Heliyon 10 (2024) e27724

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon

Review article

Pb uptake, accumulation, and translocation in plants: Plant physiological, biochemical, and molecular response: A review

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ARTICLE INFO

Keywords:
Lead (Pb)
Pb-uptake
Phytotoxicity
Pb-tolerance
Remediation techniques

ABSTRACT

Lead (Pb) is a highly toxic contaminant that is ubiquitously present in the ecosystem and poses severe environmental issues, including hazards to soil-plant systems. This review focuses on the uptake, accumulation, and translocation of Pb metallic ions and their toxicological effects on plant morpho-physiological and biochemical attributes. We highlight that the uptake of Pb metal is controlled by cation exchange capacity, pH, size of soil particles, root nature, and other physiochemical limitations. Pb toxicity obstructs seed germination, root/shoot length, plant growth, and final crop-yield. Pb disrupts the nutrient uptake through roots, alters plasma membrane permeability, and disturbs chloroplast ultrastructure that triggers changes in respiration as well as transpiration activities, creates the reactive oxygen species (ROS), and activates some enzymatic and non-enzymatic antioxidants. Pb also impairs photosynthesis, disrupts water balance and mineral nutrients, changes hormonal status, and alters membrane structure and permeability. This review provides consolidated information concentrating on the current studies associated with Pb-induced oxidative stress and toxic conditions in various plants, highlighting the roles of different antioxidants in plants mitigating Pb-stress. Additionally, we discussed detoxification and tolerance responses in plants by regulating different gene expressions, protein, and glutathione metabolisms to resist Pb-induced phytotoxicity. Overall, various approaches to tackle Pb toxicity

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https://doi.org/10.1016/j.heliyon.2024.e27724
Received 13 October 2023; Received in revised form 17 February 2024; Accepted 6 March 2024

have been addressed; the phytoremediation techniques and biochar amendments are economical and eco-friendly remedies for improving Pb-contaminated soils.

1. Introduction

Contamination of soil and water with heavy metals is a worldwide environmental issue, as almost all of the heavy metals are harmful to biota. Heavy metallic elements having a density higher than 7 g cm^{-3} could be non-essential (Ba, Li, Zr, and Al), less toxic (As and Sn), or highly toxic (Cd, Pb, and Hg) to plant growth and development [1–3]. Among other heavy metallic elements, lead (Pb) is one of the serious environmental contaminants because of its widespread application, high toxicity, persistency, and bio-accumulation in soil & water ecosystems.

Lead is extensively used for industrial purposes, including weight belts for diving, pigments, ammunition, lead crystal glass, cable sheathing, car batteries, radiation protection, and storing corrosive liquids [4]. Mainly, Pb is present in disseminated form, and its concentration in sedimentary and igneous rocks ranges from 6 to 30 mg kg^{-1} in granite igneous, 2–18 mg kg^{-1} in basaltic igneous, 7–150 mg kg^{-1} in black shales, $<$ 1–30 mg kg^{-1} in sandstones, and 16–50 mg kg^{-1} in shales and clays [5]. These rocks pass through weathering processes via various natural and anthropogenic activities that producing several forms of Pb, which ultimately enter water and soil ecosystems [5]. Further, it also enters into the environmental compartments (soil, water, air) through industrial waste or from household items. Globally, 800,000 t of Pb has been released into the environment during the past five decades, and a large proportion of it has been accumulated in the soil [6]. Such a huge release of Pb into the environment is a big challenge for all relevant scientific communities to tackle with it.

Lead accumulates in plants by soil-plant interaction as its adsorption has been detected in roots of many plants such as *Helianthus annus* [7], *Lactuca sativa* [8], *Chenopodium murale* [9], *Brassica juncea* [10], and *Nicotiana tabaccum* [11]. The extensive roots of plants absorb mineral nutrients along with free-Pb^{2+} ions from the Pb-contaminated soils [12]. Once they are adsorbed and accumulated passively by the roots, they attain apoplastic pathways, and are then translocated by the vascular flow system. However, a minor portion of Pb is transferred to the leaves through transporters using transpiration-driven pathways like apoplastic and symplastic pathways [13]. Adsorbed Pb is mostly stored in the roots, but some of its concentration is transported to the aerial parts of plants [14]. Plants also uptake Pb ionseither by cellular respiration from the air or by capillary action [4]. Plant leaves allow the absorption of air contaminated Pb-ions through stomatal and cuticular pathways, resulting in leaf chlorosis. Then these ions reach the endodermis area of plants and get firmly attached to the plasma membrane and cell wall [12].

Pb-affected plants show significant retardation in physiological attributes such as seed germination, sapling development, plant growth, transpiration rate, cell division, lamellar chloroplast functions, and chlorophyll production (Table 1) [15,16]. In biochemical effects, Pb causes high production of reactive oxygen species (ROS) like hydrogen peroxide (H_2O_2), superoxide radical (O_2^-), and hydroxyl radical (OH), and results lipid peroxidation [17]. These ROSs may destroy the plant metabolism and cause unrepairable injury to essential macromolecules, including proteins, DNA, lipids, and carbohydrates [17]. Additionally, Pb-induced oxidative pressure disrupts homeostasis and promotes cellular destruction. Pb toxicity alters the plasma membrane permeability, causing the reaction of sulfhydryl groups with Pb cations [18]. Pb-stressed plants also experience disruption of physiology and functioning at the cellular stage, including swelling of mitochondria, vascularized endoplasmic reticulum, membrane injury, damaged nuclei, and loss of cristae leading to programmed cell death [19].

The enigmatic entry of Pb into the food chain also causes serious threats to animals and human beings. Pb exposure to humans and animals might occur through touching contaminated soil or ingesting contaminated vegetables and fruits, which cause serious health issues like a nervous breakdown, disorders in the reproductive system, and cardiovascular and haematological systems leading to death [20]. Kids are more susceptible to Pb poisoning than adults [21], and the most common clinical symptoms include abdominal pain, arthralgia, behavioral changes, headache, and encephalopathy [21]. Therefore, Pb is considered non-essential- redundant, toxic even at a very low concentration, and serves no role in the development of plants and animals.

Regardless of definite controlling steps applied, minimizing the discharge of Pb pollutants into the soil is still an alarming issue

Table 1
Database search strategy.

Database	Search strategy	Identified
Google Scholar (January 1st, 2023)	(‘ecosystem’ OR ‘lead’ OR ‘Pollutants’) AND (‘Pb and Plants’ OR ‘anthropogenic activities and Pb’ OR ‘Pb toxicity and humans’) AND (‘Plants response’ OR ‘Pb tolerant genes’)	1500
EMBASE (January 5th, 2023)	(‘Lead and phytoremediation’ OR ‘Pb and environment’ OR ‘Pb and phytoextraction’) AND (‘Pb and genetic engineering’) AND (Pb and adaptation)	700
PubMed (February 3rd, 2023)	(‘Pb potential sources’ OR ‘Pb translocation and uptake’ OR ‘Plants and Pb’ OR ‘Pb toxicity and tolerance’)	550
SCOPUS (February 1st, 2023)	(‘Lead toxicity and Plants’ OR ‘Pb toxicity in human’ OR ‘Pb adaptation strategies’ OR ‘Pb phytoremediation strategies’)	1100
Science Direct (February 5th, 2023)	(‘Plants’ OR ‘Pb toxicity’ OR ‘environment and Pb’ OR ‘Plants and HMs’ OR ‘HMs and phytoremediation’)	1000
Web of Science (January 25th, 2023)	(‘Phytoremediation and HMs’ OR ‘environmental biodiversity and HMs’ OR ‘Plants and Pb toxicity’ OR ‘sustainable environment and Pb-tolerant varieties’)	900

[22]. Physiochemical methods for removing Pb from the contaminated soils are ineffective and very expensive, and may result in noticeable devastation of soil fertility and structure and thus are considered useless applications. A lot of studies have been conducted to identify highly efficient and cost-effective techniques for preventing soil contamination from Pb [23]. However, except from addressing the issue of Pb discharge into the soil environment, more studies are urgently required to find the underlying mechanisms and potential approaches to combat the serious challenge of Pb toxicity in plants for a sustainable agro-ecosystem. The current review discusses the biomagnification of Pb, its influences on plants, and techniques to reduce Pb accumulation in soil and plants. This review explains the physiological, biochemical, and morphological characteristics of Pb-toxicity in plants, and also mechanisms adopted by plants for detoxification and tolerance against Pb metallic elements.

2. Review methodology

2.1. Protocol

Preferred Items for Systematic reviews and Meta-Analyses Checklist (PRISMA) standard was used to conduct this review study. Basic aim of this study was to find the logical and mechanistical answers of the following research questions: “what are the potential sources of lead (Pb) in environment? How Pb uptake, translocate and accumulate in plants? What are the toxic effects of Pb on plant physiological and biochemical attributes? and what are the adaptation and phytoremediation strategies of plants against Pb?”

2.2. Search strategy

The search strategy (“Pb pollution in environment” OR “Pb potential sources in ecosystem” OR “Pb translocation and accumulation”) AND (“Pb toxicity and Plants” OR “Pb and humans” OR “Pb and phytoremediation” OR “Pb toxicity and Plants response”) AND (“Pb tolerant varieties and sustainable agriculture” OR “Pb toxicity and phytoextraction” OR Pb adaptation strategies”) was used in Science Direct, SCOPUS, Google Scholar, EMBASE, PubMed/Medline, Elsevier, and Web of Science database on January 01, 2023, as demonstrated in Fig. 1. For each database, the custom search strategy was applied (Table 1).

2.3. Selection process

The article selection process was completed in two steps: in first steps the authors read the title and abstracts of the searched articles. In second step, the selected articles were read in full length and applied the eligibility criteria. A consensus meeting was held with the all coauthors to resolve the disagreements on the selected articles. The data extracted from the included articles were tabulated in a Table 1.

2.4. Eligibility criteria

Studies that made logical conclusion of HMs translocation from several sources to environment, them accumulated in soil sediments and up taken by plants and finally adapted or remediated by several plants were included. And excluded, if.

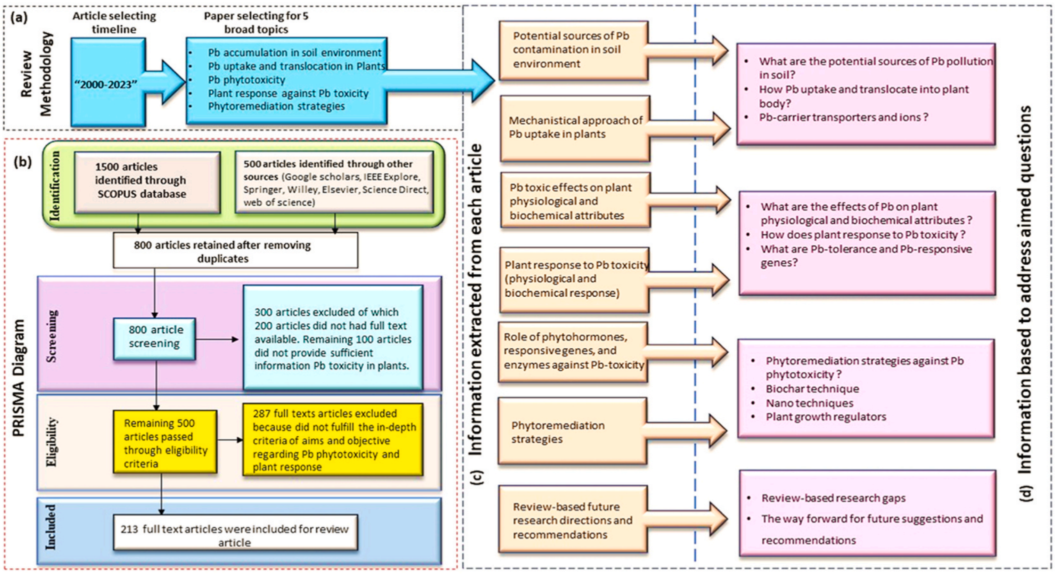

Fig. 1. Flowchart of review methodology.

1. Articles made same conclusion with same layout
2. Articles with same plant species and Pb concentrations

3. **Articles did not fulfill the basic aims of review article**

4. laboratory trials, animal studies, review articles, observational studies, letters to the editors, case reports, book chapters, patent, conferences, editorials;
5. Articles with another language that is not English

3.1. Risk of bias analysis

The quasi-experimental studies (non-randomized experimental studies) of the Joanna Institute (JBI) were used to analyze the risk of bias. To rate the methodological quality of the studies, each research question was tagged with a "low", "high" and "unclear" risk of bias.

4. Lead in the soil environment

The bedrock being a natural source of Pb causes Pb-contamination in soil and water environment when it decomposes through weathering processes [24]. Pb is found in the earth's crust and usually exists as rust and as traces in soils, water bodies, and plants. Cerussite ($PbCO_3$) and galena (PbS) are the important Pb minerals and mainly causes of Pb contamination in soils while, pyromorphite ($Pb_5(PO_4)_3Cl$) and anglesite ($PbSO_4$) are presented in small quantities. Pb is present in numerous forms, such as Pb (II), ionic, hydroxides and oxides, and complexes of oxyanion, in which the most stable forms are Pb-hydroxy complexes and Pb (II). Pb can replace Ca, Ba, K, and Sr at mineral sites [25].

In terrestrial environments, soil is a final sink for heavy metal contaminants, including Pb. The presence of Pb in the soil ecosystem is strongly associated with several anthropogenic sources such as automobile exhaust, coal combustion, release from transport vehicles, and refinery industries discharge [26,27]. Out of all lethal elements, Pb is the main toxin introduced through municipal refuse dumps, wastewater discharge, mineral mining, and excessive pesticide and fertilizer usage [28,29]. Previously, Selvi, Rajasekar [27] stated that about 10% of total toxic waste is formed by Pb metal out of all other heavy metals. Another study reported that Pb-contaminated soils may contain up to 400–800 mg kg^{-1} concentration of Pb, while the corresponding concentration in industrialized regions may rise to 1000 mg kg^{-1} soil [4].

Anthropogenic Pb commonly accumulates on the soil surface, and the concentration declines with depth [30,31]. Initially, Pb is quickly adsorbed, followed by slow adsorption in the soil, and then is reorganized into various compounds with changes in toxicity, bioavailability, and mobility [5]. After entering into the soil, the distribution and fate of Pb may be as follows (i) precipitation of

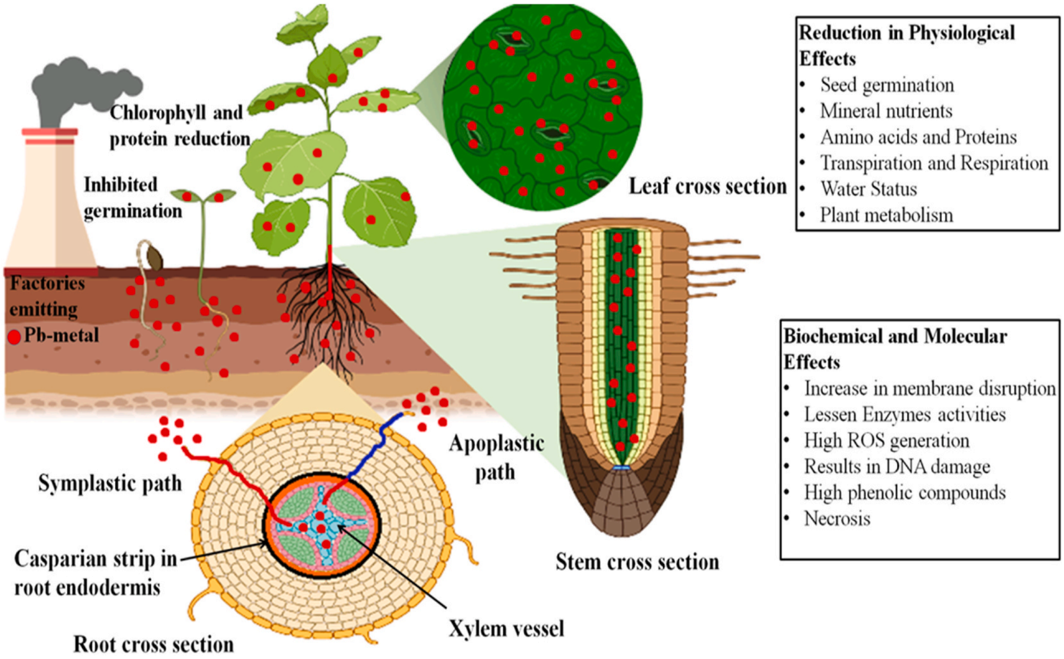

Fig. 2. Pb uptake, accumulation, and translocation in plants and its physiological and biochemical effects.

Table 2
Summary of Pb-metal's observed physiological and biochemical effects on different plant species.

Plant	Pb-concentration	Pb-exposure (days)	Experimental conditions	Plant parts	Physiological effects	Biochemical effects	References
Helianthus annuus L.	$PbNO_3$ (300, 600, and 900 mg kg^{-1})	105- days	Pot experiment	Roots, stem, and leaves	Decreased Chlorophyll *a*, *b*, and carotenoid contents. High proline contents	Increase in antioxidant activities (glutathione reductase, Ascorbate peroxidase, catalase and superoxide dismutase)	[66]
Zea mays	Pb (19.11) mg kg^{-1}	90-days	Pot experiment	Leaves	Damaged chlorophyll, high proline contents, and cell membrane permeability	Upregulation of anti-oxidative enzymes	[67]
Oryza sativa	($Pb(NO_3)_2$) (0.6 mM or 1.2 mM Pb)	30-days	Pot experiment in green house	Vegetative parts	Reduced biomass dry weight, total protein, and chlorophyll contents	ROS-overproduction	[54]
Gossypium Hirsutum	$Pb(NO_3)_2$ (500 μM)	10-days	Growth chamber	Leaves	Reduction in total soluble protein contents, leaf length, width, and petiole size	Increase in activities of antioxidant enzymes	[68]
Triticum aestivum	$Pb(CH_3COO)_2$ (0.15, 0.3 and 0.6 g L^{-1})	8-weeks	Pot cultivation	Root, stems, and leaves	Inhibition of cell metabolism. Negative effects on total protein contents and soluble sugars	Reduction in antioxidant enzymes	[53]
Glycine max L.	$PbCl_2$ (0.5, 2.5, 4.5 and 6.5 mM)	7-days	Pot cultivation under greenhouse conditions	Reduction in roots, shoots, and plant height	Increase in germination %. Reduction in respiration and photosynthesis	Increased catalase and peroxidase activities	[69]
Solanum lycopersicum L.	Pb (75, 150 and 300 mg L^{-1})	30-days	Pot cultivation under greenhouse conditions	Roots, shoots, and leaves	Reduction of mineral nutrient uptake and water contents. Chlorophyll *a*, *b*, *a*+b and biomass reduced	Disordered respiration and oxidative phosphorylation.	[70]
Brassica juncea L.	$Pb(NO_3)_2$ (0.25 mM, 0.50 mM and 0.75 mM	30-days	Earthen pots cultivation	Roots and shoots	Reduction in dry matter content	Increase in oxidative and ant-oxidative enzymes. High gene expressions. Reduction in osmolytes	[71]
Vicia faba	$Pb(NO_3)_2$ (0, 50 μM)	14-Days	Hydroponic cultivation	Shoots	Necrotic symptoms on leaves	Over production of ROS. Increase lipid peroxidation	[72]
Talinum triangulare	$Pb(NO_3)_2$ (0, 0.25, 0.5, 0.75, 1.0 and 1.25 mM)	7-Days	Hydroponics experiment	Root, stem, and leaves	Reduction in water contents and nutrients in leaves causes necrosis and chlorosis. Reduction in photosynthetic pigments	Induction of lipid peroxidation. Higher production of ROS. Reduction in Glutathione (GSH) level	[73]
Sedum alfredii	$Pb(NO_3)_2$ 200 μM	21-Days	Pot cultivation under greenhouse conditions	Root, stem, and leaves	Loss of plasma membrane and root cell death	Overproduction of ROS. Increase in anti-oxidative enzymes	[74]
Saccharum officinarum	$Pb(NO_3)_2$ (0.1, 0.2, 0.3, 0.4, 0.5, 1 mM)	150-Days	In vitro under Lab. conditions	Roots and shoots	Reduction in callus fresh and dry weight. Necrosis of callus	Increase in anti-oxidative enzymes.	[75]
Pisum sativum	$PbCl_2$ (1000 mg kg^{-1})	28-Days	Growth climate chamber	Roots and stem	Decrease in dry plant mass. Nutrients imbalance	RuBisCO activity was reduced strongly. Higher assimilation rate of CO_2	[76]
Spinacea oleracea	$Pb(NO_3)_2$ (0, 2.42 and 4.83 mM)	10-Days	Plant growth chamber	Roots and shoots	Plant biomass decreased	Diminished activities of anti-oxidative enzymes, over-production of ROS increase in lipid	[77]

(*continued on next page*)

Table 2 (*continued*)

Plant	Pb-concentration	Pb-exposure (days)	Experimental conditions	Plant parts	Physiological effects	Biochemical effects	References
						peroxidation, loss of membrane integrity	
Chrysopogon zizanioides	Pb $(NO_3)_2$ 1200 mg L^{-1}	10-Days	Hydroponics experiment	Roots and stems	Higher production of organic acids, amino acids, and coenzyme metabolites	Upregulation of antioxidants, ROS, Lipid peroxidation	[78]
Chrysanthemum indicum	Pb $(NO_3)_2$ (10, 20 and 50 mg kg^{-1})	60-Days	Pot cultivation under greenhouse conditions	Roots and stems	Decrease in Plant height, root length, and dry biomass. Alternation in chlorophyll-a, b, and carotenoid contents	Increased Pb-mediated oxidative burst, overproduction of ROS	[79]
Zygophyllum fabago	$Pb(NO_3)_2$ 500 μM	7-Days	Hydroponic system	Root, stem, and leaves	Irregular chlorotic spots on leaves. Reduction in dry mass, RuBisCO activity chlorophyll-a, b, and nutrients, mainly zinc	Decrease in total antioxidant activity	[80]
Pluchea sagittalis	(Pb $(CH_3COO)_2.3H_2O$) (0, 200, 400, 600 and 1000 μM)	30-Days	Plant growth chamber	Root, stem, and leaves	Reduction in nutrient contents, transpiration ratio, and dry weight	Alternations in non-enzymatic enzymatic antioxidants	[81]
Ficus microcarpa	Pb $(CH_3COO)_2$ (0, 25, 50, 100, and 200 μM)	1-Day	Plant growth chamber	Roots	Over-production of ROS in the aerial roots	Upregulation of antioxidant and ROS	[82]
Medicago sativa	500 mg/L	10-Days	Culture dish under Lab. conditions	Root, stem, and leaves	Inhibition of seed germination. Reduced Chlorophyll and protein contents	High generation of ROS. Increase in Lipid peroxidation and antioxidant enzyme activities	[83]
Medicago sativa	Pb (200 mg/L Pb $(NO_3)_2$)	4-Days	Natural growth chamber	Roots and shoots	Retardation in seedling growth. Protein contents reduced	Differentially expressed genes in association with upregulation of antioxidants	[84]
Gossypium hirsutum	$Pb(NO_3)_2$ (50 and 100 μM)	6-Weeks	Natural growth chamber	Roots and shoots	Inhibits seed germination. Reduction in biomass, root and shoot length, total chlorophyll, carotenoids, transpiration and photosynthetic rates	Lessen the antioxidant enzyme activities	[85]
Oryza sativa	$Pb(NO_3)_2$ (150 and 300 μM)	90-Days	Hydroponics experiment	Roots and leaves	Decrease in Photosynthetic pigments. Increase in proline contents	Decrease the activities of antioxidant enzymes	[86]
Solanum lycopersicum L.	$Pb(NO_3)_2$ (0.25, 0.50, and 0.75 mM	15-Days	Petri dishes under control conditions	Seedlings	Decrease in photosynthetic pigments, organic acids, secondary metabolites, osmoprotectants.	Over expression of stress-related genes	[87]

minerals, (ii) ionic-desorption and adsorption, (iii) complex formation with water, (iv) biological mobilization, immobilization, and (v) plants uptake [32,33]. Distribution and migration of Pb within the soil also relate to chemical aspects such as oxidation and reduction processes, chelation by organic matter, absorption of cations on complexes, and uptake by vegetation or other metallic oxides. Many of these chemical processes are topological challenges in the area affecting soil development, biota, climate, and parental material [34].

The physiochemical characteristics of soil, like soil type, soil pH, cation exchange capacity (CEC), organic matter, and soil texture, affect the Pb uptake by the plant roots [35]. Among these characteristics, soil pH has a key role in plant uptake by producing protons in roots and resulting in an acidic rhizosphere that favors the dissolution of Pb. Thus, it has been found that with the decrease in soil pH, Pb absorption also increases and becomes easily accessible to plants [35]. Additionally, it has been revealed that Pb translocated to shoots when Pb ions cannot precipitate and retain in the cell walls of plants due to the low pH [36]. Alternatively, high pH decreases Pb transformation, dissolution, and weathering, thus limiting its uptake by the plant's roots [37]. Wan, Zhang [38] reported that the soil organic matter formed organo-Pb complexes in the Pb-contaminated soils, which resulted in bioavailability and mobility of Pb for plant uptake. As far as soil texture is concerned, it has an important role in Pb availability to the plants as fine sandy soils facilitates more Pb uptake as compared to clayey soils which have strong bindings with Pb, and thus result in immobilization of Pb and unavailability to the plants [35]. Soils contaminated with Pb are a serious risk to public food safety and sustainable agriculture [39,40]. Thus, measures should be taken in advance to avoid the upcoming Pb toxicity challenges.

5. Uptake, accumulation, and transportation of Pb-metal in plants

Plant roots are the main parts through which plants uptake heavy metallic ions such as Pb [41], as shown in Fig. 2. Root exudates in rhizopheric region, root surface area, mycorrhizal relations in the rhizosphere, transpiration pull, and wide root ranges may upset the Pb-solubility in the soils [42]. It is known that Pb has less solubility and low absorption availability to plants because it precipitates as sulfates such as anglesite ($PbSO_4$) and phosphates like hydroxy pyromorphite [$Pb_5(PO_4)_3OH$], lead(II) phosphate [$Pb_3(PO_4)_2$] [43,44]. In a Pb-polluted soil solution, a portion of Pb is adsorbed in roots, which then bind to carboxyl groups of uronic acids or directly to the polysaccharides of the rhizoderm. This adsorbed Pb penetrate the roots by passive method & pursue channels of water translocation [45].

Pb uptake depends upon various aspects like plant species and related genotypes, soil chemical and physiological conditions, and total Pb metal content in the soils [46]. The mechanism by which Pb adsorbs onto the surface of roots at the cellular level is still unknown and requires further studies. Out of several pathways for the uptake of Pb through the roots, the ionic passageway is one of the definite paths [47]. The uptake of Pb relies on the operation of H+/ATPase pump in order to retain a high negative membrane potential in rhizodermal cells [45]. As a result of the concentration gradient, which can be determined from the root apex, Pb uptake is not uniform through the plant roots [48,49]. Nonetheless, numerous root cells in the root apices have thin cell walls and are young, providing a large surface area for absorption and containing a larger concentration of Pb [50].

After uptake, some Pb part accumulates in the roots, while the rest is transferred to the aerial parts of plants [51,52]. According to previous studies, it was observed that more than 95% of absorbed Pb gets deposited in the roots, while a non-significant amount of it is transferred to the aerial parts in many plants such as *Phaseolus vulgaris* [45], *Pisum sativum* [42], *Triticum aestivum* [53], and *Oryza sativa* [54]. Li, Zhou [55] clarified that Pb accumulated in the cells of roots closer to the cell gap and inner cell wall of plants, which was confirmed by the transmission electron microscope. Usually, it has been observed that monocots accumulate less Pb in their roots than dicotyledonous plants because they have higher divalent cation binding places [56].

Transport of Pb from roots to other tissues is restricted by the barrier present in the root endodermis [13], that is the casparian strips which limit the transport of Pb from endodermis tissues into vascular tissue [57]. Generally, the casparian strip in endodermis precipitates the Pb that translocate through the symplastic pathway which breakdown during the plant's detoxification process [57]. Previously, Gul, Manzoor [58] studied Pb-ions' translocation from roots to the vegetative regions and stated that Pb may require transportation through the xylem [58]. Further, the accumulation of high concentration of Pb was observed near the phloem and xylem cells in many plants through the X-ray mapping technique, which further confirmed that phloem vessels are also involved in Pb transport along with xylem vessels [59].

6. Lead phytotoxicity

Pb is known to have harmful effects on plants in different ways, affecting the germination of seeds and seedling development, enzymatic activities, photosynthesis, dry mass of shoots and roots, water status, and mineral nutrients in plants [60,61], as demonstrated in Table 2. Generally, injurious effects such as chlorosis, stunted growth, necrosis, and leaf senescence become more prominent under Pb persistence, even at low concentrations [62]. Various plant growth stages, like seed germination and shoot/root growth at the sapling stage, are very sensitive and severely affected by high concentrations of Pb. Further, it causes the unavailability of nutrients to plants by affecting their absorption and transport [63]. Consequently, Pb also inhibits many biochemical and physiological processes, but photosynthesis is the most affected process [64,65]. Fig. 2 and Table 2 show plants' Pb uptake, accumulation, and translocation and its physiological and biochemical effects on several plants.

6.1. *Lead toxic effects on plant germination and growth*

Pb affects the plants by reducing germination levels, shoot and root length, seedlings development, level of tolerance, and dry weight of plants [88,89]. Initially, the seed coat inhibits Pb entry until the germinating seed radicle breaks it down. Pb moves faster in the meristematic cells of hypocotyl & radicle after the testa breakdown, where it is translocated in vascular tissues and accumulates in distinct root areas [90]. Previous studies found that the application of Pb suppressed the germination of *O. sativa* and *Elsholtzia argyi* and induced negative effects on the size of hypocotyls and radicals [45,88,91]. Moreover, Pb toxicity also inhibits seed germination by delaying radicle emergence, disturbing the polyphenol oxidases and oxidizing capability of roots, and generally reducing the carbohydrate metabolizing enzymes, i.e., α-amylases and β-amylases [92]. Pb may also interfere with acid phosphatases, proteases, and acid invertases [34] and alter the genomic profile of seeds, which results in the inhibition of plant germination [93].

Cai, Wu [94] evaluated the effects of Pb on *Oryza sativa* seedling germination and plant growth and found that the growth and development of *Oryza sativa* were not affected after treating the rice seedlings with Pb. Lamhamdi, Bakrim [95] found that seed permeability was enhanced with the reduction of water at the final germination stage, which ultimately reduced the germination of

Pb-stressed *T. aestivum* seeds. Moreover, the presence of Pb leads to a reduction of radicle formation, destruction of osmoregulation, and proteolytic activities of the seed cells that may reduce the stored food and finally inhibit germination and seedling development [45].

6.2. Noxious effects of Pb on nutrient uptake

Pb seriously affects the nutrient uptake by plants, as proved by several studies [96,97]. Previous studies stated that Pb exposure to the plants declines the cation concentrations (Mn^{2+}, Zn^{2+}, Fe^{2+}, $Ca^{2+,}$ and Mg^{2+}) in *Vigna unguiculata* [98], *Brassica oleracea* [99], *Z. mays* [100], *Medicago sativa* [101], *O. sativa* [102], *Brassica oleracea* [99] and *Raphanus sativus* [103]. Mainly, the nutrient uptake in aerial plant parts may show a similar trend in all plants grown in Pb effected soils. However, the trend in the roots might depend on the type of species of plants or intensity of the induced-stress [101,103]. The nutrient uptake can be reduced due to variations in the physiological activities of plants or the presence of Pb, which may create ionic competition (e.g., those ions having the same atomic size as Pb). According to Morais, Boechat [104]), minerals having similar radii, like K^+ and Pb^+ ions (K^+: 1.33 Å and Pb^{2+}: 1.29 Å), enter into the plants through similar potassium channels. Likewise, Pb influences –SH groups and K^+-ATPase of proteins within the cell membranes, which results in the discharge of potassium ions from the plant roots, while nitrogen efflux is not affected by Pb [104]. Generally, the inorganic nitrogen concentration of all plant parts is reduced due to the rate-limiting enzymes and slow nitrate reductase activity during the nitrate (NO_3) reductase process [105,106]. Xiong, Zhao [106] observed a significant reduction in nitrate (70 and 80%) and amino acids (81 and 82%) and activity of nitrate reductase enzyme (100 and 50%) in shoots of *Brassica pekinensis* after (4 and 8 mmol kg^{-1}) Pb-exposure.

6.3. Pb effects on the water status of plants

The water status, such as transpiration and moisture content of plants, are also disrupted after Pb entrance, as proved by previous studies [34,107]. The presence of Pb affects the various plant mechanisms, such as the reduction of leaf growth and leaf surface area, that ultimately decrease the plant transpiration process, as the leaf area is the major organ for transpiration [65]. Previous studies observed that water use efficiency and transpiration rate were suppressed in Pb-treated *Citrus aurantium* [65]. Additionally, Pb may cause a reduction in amino acids and sugar contents that sustain the cell wall plasticity and cell turgidity [108]. Abscisic acid (ABA), the first plant growth regulator induced by drought helps to control the stomata opening and closing [109,110]. Higher accumulation of ABA in the roots and leaves of the plants could also be because of Pb^{2+} ions, which results in the closure of stomata that finally disturbs the transpiration system of the plant [110]. According to Zulfiqar, Farooq [34], the respiration process in *G. max* was decreased due to the deposition of Pb in the cuticle layer or surface of leaves. Furthermore, Pb-induced respiratory problems and oxidative phosphorylation may cause O_2/CO_2 imbalance and disturb the water status in plants [111].

6.4. Lipid peroxidation and oxidative stress

During the normal metabolism process in the chloroplast of a plant cell, ROS are formed either due to the excitation of highly energized pigments or as byproducts formation under the consequences of O_2 reduction. Similarly, ROS like radicals of hydrogen and oxygen are also produced due to exposure to specific environmental stresses in aerobic cells of an organism, and the process is known as oxidative stress, which is also a distinguished character of the noxious nature of Pb-metal [112]. ROS consumes all cellular anti-oxidants, quickly oxidizes, and attacks all biomolecules, i.e., proteins, lipids, and nucleic acids, leading to irreversible defective metabolism and causing programmed cell death [113]. ROS produces reactive aldehydes and lipid radicals by oxidizing the unsaturated fatty acids, eventually affecting the lipid bilayer. Thus, exposure of plants to Pb destroys the cell membrane structure and lipid composition because polyunsaturated fatty acids in the lipids are very sensitive to ROS [112]. Małkowski, Sitko [114] observed the potassium ion leakage and various changes in lipid composition in Pb-exposed *Z. mays*. In some cases, Pb ions also cause lipid peroxidation by reducing the saturated fatty acids and increasing the unsaturated fatty acids in the membranes of numerous plants [115]. Additionally, the presence of Pb leads to lipid membrane alterations that result in abnormalities or changes in cellular structures or organelles, i.e., chondriosomes, peroxisomes [112], chloroplastids [116], and plasma membrane [117].

6.5. Pb effects on phenolic compounds

Phenolics are one of the most important groups of secondary metabolites that plants widely produce. These compounds are categorized due to the existence of one or more than one hydroxyl group (-OH) within one aromatic ring having six carbon atoms. Phenylalanine ammonia-lyase (PAL) is the chief precursor that takes part in the formation of phenolic compounds that play their roles in the production of pigments, antioxidants, regulation of plant growth, and have a stimulating role in physiological responses of plants [118]. Phenols such as cinnamic and coumaric acid synthesize some complex phenolic compounds like flavonoids, anthocyanin, and lignin [18]. Various stresses and environmental factors disturb the metabolism of phenolic compounds, such as phenylpropanoid in plants, which act as antioxidants. The anti-oxidative nature of these compounds is due to the carboxyl and hydroxyl groups, which can chelate with the other metallic ions [119].

In plants, phenolic compounds also exhibit an extensive range of reactions to regulate the adverse effects of metallic toxicity, solar radiation, and microbial infections [120]. A high endogenous concentration of flavonoids and phenols has been observed in *Tithonia diversifolia* plants post-exposure to Pb-acetate, proposing their significant role in resisting Pb toxicity [121]. Similarly, *Hippophae* *rhamnoides* grown in Pb-affected soil had increased levels of phenylpropanoids, phenols, anthocyanin, and flavonols, which possess antioxidant activities [122]. Wiszniewska, Muszyńska [123] reported that the use of exogenous phenolic acids caused tolerance in *Daphne jasmine* by enhancing antioxidant activity against Pb-stress. Lower levels of all phenolic compounds were reported in *Triticum aestivum* plants after exposure to Pb-metal [124]. Pratima and Pratima [125] conducted an experiment on *Brassica juncea* plants and found that polyphenol contents were increased after exposure to Pb at high concentrations (10, 20, 30, and 40 mM).

7. Pb tolerance mechanisms in plants

Plants respond to the harmful effects of Pb in different ways, such as tactical metal uptake, metallic binding to the root surfaces, stimulation of the antioxidative defense system, gene regulation, and activation of phytohormones. However, the response behavior varies with metal concentration, plant species, and exposure circumstances.

7.1. Passive mechanisms

Plants accumulate the Pb in their cell wall upon exposure to Pb because the cell wall is the region that has an abundance of Pb-binding compounds. Transport of even a small concentration of Pb into the cell membrane results in its interaction with the cellular components that lead to an increase in the thickness of the cell wall, showing their defensive mechanism [126]. Pectin is an important cell wall component, forming a pectin-Pb complex with Pb ions through which plants can resist Pb toxicity [49]. Previously, it was reported that *Funaria hygrometrica* had JIM5-P, i.e., monoclonal antibodies that acted as a physical barrier limiting Pb ions' uptake into the plant cell wall [18]. Additionally, it was also observed that Pb bound to JIM5-P within the cellular parts can be re-mobilized or taken up by endocytosis. Similarly, cellular wall thickening in various groups of plants like *Lemna trisulca* [127] and *Arabidopsis hybrids* [128] was also noticed. These cellular thickenings are formed on the tip of growing cells like root caps, root hairs, and meristematic tissues, which consist of a high quantity of JIM5-P in response to Pb contamination at high concentrations. Further, it was concluded that protoplast toxicity was prevented by cell wall sequestration and compartmentalization of Pb metal ions.

7.2. Antioxidative responses

Antioxidative responses are stimulated in plants to counter the toxic effects of Pb metal ions. The first mechanism of the defense system is to avoid Pb-entry into the cells, while the second is the involvement of antioxidants and their activities to cope with high ROS levels produced by Pb ions [129,130]. The defense mechanism activates some enzymes like glutathione (GSH), APOX (ascorbate peroxidase), vitamin C (ascorbic acid), SOD (superoxide dismutase), CAT (catalase), carotenoids, and vitamin E (tocopherol), which are evenly disseminated within the cells of plants [131]. The distribution of antioxidants in plant cells is as follows: 73% in vacuoles (glutathione, ascorbic acids, and peroxidases), 17% in the chloroplasts (DHAR, Zn-SOD, GR, MDHAR, Cu-SOD, APOX, GSH, vitamin C and E), 5% in the cytosol (GSH, POD, APOX, Cu/Zn-SOD, Zn-SOD, CAT, Mn-SOD, vitamin C, and GR), 4% in the apoplast (vitamin C and POD), and 1% in chondrium (GSH, MDHAR, GR, Mn-SOD and CAT) and peroxisomes (Cu/Zn-SOD and CAT). Previously, high rate of antioxidant enzymatic activities i.e., GST, CAT, APOX, GR, SOD, and GPOX, were observed in Pb-treated plants [132,133].

ROS are generated as a result of Pb-toxicity, which is regulated by the antioxidative enzymes. In addition to antioxidant enzymes, a plant cell has a non-enzymatic antioxidant defense system to resist ROS damage. These non-enzymatic antioxidants include glutathione, flavonoids, carotenoids, phenols, and primary and secondary metabolic compounds [19]. Phenolics such as flavonoids and lignin precursors are critical antioxidants that can efficiently encounter ROS toxicity [134]. Anthocyanins (in vacuole) and α-tocopherols (membrane-related) are the major secondary metabolites, which generally show an important defense role against oxidative damage [134]. These secondary metabolic compounds efficiently alleviate the active free radicals by reducing them and saving the plant cells from the deleterious effects of Pb-induced oxidative stress [19]. Previously, it was found that phenylalanine ammonium lyase (PAL) is a key enzyme in resisting metals-facilitated toxicity and helps in changing the accumulation and biosynthesis of anthocyanin metabolites [135]. On the other hand, α-tocopherol also can alleviate active radicals and lipid peroxides [136]. Kumar, Prasad [73] reported that Pb exposure to *T. triangulare* leaves induced a significant rise in α-tocopherol (124%) and anthocyanins (70%) as compared to the control group, which shows their obvious relationship in response to oxidative stress.

7.3. Metal-chelating compounds and osmolytes

Under Pb-stress conditions, plants have evolved specific tolerance mechanisms comprising of (1) decrease in uptake of Pb; (2) driving out Pb at the cellular level; (3) formation of Pb-chelators using thiol compounds in the cytoplasmic matrix, i.e., metallothioneins, phytochelatins, and GSH; (4) detoxification of Pb-stimulated ROS; and (5) sequestration of Pb ions in the organelles like vacuoles [137]. Chelation is one of the most important tolerance mechanisms to minimize the toxic effects of Pb-metal. The metal-stress environments cause an increased level of GSH, resulting in the synthesis of phytochelatins (PCs), which is an important metal-chelating compound [138–140]. The PCs are formed by γ-glutamylcysteine (γ-Glu-Cys) with repeating units of 2–11 ranges followed by a single C-terminal glycine [138]. Further, PCs are catalyzed by phytochelatin synthase (PCS) through the consequent movement of γ-Glu-Cys to the substrate glutathione during enzyme-catalyst reactions [19,141]. Jiang, Wang [142] found that Pb-treatment resulted in the enhancement of intracellular GSH along with the rise in PC by 1.8 folds in *A. thaliana* APX1–3 mutant strains as compared to wild strains. High production of PCs reduces free Pb-ions in the cytoplasmic matrix, which strongly correlates with reducing negative responses in stressed plants [143]. During Pb-stress conditions, PCs efficiently bind with Pb and transfer it to the vacuoles, where Pb is successfully detoxified. Further, metal complexes with PCs, glutathione, and amino acids are moved to the tonoplast, where active toxic compounds are detoxified and removed from the cells.

Plants can also detoxify Pb-induced toxicity by a resistance approach called osmoregulation, which is facilitated by compatible osmolytes or solutes like mannitol, sugars, glycinebetaine, and proline [144]. It was observed that the production of osmolytes is the main characteristic of the survival and protection of plants under metal-stress conditions [19]. Along with the osmotic adjustments, these osmolytes can play a vital role in ROS scavenging in metal-stressed environments [145]. Different osmolytes including sugars, i.e., sucrose, glucose, raffinose, fructose, trehalose, and amino acids such as alanine betaine, proline betaine, and polyamines perform a defensive part in damage caused by Pb toxicity [146]. In amino acids, proline is a well-known organic osmolyte that accumulates in plants during stress conditions and often displays a positive relationship with stresses [19,144].

Additionally, soluble proline is most studied molecule/amino acid in the perception of plants' defense mechanisms. It copes with ROS and maintains the structure of protein during a stressful environment [147,148]. High proline accumulation is observed either by increased glutamate biosynthesis or ornithine pathways. Previous studies reported that plants may use glutamate instead of ornithine pathways during stress conditions [19,149]. Yang, Zhang [149] investigated the reason for proline accumulation in two cultivars (*Ningchun* and *Xihan*) of *T. aestivum,* after treatment with Pb metal. The results of their study showed that higher activities of the r-glutamyl kinase (GK) and ornithine-δ-aminotransferase (OAT) enzymes in *Xihan*, and only high GK activity in *Ningchun* leaves resulted in more accumulation of proline [149]. Along with the synthesizing enzymes like OAT and pyrroline-5-carboxylate synthetase (P5CS), the proline dehydrogenase enzyme also regulates the proline at the cellular level. This was further confirmed by

Table 3

Pb-responsive genes and their regulatory role in different plants against Pb toxicity.

Pb-responsive genes	Family name	Plant parts	Plant species	Regulatory role of gene	References
BJMInd-1,	DMP2 (transmembrane protein, putative)	Stem	*Brassica juncea*	Up-regulation	[93]
BJMInd-2	ACA1 ((auto-inhibited Ca^{2}+ -ATPase 1)	Stem		Enhances calcium-transporting ATPase/calmodulin binding	
BJMInd-3	CAD9 (Cinnamyl Alcohol Dehydrogenase 9)			Increase in binding/catalytic/oxidoreductase/zinc ion binding	
, BJMRep-1	VHA-A1 (VACUOLAR PROTON ATPASE A 1)	Stem		Down-regulation ATPase	
BJMRep-2	SCAMP5 (secretory carrier membrane protein family protein)	Stem		Reduce proteins	
bHLH	Protein Family Transcription factor bHLH104	Root	*Louisiana iris*	Iron acquisition	[157]
ERFs	Protein family Ethylene-responsive transcription factor ERF071	Root		Involve in hormonal responses.	
IRT3	Iron-regulated protein 3	Root		Ferrous iron transporter	
LAX2-2	Protein 2	Roots	*Raphanus sativus*	Regulation	
aquaporin PIP1-6	Plasma membrane protein	Roots	*Zea mays*	Downregulation of cell membrane intrinsic proteins by Pb-ions	[158]
GST 27	Glutathione S-Transferase	Roots	*Zea mays*	Regulatory role of antioxidant defence system against Pb-ions	[159]
Histidine kinase 1	Histidine Protein	Leaf	*Arabidopsis thaliana*	Regulatory role in cell signalling	[160]
GST gene	Glutathione S-Transferase	Roots	*Medicago sativa*	Regulate the metal-chelating compounds in tolerance	[84]
Chalcone synthase (CHS) genes	polyketide synthase	Roots	*Medicago sativa*	Regulate flavonoid paths against Pb	[84]
HMAs PCS1 PCS2 ABCC1	Transporter proteins	Roots and leaves	*Oryza sativa*	Regulatory role in transport and detoxification of Pb metallic ions	[86]
Chlorophyllase *Chalcone Synthase* *Phenylalanine ammonia lyase*	Phytochrome proteins	Seedlings	*Lycopersicon esculentum*	Regulate the chlorophyll enzymes' secondary metabolites against Pb	[87]
PCS1.1, ABCC1.1, ABCC3.1	Transporter proteins	Roots	*Populus* × *canescens*	Downregulation of transport and accumulation of Pb-ions in roots	[161]
PCS1.1, ABCC1.1, ABCC3.1	Transporter proteins	Roots	Populus × nigra	Downregulation of transport and accumulation of Pb-ions in roots	[161]
aNAAT1 and TaDMAS1	nicotianamine aminotransferase and deoxymugineic acid synthase proteins	Roots	*Triticum aestivum*	Control iron uptake and Fe-chelation under a Pb-stress environment	[162]
GRXC2, GSTU12, GSTU13	Glutathione S-transferase family	Roots	*Raphanus sativus*	Control the glutaredoxin in GSH metabolic pathways	[163]
TCP4, TCP10, TCP24	Transcription factor gene family	Roots	*Raphanus sativus*	Stimulates lipoxygenase to regulate jasmonic acid pathways	[164]
MYB1R1	Transcription factor protein	Roots and leaves	*Salvinia minima*	Regulatory role in DNA transcription	[165]
At2g28660	Chloroplast-targeted copper chaperone protein	Leaves	*Hirschfeldia incana*	Control the metal handling	[166]

Rucińska-Sobkowiak, Nowaczyk [144], in which *Lupinus luteus* was treated with Pb concentrations (150 and 350 mg L^{-1}). The activities of OAT and P5CS were enhanced at 150 mg L^{-1} as compared to 350 mg L^{-1}. Interestingly, the proline dehydrogenase activity was higher under 150 mg L^{-1} than 350 mg L^{-1} representing its prominent role in the proline regulation [144]. Likewise, it was reported that several Pb-affected plants such as *T. triangulare* [150], *T. aestivum* [95], and *Armeria maritima* [151] showed an increase in proline contents.

7.4. Pb transporter protein and gene expression

Gene expression, and transporter proteins are the major defense mechanisms in cellular metabolisms to counter the Pb stress [152], as shown in Table 3. Such defense mechanisms can be activated through mitogen-activated protein (MAP) kinase pathways [36] by stimulating and organizing the various cellular organelles against oxidative stress. The synthesis of proteins and expression of genes are modified by signal transduction during the MAP phosphorylation reactions [36]. Previously, gene expression patterns were studied for cellular functioning and defense metabolisms, which gave a new concept of metal interactions with molecular mechanisms of plants [153]. In an experiment, about 16,246 unigenes were distinctively expressed through sequencing in *Platanus acerifolia* grown under Pb-contaminated conditions [154]. Many of these expressed genes were associated with metal transporters, antioxidants, and plant chelators. Additionally, the identified unigenes also involved gibberellins, glutathione, photosynthesis, plant detoxification, and defense mechanisms [154]. Li, Hu [155] conducted an experiment to observe the molecular responses of the Pb-stressed *Festuca arundinacea* plant and found different expression of 25,415 genes that were involved in many important cellular metabolic pathways like polyketides, carbohydrates, terpenoids, and energy. Expressions of genes directly or indirectly affect the plant tolerance responses against Pb accumulation [155]. Besides inducing cellular metabolisms, previous studies also reported increased antioxidative gene expression like GPX, Cu/Zn-SOD, glutathione and APX in Pb exposed plants [156]. Previously, an experiment was performed on Pb-exposed *Arabidopsis thaliana* wild plant and its mutant knockout for APX1 protein (KO-APX1), it was revealed that APX1-plants showed high resistance against Pb-metal [142]. *A. thaliana* mutants APX1 expressed GPX1 gene (280%) and exhibited significantly higher CAT (33%) and GPX (170%) activities in contrast to wild-plants [142].

Venkatachalam et al. (2017) found a reduction in intensities and number of protein bands in Pb-exposed *Azadirachta indica* leaves as compared to the control [167]. However, it was interesting that six new bands of various molecular sizes were observed as new polypeptides in the Pb-exposed leaves. Furthermore, the heat-shock proteins (HSP) performed a major role in defense mechanisms against oxidative Pb-stress by restoring cell-homeostasis [168]. HSP may also involve numerous cellular metabolic functions, i.e., translocation, protein foldings, degradation, transportation of proteins across cellular membranes, and avoiding the proteins from haphazard accumulation under Pb-stress circumstances [169]. A high level of HSP70 (a type of HSP) has been detected under Pb-stress in various plants such as *Miscanthus sinensis* [170] and *Madia sativa* [156]. It has been concluded that the over-expression of genes and proteins was possibly associated with the cellular defensive mechanisms against Pb-stimulated oxidative damages.

Liu, Shen [171] used proteomics techniques and found a total of 24 responsive proteins expressing significant alternations in Pb-stressed *Suaeda salsa* plants. Different behavior of such proteins was associated with defence mechanisms, cysteine metabolisms, Calvin and Krebs cycles, energy synthesis, pentose phosphate pathway, photosynthesis, cellular signalling, and protein biosynthesis [171]. Besides these proteins, expression of the following genes, such as malate dehydrogenase, ribulose-1, 5-bisphosphate

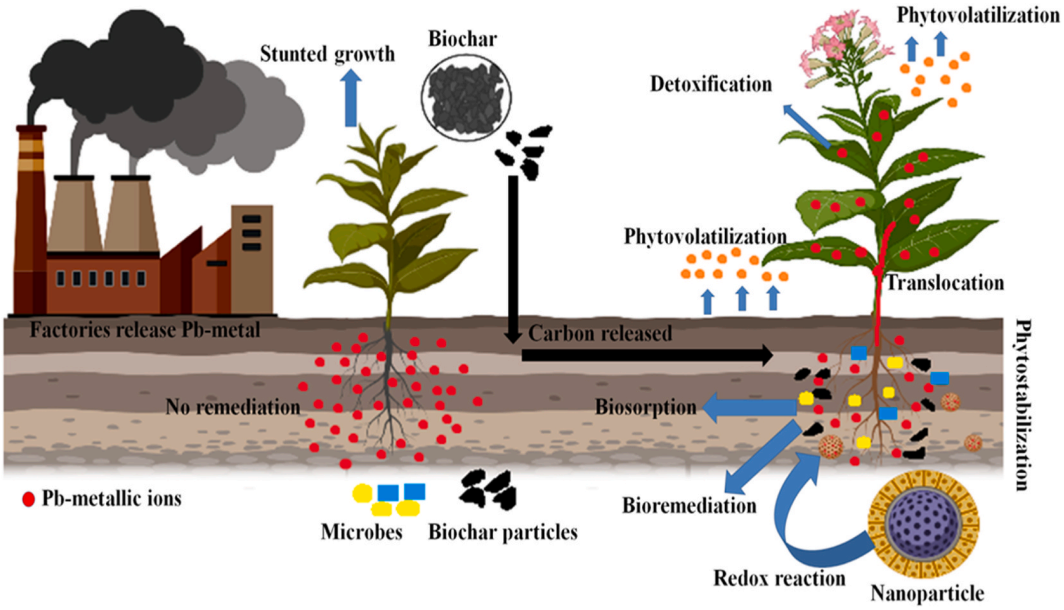

Fig. 3. Reduction of Pb accumulation in plants and soil through remediation techniques.

carboxylase oxygenase, Chl *a*, *b* binding proteins, glutathione peroxidase, and carbonic anhydrase have also been observed in Pb-stressed *S. salsa* plants [171]. Thus, the gene expression during Pb stress further confirmed the constancy of proteomic reactions. Moreover, Kumar and Majeti [168] conducted an experiment on a high level of proteins during the glycolytic pathways and carbohydrates metabolism, i.e., triosephosphate isomerase and 2,3-bisphospho glycerate independent phosphoglycerate mutase in *Talinum triangulare* after exposure to Pb metal. Different expressions of genes linked with glycolysis and metabolic pathways like glyceraldehyde 3-phosphate dehydrogenases, aldolases, S-adenosylhomocysteinases, glucose-phosphate isomerases, and enolases have also been identified in Pb stress conditions [168]. Further, it was proposed that during Pb stress conditions, the optimum performance of plants can be maintained by the upregulation of S-adenosylhomocysteinase which is considered as potential protein regulator in plant metabolisms.

8. Promising remediation strategies to reduce Pb toxicity in soil-plants system

Pb-metal is lethal to all living organisms, including plants, creating an alarming condition worldwide. It has long-term effects after its entrance into the soil environment because of its non-biodegradable property [172]. Ecologists have already developed numerous approaches to combat the Pb-metal, and some of them are already used but have not proved effective due to some technical and financial restrictions in their implementation [173]. Remediation of Pb-contaminated soils through thermal and chemical methodologies is ineffective as these are costly, difficult to operate, and cause soil degradation and sludge production [174]. Disposal of polluted soils after soil washing is also not useful as it deteriorates soil fertility due to the transportation of metals from one place to another [175]. Therefore, potential strategies are necessary for contaminated soils to avoid environmental disorders, as shown in Fig. 3. However, the following techniques can be used to reduce Pb toxicity in soil-plant systems.

8.1. Nano techniques

Nanotechnology approaches are one of the most modern strategies used to remove various contaminants from the soil environment and plants [176,177]. This technique uses nanoparticles, nanotubes, nanofiltration, carbon-based nanomaterials, nanocomposites, nanofibers, and nanoclusters [178]. Previously, HELAL, KHATER [179] performed an experiment to immobilize the Pb metallic ions in Pb-contaminated soils by using nanoscale zero-valent iron (nZVI), nZVI-bentonite, nanocarbon, and nanoalginites. Moreover, application of zinc oxide nanoparticles (ZnO NPs) with bacteria (Bacillus cereus and Lysinibacillus macroides) reduced Pb-toxicity and improved growth in *O. sativa* plants grown in Pb contaminated soils [180]. Previously, a study by Abdel-Razik, Azmy [181] reported that aerobic denitrification in *Halomonas* sp. strain WQL9 of halophilic bacterium resulted in the synthesis of lead (Pb) nanoparticles in cytoplasm and periplasm as a result of reduction of $(Pb(NO_3)_2$. Thus, nanotechnology is the advanced technique to remediate toxic metals from contaminated soils.

8.2. Remediation of Pb through stabilization/solidification technology

Solidification is one of the most appropriate techniques for the remediation of Pb-contaminated soils due to its effectiveness and suitability. It involves reducing Pb metallic element through different chemical additives such as zeolite, activated carbon, steel slag, clay, red mud, carbide slag, sand, lime, and cement [182,183]. However, it was also reported that cement and lime were effective in immobilization of Pb in artificially Pb-contaminated soil samples, while clay, activated carbon, sand, and zeolite were not effective in those soil samples [184]. Ge, Jiang [185] conducted an experiment to observe the stabilization/solidification of high Pb-contaminated soils using insoluble porous, neutral, and green material (humin) extracted from natural peat soils and found that humin reduced the bioavailability and mobility of Pb metallic ions due to its high adsorbent capacity, [185]. Wu et al. (2022) stated that solidification/stabilization technologies are attractive and economical options for the remediation of heavy metal contaminated soils, including Pb, and are expected to be progressively more used [186].

8.3. Biochar techniques

Multiple findings have reported that the application of biochar results in improving soil productivity through changes in soil structure, re-cycling of minerals nutrients (Si, P, and K), soil organic carbon (SOC) contents, and soil-pH [187]. Additionally, biochar application to contaminated soil is considered a promising approach for HMs, including Pb immobilization, because biochar can adsorb and immobilize HMs as its surface area (SA), microporosity, surface functional groups, pH, and cation exchange capacity are superior to those of raw feedstock [188]. Biochar surface has metallic cations, which may react with cations, anions, and organic contents in the soil solution, resulting in the formation of precipitates, i.e., lead hydroxyapatite is formed after reaction of phosphate ions with surface-absorbed Pb metal [189]. However, metal anions' adherent ability is less than that of cations [189]. Generally, Pb ions may attach to the clay particles through hydrogen, covalent, and ionic bonding [190]. The application of biochar improves plant growth by improving soil microbial activity, water-holding capacity, and soil structure in Pb-exposed soil [191]. Biochar has high porosity, CEC, pH, and active functional groups, which enable it to sustain Pb metallic ions [192]. The immobilization of Pb metallic ions in paddy field-soil and reduction in Pb-accumulation in paddy crops were found by Zhang, Wang [193] and Uchimiya, Chang [194], which might be because of change in soil CEC under biochar application. Long-term effects regarding the immobilization of Pb and its responses to biochar are not logically studied; however, limited studies, such as laboratory experiments with biochar modifications, exhibited a significant decrease in Pb contents in contaminated rice [193]. Therefore, inorganic as well as organic improvements along with biochar application are needed in several environmental conditions to improve and sustain the soil structure [195,196].

Several biochars may bind with other mineral items within the soil solution, consequently enhancing the efficiency of nutrients, but can decrease the nutrient accessibility to plants in barren-soils [197]. However, the use of organic amendments with biochar could be more useful in soil remediation techniques, as it retains equilibrium between nutrient acquirement and elimination or immobilization of contaminants like Pb [198]. Therefore, high CECs of biochar with organic amendments (such as compost) may be an attractive technique to remediate Pb-polluted soils. Still, there is a need to find the underlying mechanisms of how biochar with organic amendments can reduce soil contamination. In conclusion, biochar is an ecological-sound strategy to reduce Pb-contents from contaminated soils.

8.4. Plant growth regulators

Plant growth regulators (PGRs) are applied to improve plant tolerance against metal ions, particularly Pb [199]. The protective role of PGRs against Pb-uptake, accumulation and translocation within plant bodies varies with plant species and PGR types [200]. For instance, the application of PGR (nitric oxide) decreased oxidative stress in hydroponically grown *T. aestivum* plants under several levels of Pb toxicities [19]. Similarly, better growth and development were observed in *T. aestivum* after the application of polyamines in Pb-affected soil [201]. Wang conducted an experiment on applying exogenous indole-3-acetic acid in *Z. mays* grown under hydroponic conditions and found more Pb ions in the roots and less accumulation in shoots [202]. It was suggested that using brassinosteroids in Pb-contaminated soils reduced the Pb accumulation in *T. aestivum* [203]. The findings regarding PGRs studies on Pb-uptake have been presented in short-term hydroponic environments; thus, further long-term field studies are required for sustainability.

8.5. Phytoremediation techniques

Phytoremediation is a technique that involves plants (known as hyper-accumulators) that can uptake both inorganic and organic contaminants from contaminated soils and accumulate their high concentrations (more than 0.1%) in their different organs (roots, shoots, leaves). The technique involves phytoaccumulation, phytoextraction, phytovolatilization, phytodegradation, rhizodegradation, phytostabilization, and rhizofiltration for organic and inorganic contaminants [178]. In phytoremediation mechanisms, plants decontaminate or break down toxic metallic ions externally through chemicals/enzymes secreted by plant roots and internally through plant physiological activities [204,205].

This approach is widely applied for the eco-friendly restoration of Pb-contaminated soils, as the metallic elements are not biodegraded due to their inorganic nature [58]. The most extensively applied technique for Pb-phytoremediation is phytoextraction, in which plants extract the metallic ions, including Pb, from the soil profiles into their vegetative parts, which can be harvested through many agricultural practices. Pichtel and Bradway [206]) estimated the capabilities of *S. oleracea*, *B. oleracea*, *F. rubra*, *L. perenne,* and *V. faba* for phytoextraction of Pb metallic ions, and their results demonstrated that these plant species accumulated 8–467 mg kg^{-1} of Pb into their several plant organs depending on soil types, plant species, and environmental conditions from Pb-contaminated soils Phytoextraction abilities may vary from plant species to species. Salido, Hasty [207] observed that *B. juncea* exhibited high phytoextraction of Pb metallic ions as compared to *Z. mays*. Butcher [208]) stated that *Brassica carinata* showed maximum accumulation of Pb as compared to the other nine species of plants grown hydroponically.

Phytostabilization is another phytoremediation technique in which plants' adsorption and demobilization of toxins occur within the soil as plants limit their movement to other surroundings. Mainly, this type of phytoremediation includes plants that can adsorb and accumulate toxins within the roots, store them in the rhizosphere, restrict the movement of metallic ions, and hence lessen their accessibility to the plants [209,210]. Previously, Houben, Couder [211]) reported that *Armeria maritima* accumulates Pb metallic ions from metal-contaminated soils and decontaminate the soils through reducing Pb ions in the soils. In the case of rhizofiltration, the toxins and extra minerals present in the soil solutions are absorbed and sequestered into the plant roots [212]. Different plant species, including *B. juncea*, *H. annuus*, *Z. mays,* and *Nicotiana tabacum,* have been studied to eliminate Pb metallic ions, and it was found that *H. annuus* has the highest rhizofiltration ability [213].

Phytovolatilization involves the uptake of soil pollutants through plants, and then the contaminants are eliminated through volatilization. Generally it involves higher plants that take high water content besides toxic compounds from the soil through their roots and then remove them through transpiration [214]. However, in the rhizodegradation process, the soil pollutants are degraded through soil microorganisms existing within the plant root zones. Plant roots release some natural substances comprising sugar, alcoholic contents, carbon, and acids, which microorganisms use to attain their nutritional necessities [215]. Overall, phytoremediation is socially acceptable, cheapest, low-cost, and esthetically pleasant, which can be applied to amend contaminated soils.

Phytoremediation techniques are useful in concerning soil remediation in environmentally sound and economical ways, but here we also discussed definite restrictions that must also be acknowledged before applying them. First, it is a laborious technique that may take a long period to decontaminate a particular place, as mixtures of inorganic and organic toxic chemicals are present in the soils [216]. Secondly, the quantity of detoxified soil pollutants depends on the production of plant biomass as well as on yield, which might be influenced by various plant species, climatic conditions, soil toxicity level, and the plant's ability to remove the metal [217]. Third, root contamination and plant root depth are essential to access soil contaminations. Plants with shallow roots detoxify soils from toxins in the upper layers, whereas lower soil layers need deep-rooted plants to decontaminate pollutants [218]. Fourth, phytoremediation is dependent on specific metallic ions to detoxify in soil, contamination level, and plant age; for example, weak and older trees might eliminate lesser metallic components than young and healthy ones [219]. Finally, the plants harvested from toxic soils can be considered lethal waste, so they must be thrown away properly; on the other hand, using such plants may lead to the entry of pollutants into the food-web, which could again be a serious risk.

9. Conclusion and future strategies

In conclusion, the current review highlights the environmental consequences of Pb on soil-plant systems. The findings from the literature on Pb effects and its biogeochemical nature can be summarized as follows.

1. Despite its usefulness, Pb accumulation in soil systems through various industries has led to severe environmental issues.
2. Pb binds with soil particles and forms various complexes that affect soil health. However, different factors, including soil structure, texture, pH, CEC, and living biota in soil, regulate the transport and bioavailability of Pb.
3. Generally, Pb accumulates in the root cells after entering through the roots, while a very small portion is translocated to the shoot due to natural endodermis barriers.
4. Accumulation of Pb in plants leads to negative effects on plant growth and development, like seed germination, root elongation, plant biomass, chlorophyll biosynthesis, enzymatic reactions, and nutrient availability.
5. Pb-induced production of reactive oxygen species (ROS) that disrupts the oxido-reduction processes in cells, resulting in oxidative stress, DNA injury, metabolic deterioration, and cell death.
6. Plants use various detoxification mechanisms to tackle Pb toxicity, such as binding Pb to cell walls and activating the antioxidative enzymes to counteract ROS formation. Some plants with efficient detoxification abilities, known as hyperaccumulators, are used for bioremediation. Various approaches, like phytoremediation, phytoextraction, nanotechnologies, etc., can remediate Pb-contaminated soils.

Based on scanning the literature, many questions were raised that are still unanswered because of complex interactions between Pb and the soil systems. The various metabolic mechanisms of action against the toxic behavior of Pb-metal in plants are still unidentified. Therefore, studies regarding the biogeochemical behavior of Pb in various environments, direct and indirect effects on the plant genetic makeup, and the underlying mechanisms regarding Pb toxicity in plants must be conducted for sustainable and eco-friendly soil-plant systems. Furthermore, the investigations focusing on the sorption and speciation of Pb in different plant species should be made in realistic environmental conditions to enhance the understanding of the ecological influences of Pb and to develop potential strategies for its mitigation.

10. Summary

Pb metal, the most toxic persistent, an important industrial and structural material, comes into the soil through anthropogenic and pedogenic activities. The objective of the recent review is to report the uptake process of Pb metallic ions and their toxicological effects in plants. Furthermore, we discussed the detoxifying agents responsible for detoxifying or resisting the toxicological effects of Pb-metal. Pb has many stimulating chemical and physical characteristics, making it an advantageous metallic element. However, it has been used by humans from the beginning of human culture. Many other anthropogenic events, such as urbanization, industrialization, and mining, have caused the rearrangement of Pb-metallic elements from the earth's crust to the environment and the soil. Pb makes different complexes with soil constituents, while a few of these complexes in the soils are considered photo-available. In spite of its absence of a necessary role in plants, it is up taken by them mostly through the root cells from the rhizosphere and consequently may enter the food web. Pb-uptake by roots happens through symplastic or apoplastic pathways. Pb-ions' performance in the soil and plant uptake is accomplished by their speciation and particle size of soil, soil-pH, CEC, root exudation, rhizosphere, and extent of plant transpiration. Pb-ions mainly accumulate in the roots after their uptake through soil solutions due to the barriers caused by Casparian strips within the root endodermis. Moreover, root cell walls have negative charges, which cause the blockage of Pb-ions. High accumulation of Pb-ions in plant tissues damages directly or indirectly and disrupts physiological, biochemical, and morphological functions. Pb-ions react with phosphate groups of ADP or ATP or with various enzymes of plant metabolism, and they also alter the cell membrane structure, which ultimately causes phytotoxicity. Toxicological effects of Pb ions include DNA denaturation by overproduction of ROS, lipid peroxidation, and inhibition of ATP production. Moreover, Pb-ions strongly inhibit plant growth, seed germination, seedling development, root elongation, chlorophyll production, transpiration, and protein and water contents. It also causes harmful effects on the vegetative parts due to the following aspects: obstructed electron transport, alteration of chloroplastids, weakened uptake of mineral ions like iron and magnesium, induced deficiency of CO_2 due to stomatal closure, and disturbance of enzymes involved in Calvin-cycle. Plants have numerous defense approaches to resist the Pb-toxic effects in Pb-stressed environments. These strategies are sequestration of Pb into vacuoles by the complex formations, less Pb-uptake into the cell, synthesis of osmolytes, and binding of Pb-ions by glutathione, amino acids, and phytochelatins. Furthermore, the activation of different antioxidative enzymes to cope with the high assemblage of Pb-prompted ROS contents is a secondary defensive mechanism. However, it was recommended that some remedial techniques be applied to reduce Pb metallic elements from the soil and plants through phytoremediation, phytoextraction, phytovolatilization, biochar applications stabilization/solidification nanotechnologies, etc. Phytoextraction, biochar, and nano techniques are ideal for decontaminating Pb from contaminated soils. Lastly, the implementation of the principles of sustainable progress and change in human behavior can help in the holistic management of all ecological difficulties.

Data availability statement

All data required to support this study is already mentioned in the manuscript.

CRediT authorship contribution statement

Shafeeq Ur Rahman: Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Anzhen Qin:** Resources, Project administration, Investigation. **Muhammad Zain:** Visualization, Validation, Resources. **Zain Mushtaq:** Writing – review & editing, Investigation, Data curation. **Faisal Mehmood:** Writing – review & editing, Visualization, Validation. **Luqman Riaz:** Writing – review & editing, Visualization, Validation, Software. **Sadiq Naveed:** Writing – review & editing, Validation, Formal analysis, Data curation. **Mohammad Javed Ansari:** Writing – review & editing, Visualization, Validation, Software, Resources. **Mohd Saeed:** Writing – review & editing, Visualization, Validation, Software, Resources. **Irfan Ahmad:** Writing – review & editing, Validation, Software, Resources. **Muhammad Shehzad:** Validation, Supervision, Software.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

The authors extend their appreciation to the Agricultural Science and Technology Innovation Program (No. ASTIP) of CAAS, and the National Agricultural Key & Core Technology R&D Program (No. NK202319080301). The authors are thankful to the Deanship of Scientific Research, King Khalid University, Abha, Saudi Arabia, for financially supporting this work through the small Research Group Project under Grant no. R.G.P.1/323/44.

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