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INFLUENCE OF LEAD POLLUTION ON THE GROWTH, DEVELOPMENT, AND METABOLISM OF CEREAL CROPS: THE PROTECTIVE ROLE OF SALICYLIC ACID

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Cereal crops are the world's main source of food. They provide more than half of the world's total calorie needs. Sustainable access to quality cereals is important in addressing food security challenges. Soil contamination with lead (Pb) seriously threatens sustainable cereal production. In Ukraine, this problem has become particularly acute due to the intense hostilities. By inhibiting important functional groups in proteins, displacing critical metal ions, and accumulating reactive oxygen species, lead, a non-essential heavy metal, has a complicated harmful effect on plant organisms. According to studies, lead considerably reduces the germination of seeds and the growth of cereal seedlings; the degree of this effect varies according to the concentration, length of exposure, and type of plant. At high concentrations of Pb, seed germination decreases by 30—40 %, root length decreases by 45 %, and the stress resistance index decreases significantly. At the cellular level, Pb disrupts the structure and functions of photosystems, causes oxidative stress, destabilizes membranes, and loses the integrity of cellular organelles. Salicylic acid (SA), a phenolic plant hormone, plays a key role in the regulation of numerous plant physiological processes, including growth and development, photosynthesis, respiration, transpiration, and provides for the formation of defense responses, increasing the resistance of cereals to a wide range of abiotic and biotic stressors. The SA plays a special role in shaping the resistance of cereals to Pb contamination through its participation in the transmission of stress signals, antioxidant defense mechanisms and modulation of physiological processes. In this review, we present a contemporary summarization of existing data on the impact of Pb toxicity on morphophysiological and biochemical responses of major cereal crops. We also highlight the data on the mechanisms of lead ion uptake and translocation in plants, critically discuss possible strategies for phytoremediation of soils and ways to overcome the threat of lead toxicity for cereals.

Key words: cereal crops, lead contamination, salicylic acid, growth, metabolism, tolerance.

The toxic effects of heavy metals (HMs) on plants are attracting considerable attention worldwide as they directly threaten the food supply [1, 2]. Among these, soil contamination with lead (Pb) poses a serious risk to cereal crops' growth, development, and productivity. As a non-essential

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heavy metal, Pb disrupts plant metabolic processes, leading to toxicity [3, 4]. Among the metal pollutants, Pb is the most worrisome due to the scale and intensity of its impact. In soil, Pb^{2+} ions, like most metals, are present in various substances, but not all of them are equally available for plant assimilation.

The extent of Pb absorption by plants depends on the soil's physico-chemical properties, including pH, cationic composition, and soil particle characteristics that influence metal bioavailability [5, 6]. Pb accumulation is most intense in acidic soils with low phosphate and sulfate concentrations [7]. Absorbed Pb^{2+} ions interfere with the uptake of essential macro- and micronutrients such as calcium (Ca), iron (Fe), magnesium (Mg), manganese (Mn), phosphorus (P), and zinc (Zn), leading to nutrient deficiencies and impaired cereal growth and development [8, 9, 10].

Cereals play a crucial role in global food security due to their high yield, resource efficiency, storage stability, and nutritional value. However, their interaction with HMs, particularly Pb, has complex implications for agriculture, nutrition, and human health. As the global population continues to grow, ensuring the sustainable production of cereals remains vital for addressing hunger, malnutrition, and food insecurity [11]. According to WHO/FAO statement [12], the permissible Pb content in cereal grains should not exceed 0.20 mg/kg.

Cereal crops exhibit varying responses to Pb toxicity and can be classified as metal excluders, indicators, or accumulators. Excluders prevent metal uptake and translocation to shoots, indicators reflect accumulated HM levels (detectable via aerial imaging), and accumulators absorb, transport, and store metal ions at concentrations higher than those in the surrounding soil [13, 14].

In Ukraine, lead contamination of agricultural soils is increasingly linked to military activities during the large-scale Russian-Ukrainian war [15, 16]. This review aims to analyze and summarize current research of Pb effects on the growth, development, and metabolism of key cereal crops — wheat, maize, and rice — along with its uptake, translocation, adaptation mechanisms, and strategies for mitigating its toxicity. Our review focuses on cereal crops, but lead contamination is a broader issue affecting other plant species and entire ecosystems.

Impact of lead pollution on seed germination and seedling growth of cereals. Lead pollution has a detrimental impact on the morphology and physiology of seeds [17]. It inhibits germination, root elongation, seedling development, plant growth, transpiration, chlorophyll biosynthesis, and the water and protein content of plants. These effects occur due to lead-induced changes in chloroplast structure, interference with the electron transport chain, inhibition of Calvin cycle enzymes, disruption of essential element uptake (Mg and Fe), and CO_2 deficiency caused by stomatal closure [18].

The extent of lead's impact on seed germination and growth depends on species characteristics, plant developmental stage, metal concentration, and exposure duration [19]. Lead inhibits protease and amylase activity, slowing the utilization of nutrients stored in the endosperm [20]. Nolan et al. [21] found that in winter wheat, Pb phytoavailability is determined by its concentration in the soil solution, rather than its supply from the solid phase. Kanwal et al. [22] reported that lead reduced winter wheat grain germination by 30 % and significantly affected morphophenological traits. Biomass accumulation decreased, the stress resistance index dropped by 84 %, and root length was reduced by 45 %. Additionally, the number and weight of grains per plant, 1000-grain weight, and yield index declined by 90 %, 88 %, 44 %, and 61 %, respectively. Similar findings were reported by Yang et al. [23], who observed that high Pb concentrations suppressed grain germination and root and shoot growth in winter wheat while increasing reactive oxygen species (ROS) accumulation in grains and root tissues. Li et al. [24] found that low Pb concentrations in soil (up to 0.5 mg/kg) had a minor negative effect on the germination index and energy of durum wheat grains. However, concentrations above 4.5 mg/kg significantly inhibited germination [25].

Research has shown that only 2 % to 5 % of the total Pb absorbed by maize is transported from roots to leaves [26]. When soil contained 30 ppm Pb, maize hybrid productivity decreased by 76—85 % [26]. Lead concentrations were significantly higher in the roots of wheat and maize than in grains [27]. Germination of maize kernels was severely inhibited when exposed to a $Pb(NO_3)_2$ contamination gradient of 1000—3000 mg/L in a Hoagland nutrient solution. At Pb concentrations below 100 mg/L, root length, diameter, and surface area increased, but these traits gradually declined as Pb levels rose. Low Pb concentrations ($<$ 60 mg/L) stimulated shoot growth, whereas concentrations of 3000 mg/L inhibited it [28].

Gupta et al. [29] found that high Pb concentrations (1 mM) reduced rice germination by 14—30 % and suppressed seedling growth by 13—45 %. Different rice varieties responded variably to soil Pb contamination (800 mg/kg), with yield changes primarily attributed to variations in spikelet number per panicle. These changes were positively correlated with straw dry weight. Lead uptake and translocation varied significantly, with Pb concentrations declining from root to grain. Regression analysis revealed negative correlations between Pb content in adjacent organs and positive correlations between isolated organs in rice plants [30].

Thus, lead pollution induces various morphological changes in wheat, maize, and rice, including delayed germination, reduced seedling growth, biomass suppression, and impaired root development. These alterations serve as visual stress indicators and provide valuable insights into the severity of environmental Pb contamination.

Impact of lead pollution on metabolism of cereals. Elevated Pb concentrations disrupt natural physiological processes, reduce enzyme activity, interfere with nutrient uptake and hydration, and alter cell membrane permeability, ultimately leading to plant decline or death. Three primary molecular mechanisms of Pb toxicity have been identified: accumulation of reactive oxygen species (ROS), blockage of key functional groups in biomolecules, and displacement of essential metal ions (Fig. 1).

Pb, present as cations in various physiological processes, negatively affects wheat germination, seedling growth, photosynthesis efficiency, mineral nutrition, and enzymatic activity [31]. By accelerating hydroxyl radical accumulation, Pb induces oxidative damage in plants [32], disrupting

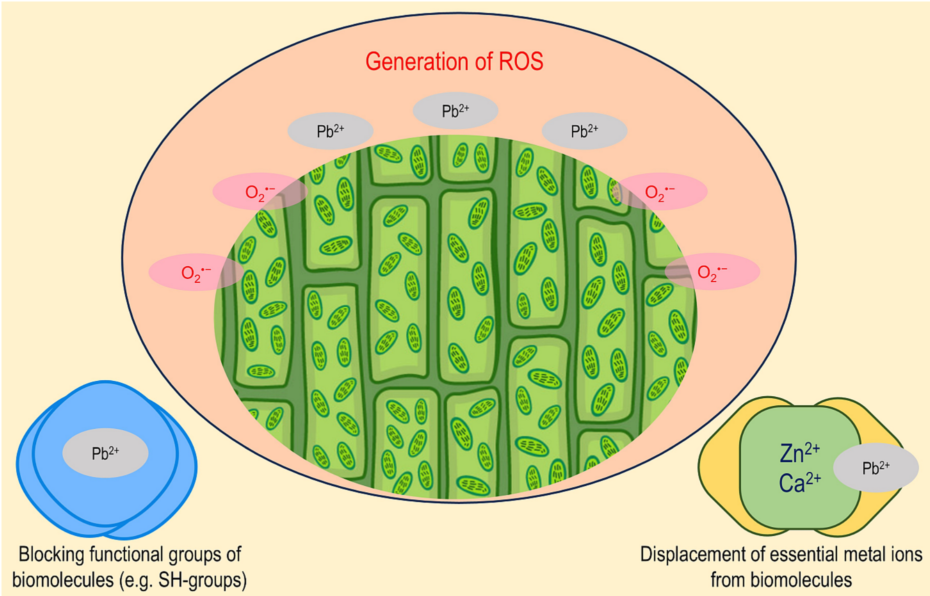

Fig. 1. Molecular mechanisms underlying Pb toxicity in cereals

macromolecular structures and impairing metabolic enzyme function. This results in reduced photosynthetic activity, ATP synthesis, and overall plant growth [33]. Pb accumulation in cereal tissues triggers oxidative stress by increasing ROS production [8, 34], leading to damage of biopolymers, lipids, proteins, and nucleic acids, ultimately impairing photosynthesis and respiration (Fig. 2). The antioxidant system, particularly catalase and superoxide dismutase (SOD), plays a crucial role in mitigating Pb-induced oxidative stress by minimizing cellular damage [18, 34]. Pb disrupts the photosynthetic apparatus, inhibits chlorophyll biosynthesis, and slows car-

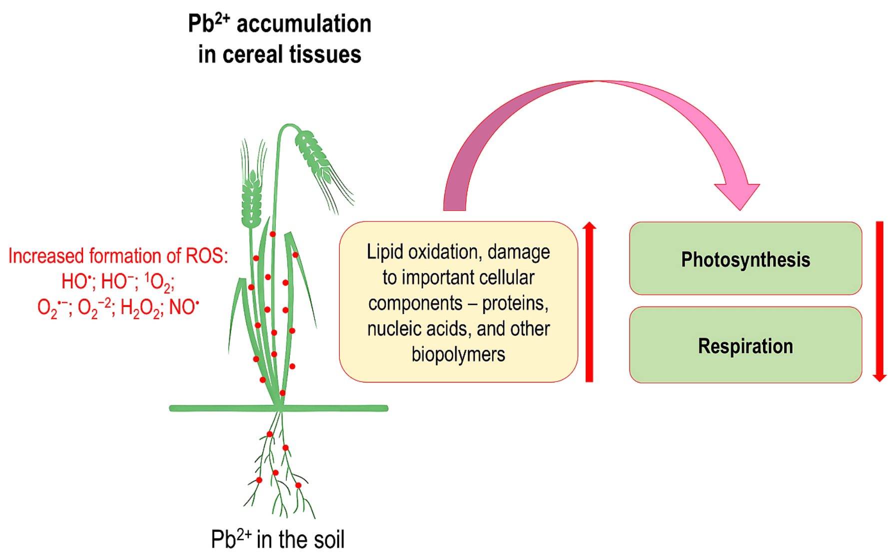

Fig. 2. Impact of lead pollution-induced oxidative stress on biopolymers and key physiological processes in cereals

bon metabolism [35], leading to chlorosis and reduced photosynthetic efficiency [5, 6]. Additionally, Pb-induced membrane damage disrupts water balance and nutrient transport in the xylem [8, 34, 36].

Plants have evolved protective mechanisms against Pb toxicity, including the synthesis of antioxidants and phytochelatins, which bind and detoxify heavy metals [18, 37]. Pb remains largely excluded from mature plant cell protoplasts, whereas actively dividing cells are more vulnerable [5].

Kanwal et al. [22] reported that high Pb concentrations (1000 mg/L) in wheat reduced stomatal conductance by 82 %, transpiration rate by 72 %, and photosynthesis rate by 74 %. Carotenoid content decreased by 41 %, chlorophyll *a* by 42 %, and chlorophyll *b* by 53 %. Pb toxicity hinders plant growth due to impaired nutrient uptake and transport [38]. Reduced seed germination and plant growth under Pb stress result from enzyme inhibition, membrane damage, and stomatal closure, mediated by ABA synthesis and Pb negative correlation with potassium [35]. Pb also interferes with chlorophyll, carotenoid, and plastoquinone biosynthesis, reduces photosynthetic enzymes activity, and disrupts respiration by altering mitochondrial cristae density [29]. Increased chlorophyllase activity under Pb stress accelerates chlorophyll breakdown [39]. Reduced chlorophyll levels, altered antioxidant enzyme activity, and differential gene expression have been observed in wheat leaves and roots, with higher responses in roots [40]. Photosystem I is less susceptible to Pb inhibition than photosystem II [41]. Pb also disrupts the mitochondrial electron transport chain, impairing cellular respiration and energy production [42].

Zeng et al. [43] found that low Pb concentrations (100—300 mg/kg) enhanced soil enzymatic activity and microbial biomass carbon accumulation, while high concentrations (500—900 mg/kg) inhibited these processes, posing ecological risks to soil microorganisms and plants. Initially, Pb increased chlorophyll content and rice biomass, but both declined at higher concentrations. Pb-induced oxidative stress also led to proline accumulation in rice plants.

Ashraf et al. [44] reported decreased chlorophyll and carotenoid content and increased hydrogen peroxide accumulation in rice exposed to 400—1200 ppm Pb. Pb stress altered the activities of SOD, peroxidases (POD), catalases (CAT), and ascorbate peroxidase (APX), and affected glutathione (GSH) and oxidized glutathione (GSSG) levels. Pb exposure reduced rice yield and grain quality, with Pb accumulating primarily in roots, followed by stems, leaves, ears, and grains.

Heavy metal pollution also affects phytohormone metabolism, increasing levels of abscisic acid, salicylic acid, brassinosteroids, ethylene, and jasmonates while reducing auxins, cytokinins, and gibberellins. Lower levels of growth-promoting hormones inhibit plant growth, enabling stress adaptation and recovery once Pb toxicity diminishes. Complex hormonal interactions activate protective and stress-response mechanisms [45, 46].

Thus, Pb pollution severely disrupts photosynthesis, respiration, enzymatic activity, membrane integrity, water balance, electron transport, and hormonal regulation in cereal crops (Fig. 3).

Protective role of salicylic acid. Salicylic acid (SA) is a phenolic phytohormone synthesized in plants primarily through the phenylpropanoid pathway [47]. It plays a crucial role in regulating various physiological

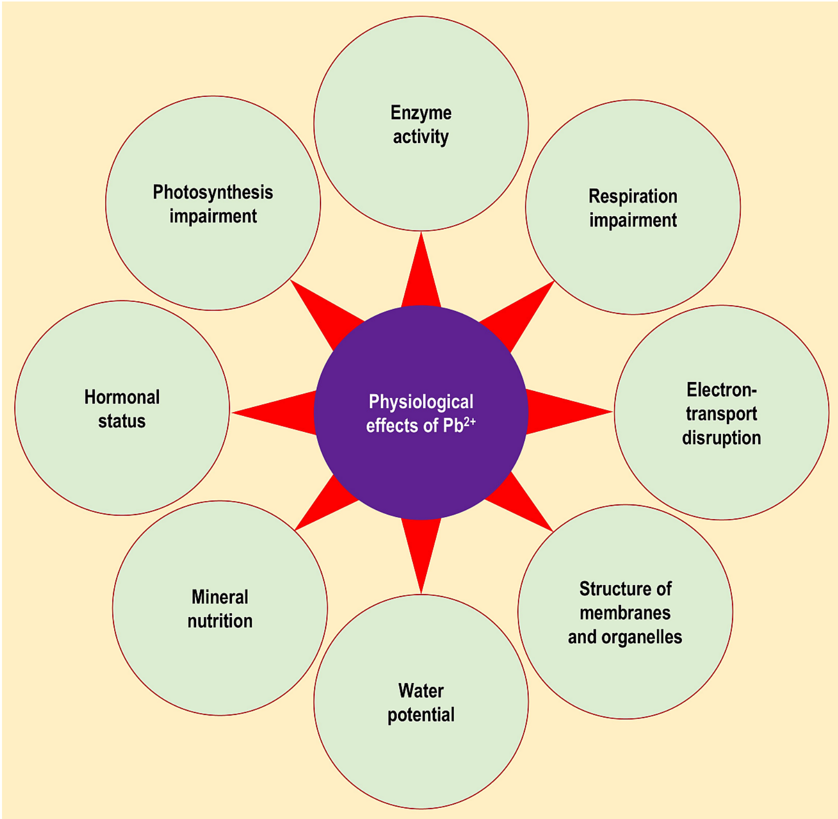

Fig. 3. Effects of lead pollution on the metabolism of cereals

processes, including growth, photosynthesis, respiration, and transpiration, while also enhancing plant defense responses against abiotic and biotic stressors [2]. SA is particularly involved in responses to drought, low temperatures, heavy metal toxicity, and osmotic stress [48]. In rice, barley, and soybean, SA content has been reported to reach 1 μg/g of fresh weight. Together with ethylene and jasmonic acid, SA is a key component in plant resistance to environmental stressors, including heavy metal pollution [49]. Regardless of whether SA interacts synergistically or antagonistically with ethylene, jasmonic acid, and abscisic acid, their combined action regulates plant responses to stress [50]. SA is particularly important in mitigating Pb toxicity by modulating stress signaling pathways, enhancing antioxidant defense, and stabilizing physiological processes. Under Pb pollution, which induces oxidative stress and metabolic imbalances, SA reduces damage and improves stress tolerance [2].

Antioxidant defense mechanism. SA enhances Pb tolerance primarily by strengthening the plant's antioxidant system. It stimulates the activity of key antioxidant enzymes, such as superoxide dismutase and peroxidase, which play critical roles in neutralizing ROS [51, 52]. Increased antioxidant activity helps reduce oxidative stress, protect cellular structures, and maintain metabolic stability [53]. SA has also been found to regulate the expression of genes involved in antioxidant defense, further enhancing resistance to oxidative stress [54].

Regulation of physiological processes. Beyond antioxidant protection, SA significantly influences physiological processes that determine plant growth and development under Pb stress. It has been shown to improve photosynthetic efficiency, stimulate root growth, and enhance biomass accumulation in maize exposed to heavy metals [55]. This is particularly important, as Pb pollution inhibits root system development and nutrient uptake, leading to stunted growth and reduced yields [56]. SA application not only mitigates these negative effects but also enhances plant productivity under Pb stress (Fig. 4).

SA also plays a critical role in maintaining ion homeostasis, essential for cellular function under heavy metal stress. It regulates the uptake and translocation of Pb and other heavy metal ions, potentially reducing their accumulation in plant tissues [57].

Impact on photosynthesis and stomatal regulation. SA regulates photosynthesis by influencing stomatal closure, chloroplast structure, and key photosynthetic enzymes such as ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and carbonic anhydrase [58]. SA treatment has been shown to improve plant physiological, morphological, and biochemical traits, ultimately increasing crop yields. Under abiotic stress, SA application enhances growth in maize [59] and rice [60]. Foliar application of SA induces SOD production in maize leaves [58], while seed priming with SA promotes photosynthetic activity, yield, and polyamine accumulation (putrescine, spermidine, spermine) in maize roots, further boosting stress tolerance [61]. Notably, seed priming with SA has been reported to be more effective than foliar application [59].

Chelating effects and hormonal signaling. The chelating effect of SA helps reduce the bioavailability of Pb, minimizing its toxic effects on plants. As a signaling molecule, SA increases plant resistance to Pb stress by regulating the expression of a number of regulatory and signaling genes, making it an effective compound for protecting cereals from HM [62].

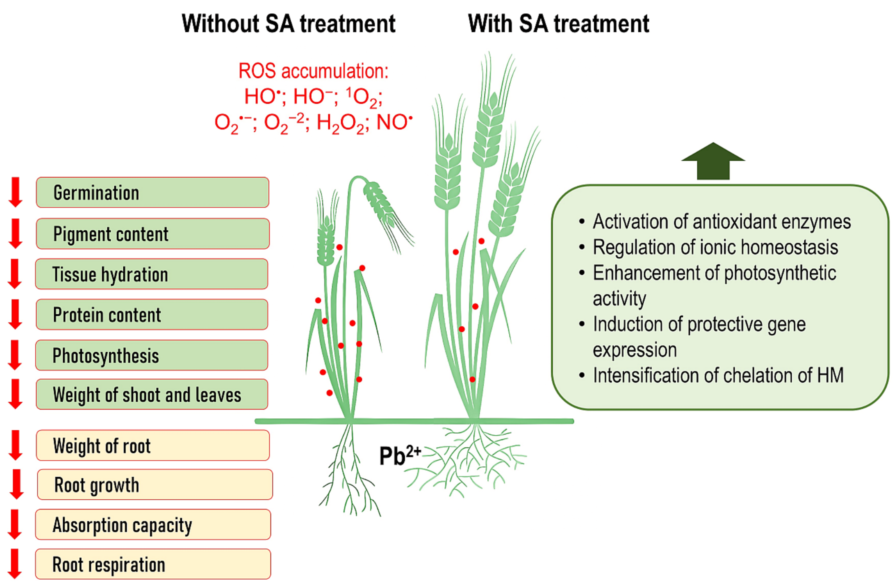

Fig. 4. The role of salicylic acid in enhancing plant resistance to stress caused by Pb exposure

Exogenous SA treatment triggers acclimatization mechanisms by activating hormonal signaling pathways, leading to increased expression of stress-responsive genes and biosynthesis of protective enzymes. In Pb-exposed plants, SA improves growth performance, boosts carbohydrate and nitrogen metabolism, and activates key enzymes such as catalase, peroxidase, SOD, and nitrate reductase. SA also helps normalize malondialdehyde levels, ROS accumulation, and electrolyte leakage, further mitigating Pb toxicity [2].

Potential risks of high SA concentrations. While SA is beneficial at optimal concentrations, excessive levels can be harmful. High SA concentrations may exacerbate oxidative stress by increasing ROS production in photosynthetic tissues, leading to cellular damage and tissue death [63]. Under severe abiotic stress, excessive SA can intensify ROS accumulation, resulting in widespread cellular damage [64]. Therefore, careful regulation of SA concentrations is essential for effectively managing Pb-induced oxidative stress and mitigating its harmful effects.

Phytoremediation in the control of lead contamination of soils. Phytoremediation is a promising approach for combating lead contamination in soils. This environmentally friendly technology utilizes plants to remove, stabilize, or detoxify heavy metals from polluted environments. Of particular interest are hyperaccumulator species, which can accumulate significant amounts of Pb, though this process is often accompanied by growth inhibition and metabolic disruptions [65, 66]. Notably, only about 0.2 % of angiosperms exhibit hyperaccumulation of HM ions [67]. The success of phytoremediation largely depends on the plant's ability to maintain essential metabolic functions despite Pb toxicity [66, 68].

The primary mechanism behind phytoremediation is phytoextraction, in which plants absorb Pb^{2+} from the rhizosphere or water and accumulate it in their biomass, significantly reducing environmental pollution [69]. Several factors influence the effectiveness of phytoremediation, including plant species, soil type, and the presence of rhizosphere bacterial communities that enhance HM uptake [70]. The ability of hyperaccumulators to compartmentalize HMs within their cells is critical for survival in contaminated environments. For example, *Sedum alfredii* (Crassulaceae) can store Pb and other HMs in vacuoles, facilitating detoxification and reducing toxicity [71]. This trait is essential for developing sustainable phytoremediation strategies, as it minimizes metal-induced damage and maintains plant growth.

Hyperaccumulator species and their Pb uptake capabilities. Various plant species have been identified as Pb hyperaccumulators, each with unique mechanisms for Pb uptake and accumulation. Let's list the most known ones.

Mustard greens (*Brassica juncea*, Brassicaceae) accumulate Pb in tissues at concentrations exceeding 600 mg/kg dry weight (DW) in stems and 3500 mg/kg DW in roots [72]. Its high tolerance to Pb while maintaining normal growth makes it a valuable phytoremediation candidate.

Common buckwheat (*Fagopyrum esculentum*, Polygonaceae) exhibits impressive Pb accumulation, reaching 8000 mg/kg (DW) in leaves, 2000 mg/kg in stems, and 3300 mg/kg in roots [73].

Common wheatgrass (*Agrostis tenuis*, Poaceae) and red spinach (*Amaranthus dubius*, Amaranthaceae) efficient at Pb^{2+} uptake from soil, though they have lower translocation efficiency to aerial parts [74, 75].

Thlaspi rotundifolium, hardy perennial plant from Brassicaceae can accumulate 8200 mg/kg DW of Pb in shoot tissues [76, 77].

Poisonbean (*Sesbania drummondii*, Fabaceae) accumulates Pb primarily as acetate salt in tissues [78].

Floating fern common salvinia or water spangles (*Salvinia minima*, Salviniaceae) is known for its strong Pb adsorption capacity, reaching 4000 mg/kg DW in tissues [79, 80].

Tufted hairgrass (*Deschampsia cespitosa*, Poaceae) accumulates up to 520 mg/kg Pb in shoots and 4915 mg/kg in roots [81].

Sand rock-cress (*Cardaminopsis arenosa*, Brassicaceae) stores 579 mg/kg Pb in shoots and 2123 mg/kg in roots [82].

Euphorbia cheiradenia, Euphorbiaceae grows on contaminated soil, it reduced Pb concentrations from 42.2 ppm to 11.88 ppm [83].

Tatar buckwheat (*Fagopyrum tataricum*, Polygonaceae) — nutritionally valuable crop with strong Pb hyperaccumulation potential. It possesses efficient Pb detoxification mechanisms, including osmolyte production and a robust antioxidant defense system [32].

Therefore, the use of HM hyperaccumulator plants offers a sustainable and eco-friendly approach to soil remediation. These plants exhibit stress resistance, rapid growth, significant biomass production, and adaptability to diverse climatic and geological conditions. Lead hyperaccumulation remains a critical area of research aimed at refining phytoremediation strategies for effective HM removal from contaminated environments.

Conclusion. Enhancing land resource efficiency and improving crop quality are among the key challenges facing modern agriculture. The contamination of terrestrial and aquatic ecosystems with heavy metals necessitates the development of environmentally friendly technologies to mitigate their negative impact. Research in this field has significantly advanced our understanding of the mechanisms underlying HM absorption, transport, and detoxification in plants.

Phytohormones play a crucial role in plant signaling systems, regulating responses to environmental stressors. Lead pollution induces numerous morphological and physiological disruptions in cereal crops, including inhibited germination, reduced seedling growth, impaired biomass accumulation, and restricted root development. Pb toxicity also affects essential physiological processes such as photosynthesis, respiration, enzymatic activity, membrane integrity, water potential, electron transport, and hormonal balance.

Salicylic acid (SA) is instrumental in mitigating Pb-induced oxidative stress by activating hormonal signaling pathways, inducing stress-responsive gene expression, and enhancing the biosynthesis of antioxidant enzymes. SA treatment significantly improves plant growth, increases carbohydrate and nitrogen compound accumulation, and enhances overall stress resistance. While phytohormone treatment cannot fully counteract the adverse effects of HMs on nutrient transport, it can reduce HM ion uptake, limit their translocation from roots to shoots and leaves, and thus mitigate toxicity.

Phytoremediation is a promising strategy for addressing lead contamination in soils. This technology leverages the ability of plants to extract, stabilize, or sequester heavy metals from polluted environments. Hyperaccumulator species, particularly those in the Poaceae family, are of special interest due to their capacity to accumulate substantial amounts of Pb in their biomass. Their unique physiological adaptations make them valuable tools for sustainable soil remediation and environmental protection.

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ВПЛИВ ЗАБРУДНЕННЯ СВИНЦЕМ НА РІСТ, РОЗВИТОК І МЕТАБОЛІЗМ КУЛЬТУРНИХ ЗЛАКІВ: ЗАХИСНА РОЛЬ САЛІЦИЛОВОЇ КИСЛОТИ

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Культурні злаки є головним джерелом продовольства у світі. Вони забезпечують більше половини загальної потреби людства в калоріях. Для вирішення проблеми продовольчої безпеки необхідно забезпечити стабільне постачання якісного зерна. Забруднення ґрунтів свинцем (Pb) є значним викликом для довгострокового виробництва зернових. В Україні ця проблема набула особливої гостроти через інтенсивні бойові дії. Свинець, як неесенціальний важкий метал, спричиняє комплексний токсичний вплив на рослинний організм через три основні молекулярні механізми: накопичення активних форм кисню, блокування ключових функціональних груп у біомолекулах та витіснення іонів біологічно важливих металів. Дослідження показали, що свинець істотно пригнічує проростання насіння й ріст проростків злаків, причому інтенсивність впливу залежить від концентрації, тривалості експозиції та видових особливостей рослин. За високого вмісту в середовищі Pb, проростання зернівок знижується на 30—40 %, довжина коренів зменшується на 45 %, значно падає індекс стресостійкості. На клітинному рівні Pb порушує структуру і функції фотосистем, спричиняє оксидативний стрес, відбувається дестабілізація мембран, втрачається цілісність клітинних органел. Саліцилова кислота (СК) — фітогормон фенольної природи — відіграє ключову роль у регуляції численних фізіологічних процесів рослин, включно ріст і розвиток, фотосинтез, дихання, транспірація, та забезпечує формування захисних реакцій, підвищуючи стійкість злаків до широкого спектра абіотичних і біотичних стресорів. Особливу роль СК відіграє у формуванні стійкості злаків до забруднення Pb через її участь у передачі стресових сигналів, механізмах антиоксидантного захисту й модуляції фізіологічних процесів. У цьому огляді ми представили сучасне узагальнення існуючих даних щодо впливу токсичності Pb на морфофізіологічні та біохімічні реакції основних зернових культур. Також висвітлюються дані про механізми поглинання й транслокацію іонів свинцю в рослинах, критично обговорюються можливі стратегії фіторемедіації ґрунтів та шляхи подолання загрози токсичності свинцю у зернових культур.

Ключові слова: зернові культури, забруднення свинцем, саліцилова кислота, ріст, метаболізм, стійкість.

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