leaves, and dry matter of sunflower plants at higher concentration (Hung et al. 2014). Blackberry plant's leaves have 4.5 folds higher Pb concentration than the fruits, and blackberry contains 71% of the Pb exceeding the WHO threshold by 29 times. The consumers are at high risks who take 100 g fresh blackberries which consist 8.51 mg Pb (Collin et al. 2022). Opeolu et al. (2010) reported less number of flowers under high concentration of Pb in sunflower, and histological changes in leaves such as thin blade leaf, minified xylem and phloem in vascular bundle, and reduction in diameter of xylem vessels were observed in soybean under Pb contamination (Hadi and Aziz 2015). Table 10.1 presents the effects of different Pb concentration on crops and vegetables.

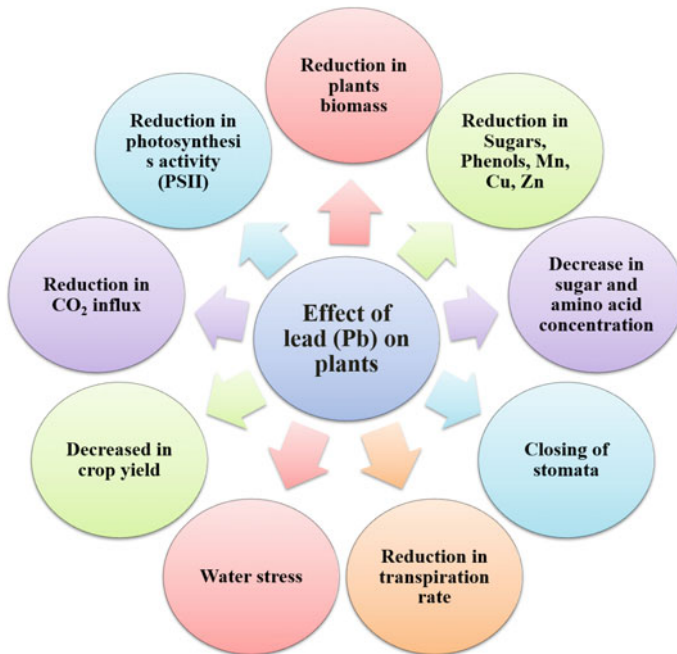


Fig. 10.2 Effects of Pb on plants

Table 10.1 Effects of Pb on some crops and vegetables

Plant species	Pb concentration	Effects on plants	References
<i>Helianthus annuus</i>	300, 600, and 900 mg/kg 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, and 5 mM	Reduction in shoot and root length, fresh weight and dry weight, Chl a and Chl b, carotenoid contents, and matter stress tolerance index were less as well	Azhar et al. (2006) and Saleem et al. (2018)
<i>Brassica juncea</i>	0.25, 0.50, and 0.75 mM	Lower dry weight, shoot and root length, total chlorophyll and carotenoid level. Water content and relative water content were enhanced	Kohli et al. (2017, 2018a, b)
<i>Lactuca sativa</i>	20 mg/l 500 μ M	Delayed in germination, significant decline in dry and fresh weight of plants and reduction in carotenoids, Chl a and Chl b content	Đurđević et al. (2008) and Silva et al. (2017)
<i>Hordeum vulgare</i>	100 and 200 μ M	Reduction in shoot length, root length, fresh weight, and dry weight	Arshad et al. (2017)
<i>Oryza sativa</i>	100 μ M 400, 800, and 1200 ppm 500 and 1000 μ M	Decrease in shoot, root lengths, fresh and dry weights, gas exchange parameters, and decrease in Chl a and Chl b, total chlorophyll, and carotenoid as compared to control	Chen et al. (2017), Ashraf et al. (2017) and Verma and Dubey (2003)
<i>Triticum aestivum</i>	100 μ M 40 and 60 ppm 1.5, 3, and 15 mM 0.05, 0.1, 0.5, and 1 g/L	Reduction in dry weight, fresh weight, shoot length, and root length and number of tendrils. Low total chlorophyll, Chl a, and Chl b. Dose-dependent reduction in growth, fresh weight, dry weight, and germination percentage	Tripathi et al. (2016) and Lamhamdi et al. (2010)
<i>Brassica juncea</i>	25, 50, and 100 μ M	Reduced growth in terms of percentage, germination, shoot length, root length, fresh weight, dry weight total chlorophyll, and carotenoid	Pratima and Pratima (2016)

(continued)

Table 10.1 (continued)

Plant species	Pb concentration	Effects on plants	References
<i>Gossypium hirsutum</i>	25, 50, and 100 μ M 500 μ M	Steep decline in biomass of leaf, stem and root in plants. Decline in plant height, root length, leaf area, and number of leaves per plant. Reduced content of Chl a, Chl b, total chlorophyll, and carotenoid content and gradual retardation in levels of, stomatal content, net photosynthetic rate, and transpiration rate. Changes in leaf morphology, viz. length, width, and petiole size, were reduced	Bharwana et al. (2013, 2014, 2016)
<i>Brassica juncea</i> L.	32, 100, 200, 400, and 800 ppm 50 mg/L	Seed germination and survival were reduced. The number of leaves, root, shoot and branches length, fresh weights, and dry weights were declined reduction in photosynthetic indices	Kaur et al. (2013) and John et al. (2012)
<i>Brassica napus</i> L.	33, 100, 200, and 400 μ M	Lowered root length and tolerance index	Mosavian and Chaab (2012)
<i>Vigna mungo</i>	25, 50, 75, 100, and 150 ppm 9, 10, and 11 mg/L	Reduction in percentage germination, lengths of root and shoot, and the number of leaves. Similarly, reduction in dry weight, fresh weight, leaf area, and number of nodules were also observed Plant height, fresh and dry weights, chlorophyll, and carotenoid content also get reduced	Kumar and Jayaraman (2014) and Gupta et al. (2006)
<i>Arachis hypogea</i> (cultivar K6 and K9)	100, 200, 400, and 800 ppm	Pb-induced reduction in biomass, and growth in term of shoot and root length	Nareshkumar et al. (2015)
<i>Vigna unguiculata</i>	200 ppm 0.025, 0.050, 0.1, 0.15, 0.2, 0.3, 0.4, 0.5, 1, 1.5, and 2.50 mM	Growth was drastically lowered. Reduction in shoot and root growth, fresh mass of roots, and shoot was also low	Ojwang et al. (2015) and Kopittke et al. (2007)
<i>Pisum sativum</i>	0.25 mg/L	Reduction was observed in number of tendrils, plant height, and leaf length, whereas in the number of leaves and leaf width got increased	Ghani et al. (2015)
<i>Vigna radiata</i>	25, 0.05 and 0.3 mM	Seed length and percentage germination were reduced	Hassan and Mansoor (2014)

(continued)

Table 10.1 (continued)

Plant species	Pb concentration	Effects on plants	References
<i>Zea mays</i> L.	1, 25, 50, 100, 200, and 500 mM 10, 20, and 30 ppm	Germination percentage and seedling growth in terms of root and shoot length were reduced significantly. Similar reduction in fresh and dry weight of seedlings, root and shoot growth got inhibited. Decline in level of total chlorophyll	Hussain et al. (2013) and Ghani (2010)
<i>Raphanus sativus</i>	2.5 mM	Decline in fresh weight, dry weight, and plant height reduced net photosynthetic rate and total chlorophyll content	Anuradha et al. (2011)

10.5.1 Germination

Germination of the seed marks the beginning of plant life. Many researchers have reported the adverse effect of Pb on germination such as such as rice, *Pinus helipensis*, *Phaseolus vulgaris*, and *Pisum sativum* (Mukherji and Maitra 1976; Nakos 1979; Wierzbicka and Obidzińska 1998). Mukherji and Maitra (1976) reported that 60 mM lead acetate lowered the activity of protease and amylase by about 50% in rice endosperm. The lead which enters through symplastic pathways leads penetration into the seed embryos and delays the germination by disrupting the activity of protease and α -amylase enzymes. These enzymes are released from aleuronic layer into the endosperm and scutellum epithelial cells, and its function is to hydrolyze the storage protein into metabolizable sugars to nourish the germinating plant (Tan-Wilson and Wilson 2012). Lead disrupts their functioning by binding at their active site and leading to inhibition of seed germination and growth (Sengar et al. 2008).

Seed coats exhibit selective permeability to Pb ions, but during imbibition of seeds, their permeability varies and become highly permeable to lead. The variation in selective permeability is a consequence of chemical and physical processes due to hydration of seed coats. Selective permeability is the function of both living and dead cells containing substances like lipids and tenins and increases with the reduction in water uptake as the final stages of imbibitions approach. Mrozek and Funicelli (1982) observed the inhibitory action of Pb in seed germination of *Spartina alterniflora* by altering their selective permeability and suggested the alteration in dormancy mechanism in halophyte seeds which aid these seeds to avoid adverse salinity conditions. In rice seedlings, 14–30% of the germination and 13–45% development reduced which adversely affects the length of radical and hypocotyls under high Pb concentration (1 mM) (Gidlow 2015). Other scientists also reported the similar result regarding the inhibition of germination by the Pb in *Hordeum vulgare*, *Oryza sativa*, *Zea mays*, and *Pinus halepensis* (Collin et al. 2022). Pb interferes with metabolic process like protease and amylase enzyme activity that ultimately leads to decrease in seed germination. Inhibition of ATPase/ATP synthase enzyme results into

decreased ATP production which is necessary for the growth of seedlings (Mench et al. 1987). When the seeds were incubated in Pb salts, their level of saturated fatty acid decreased and level of unsaturated fatty acid increased (18:3). Synthesis of DNA, RNA, and protein was decreased with increased concentration of Pb in the embryo axis and endodermis of the germinating rice seedlings (Wierzbicka 1987).

10.5.2 Photosynthetic Indices

The toxicity of Pb ions has a negative impact on photosynthetic rate. Reduction in photosynthetic rate may be due to the distortion in structure of chloroplast, reduction in the production of chlorophyll and carotenoids, impeded functioning of the enzymes involved in the Calvin cycle, crippled transport of electrons, and dearth of CO₂ which surfaced from the closing of stomata. Rebechini and Hanzely (1974) experimented with the *Ceratophyllum demersum* plants by growing them in an aqueous solution containing lead nitrate and observed well-defined alterations in the fine structure of chloroplast. A substantial fall in grana stacks and stroma content was observed along with elimination of starch grains. Stefanov et al. (1995) also noticed a modification in the lipid composition of thylakoid membranes as a result of Pb treatment. Uptake of elements like Fe and Mg by plants is critical for chlorophyll synthesis and thus adversely affects the formation of chlorophyll pigment when disturbed by Pb (Akinci et al. 2010). Owing to its intense affinity toward protein N- and S-ligands, it heavily impairs the photosynthetic machinery (Ahmed and Tajmir-Riahi 1993). Acceleration of chlorophyllase activity causes enhancement in chlorophyll degradation in Pb-treated plants. The adverse effect of Pb treatment on Chlorophyll-b is more pronounced compared to chlorophyll-a (Vodnik et al. 1999). Donor and acceptor sites of PSII, PSI, and cytochrome b/f complex are affected by Pb. PS I electron transport is less prone to inhibition by Pb than PS II (Mohanty et al. 1989; Šeršeň et al. 1998). It also leads to the dismantling of oxygen releasing extrinsic polypeptide of PS II and removal of Cl, Ca, and Mn from oxygen-evolving complex (Rashid et al. 1991). The application of Pb reduces photosynthesis indirectly by prompting stomata closure (Bazzaz et al. 1975). This reduction in carotenoid and chlorophyll content of seedlings and cuttings under high concentration of Pb stress can be regarded as a response of the plants specifically to the metal stress, which resulted in photosynthesis inhibition and chlorophyll degradation (Gajewska et al. 2006). In ryegrass, the content of total Chl, Chl a, Chl b, and Car markedly decreased under the Pb treatment by 40.50, 44.16, 28.25, and 51.11%, respectively, in comparison with control (Bai et al. 2015). In shoots, the Pb exposure decreased the K, Mg, Fe, Zn, and Cu content by 59.50, 18.51, 43.07, 28.73, and 46.85%, whereas enhancement is observed in Ca content by 92.78% in comparison with control (Bai et al. 2015). Pb at lower concentration enhances the anthocyanin content in *Brassica napus* but decreased at higher level of Pb concentration (Fatemi et al. 2021). Several study revealed that Pb toxicity has decreased the photosynthetic pigment in many plant species such as *Brassica napus* (Kanwal et al. 2014). In *Pisum sativum*, Rodriguez et al. (2015) reported

that chlorophyll A and chlorophyll B concentration increased with elevated level of Pb and reach maximum at 1000 mg kg^{-1} . *Hordeum vulgare* under hydroponic Pb condition showed toxic symptoms such as change in chloroplast morphology and decreased number of thylakoids damage to chloroplast directly inhibits photosynthesis and adversely affects the growth and development of the plants (Legocka et al. 2015). Pb reduces the photosynthetic pigments (Chl a and Chl b) of bean and pea seedlings (Hameed et al. 2010). It can be caused due to the impaired uptake of essential elements such as Mg and Fe or due to reduced leaf size (Feleafel and Mirdad 2013). Chlorophyllase (Chlase) and Mg-Dechelataase (MDCase) involved mainly in the destruction of chlorophyll, and their activity was stimulated under Pb stress. The net photosynthetic rate declines significantly in *Davidia involucreata* with increasing Pb concentration and maximum at Pb 200 mg/kg (Yang et al. 2020).

10.5.3 Growth

Contamination of lead in soil impairs the early plant growth. Hadi and Aziz (2015) attributed the poor germination of seeds and retarded growth in seedlings due to toxic effects of Pb on chlorophyll synthesis, cell division, root growth, and transpiration. Pb has harmful ramifications on growth of radish plants as observed by Tomulescu et al. (2004). When Jiang and Liu (2010) investigated Pb-induced changes in cell after 2–3 days of Pb exposure, they found that Pb caused the loss of endoplasmic reticulum, dictyosome and cristae, and the mitochondrial structure of root meristematic cells, and damaged biological membranes. The excess migration of Pb in roots declined root growth and facilitated the loss of apical dominance leading to a decline of 10% in the fresh biomass of plants as a result of Pb activity in roots and shoot, respectively, at 0.3 and $0.07 \mu\text{M}$ concentration (Kopittke et al. 2007). Pb toxicity leads to expansion of interphase stage of mitosis which reduced cell division leading to decreased plant growth (Patra et al. 2004). Pb caused a remarkable decline in the sprouting, seedling development, and growth in wheat, and inhibitory effect was also observed in *Jatropha curcas* (Dey et al. 2007; Shu et al. 2012). Even low concentration of Pb suppresses the growth of roots as well as aerial parts of the plants and detrimental effects on growth of the roots are observed than other plant parts (Kopittke et al. 2007; Liu et al. 2008).

Toxicity of lead leads to abnormalities in root morphology and structure as swollen, short, and stubby roots that exhibit a rise in the number of secondary roots and their length (Kopittke et al. 2007). As a result of Pb contamination, a reduction in the elongation of Mesquite (*Prosopis* sp.) roots was observed by Arias et al. (2010). The most obvious symptoms of growth retardation such as fewer, smaller, and brittle leaves having dark purple dorsal surfaces are clearly visible at extreme level of Pb toxicity (Islam et al. 2007). Overall, compromised nutrient metabolism, photosynthesis, and plant water relations leading to inhibition of plant growth occur as a result of Pb toxicity (Kopittke et al. 2007; Alsokari and Aldesuquy 2011). Toxic effects of Pb are different on the basis of its concentration, duration of exposure,

affected species, and stage of growth in plants (Gupta et al. 2009; Gul et al. 2019). High application of Pb (1000 and 5000 $\mu\text{g/g}$) in soil causes the reduction in root and shoot growth, ceased seedling growth, very thin stems, and small leaves in radish plant (Khan and Frankland 1983). Pb concentration significantly undermined starch solubility in endosperm and α -amylase activity in seeds in rice (Gautam et al. 2010). In seedlings of wheat, Pb causes reduction in seed germination, reduction in macro (Na, Ca, Mg, K, and O) and micronutrients (Fe, Cu, and Zn) biomass shoot and root elongation in comparison of control (Lamhamdi et al. 2011). Decrease in Cu and K concentration in maize cultivar was observed under higher level of lead contamination (Rizwan et al. 2018).

10.5.4 Crop Productivity

The most widely notable manifestation of Pb toxicity is detention of the photosynthetic carbon fixation which leads to declined crop productivity (Singh et al. 2010). Lead interferes with the synthesis of plastoquinone, carotenoids, and functioning of electron transport chain and retardation of enzymatic activities vital for CO_2 fixation as stomatal and non-stomatal constraints are accountable for carbon fixation (Mishra et al. 2006; Chen et al. 2007; Qufei and Fashui 2009). Lead stress curtailed the photosynthetic activity of sunflower plants as a consequentially affect the biosynthesis of chlorophyll which ultimately leads to reduction in plants biomass production (Mukhtar et al. 2010). Oxidative stress, synthesis and activity of chlorophyllase enzyme got promoted due to Pb toxicity which ultimately leads to decline in the rate of photosynthesis as a result of chlorophyll degradation (Liu et al. 2008). Furthermore, under Pb stress, there is also a significant reduction in the activities of delta-aminolevulinic acid dehydratase (ALAD) and ferredoxin NADP^+ reductase, which impedes chlorophyll synthesis (Gupta et al. 2009). Dissociation of chlorophyll is a four step reaction, and the final products include phytol, Mg, and a primary product of porphyrin rings. Although, level of toxicity differs among plant species, and usually it is more intimately related to Chl b than Chl a: however, decline in photosynthetic activity is more vulnerable to Pb stress than content of photosynthetic pigments (Xiong et al. 2006). Kosobrukhev et al. (2004) analyzed the extent of structural changes and photosynthetic activity of plants grown in soil contaminated with Pb and observed a decline of 40–50% in stomatal conductance. Romanowska et al. (2006) ascribed disrupted photosynthesis under Pb stress to depletion in leaf area, total chlorophyll contents, vascular bundles, and CO_2 influx due to ill-function of stomatal closure. Qufei and Fashui (2009) stated that addition of Pb in leaves of duckweed destroyed secondary structure of photosystem II and constrained the absorption and transfer of energy among numerous enzymes. It alters the actions of photosystem I and photosystem II in *Pisum sativum*. The rate of electron transport during hill reaction and halted cyclic and non-cyclic photophosphorylation got slow down due to Pb exposure (Romanowska et al. 2008). The catalysis of Melvin Calvin cycle enzymes is also affected by Pb toxicity (Chen et al. 2007). Exposure to Pb

also significantly affects ATP content and respiration of plants. Pb exposure chiefly disturbs the activity of ribulose-bisphosphate carboxylase responsible for regulating the assimilation of CO₂ in C₃ plants, devoid of affecting the oxygenase activity (Assche and Clijsters 1990). Parys et al. (1998) documented a considerable rise in CO₂ concentration in leaves of pea on being exposed to Pb(NO₃)₂ accrediting it to increased respiration with a simultaneous fall in photosynthesis. It was divulged by Romanowska et al. (2002) that photorespiration in this case remains constant and elevated respiration under Pb exposure is related to mitochondrial respiration (dark) only. The dark respiration instigated by Pb was observed in protoplast of barley and pea leaves (Romanowska et al. 2002, 2005, 2006). Furthermore, invigoration of respiration was linked with high ATP generation in mitochondria, raising the demand for more energy in order to cope up with the Pb toxic effects.

The decline in grain yield of crops under Pb stress can be accredited to poor nutrient uptake, incomplete carbon fixation as a result of stomatal and non-stomatal constraints, plant water relations, and escalated oxidative damage. Gu et al. (1989) reported a significant impact of Pb contamination in soils on productivity (grain and biological yield) of rice. Rehman et al. (2017) also documented 25–30% decline in the grain yield of wheat due to lead toxicity. Misra et al. (2010) perceived a marked decline in the economic yield of sugarcane crop grown under Pb stress. Decline in productivity of various crops is determined by Pb concentration in soil as argued by Codling et al. (2016) and Hussain et al. (2006) noticed a reduction of 28–32% and 24% in the economic yields of potato and mash bean, respectively. In maize seedlings, Pb stress causes a general reduction of macro- and micronutrient contents especially of K, Ca, and Mn which was observed (Wang et al. 2007). In seedlings and cuttings of ryegrass, photosynthetic rate (Pn) manifests a related trend of abrupt decrease as noted for conductance (Cond) and transpiration (Tr). Pn, Cond, and Tr were found to be comparatively less in leaves of seedlings than leaves of cuttings under lower Pb concentration, but an opposing trend is seen under high Pb concentration. The severely damaged thylakoid membrane of stroma and grana caused sharp reduction in rate of photosynthesis. In a study, Bai et al. (2015) observed the parallel change of Cond, and Pn in peanut leaves that reinforced the changes in Pn could be allocated to the changes in Cond.

Chatterjee et al. (2004) planted three variety of rice (Xinagyaxiangzhan, Meixiangzhan-2, Basmati-385) in Pb contaminated soil and found reduction in yield in the following order 69.12%, 58.05%, and 46.27% respectively. Reduction in grain yield may be due to the decrease in chlorophyll in leaves, carotene, sugars and Fe, Mn, Cu, and Zn. Moreover, the effects of Pb toxicity on germination, yield, and growth of different crops depend on time and concentration and also fluctuate with prevailing growth conditions and plant species. Ma et al. (2021) reported inhibition of grain yield of fragrant rice under soil Pb stress. Xian (1989) reported decrease in yield of kidney beans at high concentration of Pb. With the increasing concentration of Pb, pods per plant, seeds per pod, as well as total protein content of pea plant decreased in Sorial and Abd El-Fattah (2001) study. In spinach, ribulose-bisphosphate carboxylase/oxygenase activity was inhibited even at low concentration

of 5 μM Pb concentration (Vallee and Ulmer 1972). Pb is known as most potent metal ion for the inhibition of chloroplastic ATP synthetase/ATPase activity.

10.5.5 Biomass

Plants grown in contaminated soil, especially in high concentrations of Pb (1500 mg/kg), had dramatically lower biomass, almost 60% compared with the control plant (Fatemi et al. 2021). The plants have lower biomass when grown in Pb contaminated soil which is about 60% of control plant biomass. The Pb exposure inhibited the growth of ryegrass seedlings compared with control, and the reductions of plant height, fresh mass, dry mass, root volume, and root/shoot ratio were 35.77, 18.28, 55.18, 54.12, and 34.62%, respectively (Bai et al. 2015). Pb toxicity causes decline in biomass in *B. napus* and coriander (Fatemi et al. 2020a, b). Growth of coriander was decreased under Pb toxicity (Fatemi et al. 2021). Sidhu et al. (2016) reported that root and shoot biomass increased under Pb stress but declined at 29 mg kg⁻¹ Pb concentration in *Cronopus didymus*. Xu et al. (2018) observed that under Pb stress tea plants show poor biomass production loss of photosynthetic pigment reduction in total caffeine, free amino acid but increased catechin concentration. Compared to the control in tea plant under Pb stress, 17–65% root biomass, 3–50% stem, 20–73% leaves biomass were reduced that significantly affects the yield of the tea plants. *Chrysanthemum indicum* has caused significant reduction in root (32.7 mg kg⁻¹) and shoots (41.3 mg kg⁻¹) biomass with 50 mg kg⁻¹ Pb concentration. However, minimum application of Pb can promote the growth of the plant for some extent (Mani et al. 2015).

10.5.6 Antioxidant Enzymes

The production of hydrogen peroxide, superoxide, and hydroxyl radical increased when plants are exposed to heavy metals stress. The possible reason behind this phenomenon can be that the heavy metal stress reduces the capability of plants to assimilate carbon and escalate influx of photosynthetic electrons to molecular oxygen. Antioxidants rapidly scavenge reactive oxygen species that damaged the proteins, lipids, and pigments (Bhaduri and Fulekar 2012). ROS is collective term used for hydrogen peroxide, superoxide radical, hydroxyl radical, and singlet oxygen generated at the time of heavy metal stress (Devi and Prasad 1998). Lipids, nucleic acids, amino acids, and proteins got damaged which leads to irreversible metabolic dysfunction and cell death (Luna et al. 1994). The antioxidant system got activated to cope and repair the damage (Shu et al. 2012). A variety of mechanisms to deal with ROS effects in cellular compartments has been evolved by the plants. This is generally coped up through the production of various anti-oxidative enzymes, such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) (Wang

et al. 2007). Pb exposer shows simulative effects on electrolytes leakage H_2O_2 level MDA content and activity of antioxidant (SOD, CAT, APX, GPX, GR), but at higher concentration SOD, CAT, H_2O_2 , and MDA declined in *Cronopus didymus* (Sidhu et al. 2016). SOD, POD, and CAT were up-regulated compared to the control in maize seedlings (Wang et al. 2007). The activity of SOD and POD decreased in *Elsholzia argyi* after addition of Pb (Islam et al. 2007). SOD activities increased, but POD activities decreased under Pb stress in *S. japonica* which indicated that antioxidant system behaved differently in different plant species (Zhong et al. 2017). Ascorbate peroxidase participates in the detoxification of H_2O_2 into water and oxygen with the consumption of ascorbic acid. Glutathione reductase catalyzes the GSSH to GSH, and both these helps the plant cell to increase the antioxidants level under the metal stress (Qureshi et al. 2007). Proline not only regulates the osmotic potential of the cell but also plays a great role in the removal of reactive oxygen species and protects the cell membrane by maintaining structural stability and proton pumps from Pb toxicity (Cai et al. 2022).

10.5.6.1 Superoxide Dismutase (SOD)

SOD, a metallo-enzyme present in different cellular compartments, can catalyze the dismutation of O_2^- into H_2O_2 and O_2 , and subsequently H_2O_2 can be effectively scavenged by CAT and POD. The first step of ROS generation is superoxide formation, superoxide radicals (precursor of the other ROS) (Bhaduri and Fulekar 2012). Ashraf et al. (2017) found that SOD was the initial of scavenger of reactive oxygen species in rice under soil Pb stress. Heavy metal ions can increase the activity of SOD in oat and rice (Luna et al. 1994; Verma and Dubey 2003). Heavy metals may also decrease or not affect at all the SOD activity (Reddy et al. 2005). SOD activity of seedlings culminated at higher metal concentrations than those of cuttings of ryegrass, suggesting that SOD has better protection against oxidant damage. The decrease by 46.74% in shoots and by 55.99% in roots of SOD activity in ryegrass plant after Pb treatment has been observed (Bai et al. 2015). Multiple SOD genes encoding at least three Fe-SODs, three Cu-Zn-SODs, and one Mn-SOD had been reported in *Arabidopsis* (Bhaduri and Fulekar 2012). SOD increased but not dramatically in *B. napus* under various concentration of Pb (Fatemi et al. 2021).

10.5.6.2 Peroxidase (POD)

H_2O_2 is utilized in the oxidation of various organic and inorganic substrates by peroxidase. Guaiacol acts as electron donor when utilized by peroxidase in vitro known as guaiacol peroxidases. A strong increase in POD activity has been observed in response to Pb was reported in *rice*, *A. thaliana* and *Zea mays* (Verma and Dubey 2003; Wang et al. 2007). However, POD activity has been inhibited due to heavy metals which has also been observed in oat leaves (Luna et al. 1994). POD activity increased by approximately 2.26 times in comparison with controls at 3 mM of Pb

concentration in seedlings. The activity of POD is high at lower concentration in comparison with higher concentration, in seedlings and cuttings of *Jatropha curcas*. POD participating in lignin biosynthesis can build up a physical barrier against toxic heavy metals. A physical barrier can be build up against toxic heavy metals by participation of POD in lipid biosynthesis indication that seedlings are more efficient in avoiding damage than cuttings (Shu et al. 2012). POD activity significantly increased in *Brassica napus* by 47% at the Pb level 1500 mg kg⁻¹ (Fatemi et al. 2021).

10.5.6.3 Catalase (CAT)

CAT is a universal heme-containing and oxidoreductase enzyme that decomposes H₂O₂ to water and molecular oxygen, and acts as one of the key enzymes implicated in the removal of toxic peroxides. Generally, CAT activity gets stimulated under heavy metal stress. Shu et al. (2012) reported that at higher concentration, CAT activity is less in comparison with lower concentration. When seedlings had exposed to high Pb stress, CAT activity in leaves was quite high. CAT activity in both roots and shoots of the Pb-treated ryegrass plants increased significantly compared to control (Bai et al. 2015). CAT activity get stimulated up to 500 mg kg⁻¹ of Pb while show decline trend at higher concentration in *B. napus* (Fatemi et al. 2021).

10.5.6.4 Ascorbate Peroxidase (APX)

Ascorbate peroxidase is an important peroxidase which is ubiquitously present in plants. APX is universal housekeeping protein in the chloroplasts and cytosol of plant cells. Ascorbate work as a substrate and believed to scavenge excess H₂O₂ formed in plant cells under both stress and normal conditions (Bhaduri and Fulekar 2012). The ascorbate-free radical is the product of oxidation of ascorbate which got reduced back to dehydroascorbate with NADPH as the electron donor by the enzyme mono-hydroascorbate reductase (Asada et al. 1996). Several scientists reported increase in ascorbate peroxidase activity in response to air pollutants specially with O₃ in several species such as in wheat spinach, pumpkin, and *Picea abies* (Tanaka et al. 1985; Bender et al. 1994; Ranieri et al. 1996; Sehmer et al. 1998). The Pb stress also increased the H₂O₂ content in comparison of control by 181.86% in leaves and by 235.95% in roots of ryegrass plant (Bai et al. 2015).

10.5.7 Malondialdehyde (MDA)

When plants are subjected to oxidative stress, malondialdehyde is the term used to measure lipid peroxidation because it is a final product of the peroxidation of membrane lipid. Lipid peroxidation enhancement indicates that Pb and/or IAA caused oxidative stress in maize seedlings (Wang et al. 2007). Shu et al. (2012)

reported that the MDA contents of cuttings in rye grass increased about 100.91%, while in seedlings the increment is about 108.81% for seedlings at a highly toxic Pb level compared to the control. In *B. napus*, MDA content increased up to 1000 mg kg⁻¹ Pb concentration after that downward trend was observed (Fatemi et al. 2021). Excessive proline in the body may also participate in the clearance of reactive oxygen species and effectively keeping the MDA content low in aromatic rice and sunflowers under soil Pb stress (Liao et al. 2021). At different Pb concentration (500–2500 μM) in culture medium, there is an increase in MDA and H₂O₂ content in roots of wheat (Kaur et al. 2012). Similarly, in Maize and rice, the MDA content increased in respect of duration of exposure and dose (Thakur et al. 2017).

10.5.8 Protein

A large number of enzymes having sulfhydryl groups get inhibited at different sites when exposed to metal stress resulting in deleterious effects in the normal protein formation and folding pathways. According to Shu et al. (2012), the increase in protein content has been observed while the protein content decreased in leaves of seedlings in ryegrass plants. Soluble proteins can decrease the osmotic potential of the cell to ensure extracellular turbulence and stability (Jiang et al. 2019).

10.6 Conclusion

Pb pollution is a leading and common cause for stress in plants. The plants are adversely affected in terms of growth and physiological activities. To overcome the stress, plants evolutionally develop antioxidants system. When plants are under stress, a surge in free radical species observed which enhanced the activity of enzymatic and non-enzymatic antioxidants. The antioxidant system helps in maintaining the cell components structural integrity. This chapter detailed the Pb sources, impact and distribution in different parts, overall growth of the plants, and antioxidants activity in plants under Pb stress. Recently, world population and industrialization are growing exponentially which causes increase in food demand and at the same time reduction in cultivable land. Future agriculture requires stress-tolerant varieties, and to develop these varieties, the comprehensive knowledge of antioxidant system in plants is obligatory. Despite the advances in understanding of synthesis of antioxidants under Pb pollution, the detailed study on biochemical interaction of antioxidants and Pb is required.

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