



Feature Review

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Heavy Metal Tolerance in Aquatic Plants: Physiological Adaptations and Detoxification Strategies

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Abstract This study explores the physiological adaptations and detoxification strategies of aquatic plants, focusing on key mechanisms such as chelation, sequestration, antioxidant defense systems, and the role of phytochelatins and metallothioneins. Key findings highlight the critical roles of antioxidant enzymes, cellular compartmentalization, and metal-binding peptides in mitigating heavy metal toxicity. Case studies on freshwater and marine plants, including Canadian waterweed (*Elodea canadensis*), *Posidonia oceanica*, Eelgrass (*Zostera marina*) and duckweed (*Lemna minor*), provide unique insights into species-specific and shared tolerance mechanisms. Understanding these mechanisms is crucial for advancing phytoremediation technologies and offers potential applications in environmental management. By understanding these mechanisms and focusing on molecular and genetic advancements, we can enhance the efficacy of phytoremediation strategies, contributing to the sustainable management of heavy metal pollution in aquatic environments.

Keywords Aquatic plants; Heavy metal tolerance; Phytoremediation; Antioxidant defense systems; Phytochelatins; Metallothioneins

1 Introduction

Heavy metal pollution in aquatic ecosystems has become a significant environmental concern due to its persistent and toxic nature. Industrialization, urbanization, and agricultural activities have led to the release of heavy metals such as cadmium, lead, mercury, and arsenic into water bodies, causing severe contamination (Kahlon et al., 2018; Shrestha et al., 2021). Unlike organic pollutants, heavy metals cannot be degraded and thus accumulate in the environment, posing long-term risks to aquatic life and human health (Dixit et al., 2015; Nguyen et al., 2020). The bioaccumulation and biomagnification of these metals in the food chain further exacerbate their impact, leading to detrimental effects on aquatic biota and ecosystems (Kahlon et al., 2018).

Aquatic plants, particularly macrophytes, have shown remarkable potential in mitigating heavy metal pollution through phytoremediation. This green technology leverages the natural ability of plants to absorb, accumulate, and detoxify heavy metals from contaminated water and sediments (Demarco et al., 2023). The study of heavy metal tolerance in aquatic plants is crucial for several reasons. Firstly, understanding the physiological and molecular mechanisms underlying metal uptake and detoxification can enhance the efficiency of phytoremediation strategies (Dixit et al., 2015; Pang et al., 2023). Secondly, identifying hyperaccumulator species and optimizing their use in constructed wetlands and other remediation systems can provide cost-effective and sustainable solutions for water purification (Rezania et al., 2016; Komijani et al., 2021). Lastly, insights into the interaction between heavy metals and plant defense systems, including the role of phytohormones, can inform the development of more resilient plant varieties for environmental cleanup (Nguyen et al., 2020).

This study aims to summarize the current knowledge on the types and sources of heavy metal pollution in aquatic ecosystems, discuss the various physiological mechanisms and molecular pathways involved in heavy metal uptake, translocation, and detoxification in aquatic plants, highlight the potential of different aquatic plant species in phytoremediation applications, with a focus on the aquatic plants such as Canadian waterweed (*Elodea canadensis*), *Posidonia oceanica*, Eelgrass (*Zostera marina*) and duckweed (*Lemna minor*), explore the role of

phytohormones and other plant defense systems in mitigating heavy metal toxicity, and identify future research directions and technological advancements needed to enhance the effectiveness of phytoremediation in heavy metal-contaminated water bodies.

By addressing these objectives, this study seeks to contribute to the growing body of knowledge on phytoremediation and support the development of innovative and sustainable approaches for managing heavy metal pollution in aquatic environments.

2 Physiological Adaptations to Heavy Metals

2.1 Cellular mechanisms of tolerance

Aquatic plants employ several cellular mechanisms to tolerate heavy metals. These mechanisms include the binding of metals to cell walls and extracellular exudates, reducing metal uptake or pumping metals out of cells via efflux transporters, chelation of metals in the cytosol by peptides such as phytochelatins, repairing stress-damaged proteins, and compartmentalizing metals in vacuoles through tonoplast-located transporters. Mycorrhizal associations also play a significant role in restricting heavy metal uptake by plants (Kushwaha et al., 2016). Additionally, the secretion of substances into the soil and metal immobilization are crucial for avoiding metal uptake (Skuza et al., 2022).

2.2 Biochemical pathways involved

The biochemical pathways involved in heavy metal tolerance include the synthesis of metal-binding peptides like phytochelatins and metallothioneins, which chelate and sequester heavy metals, thereby reducing their toxicity (Kushwaha et al., 2016). Organic acids and amino acids also play a role in chelation and detoxification processes. The expression of genes encoding heavy metal transporters, such as the ZIP family, Nramp, and P1B-type ATPase, is crucial for regulating metal uptake and transport within plant cells. Additionally, the production of heat-shock proteins helps in the repair and stabilization of proteins damaged by heavy metal stress (Skuza et al., 2022).

2.3 Structural and morphological changes

Aquatic plants exhibit various structural and morphological changes to mitigate the effects of heavy metal stress. These changes include modifications to the cell wall, which can bind and immobilize heavy metals, thereby preventing their entry into the cytoplasm (Figure 1) (Kosakivska et al., 2020; Skuza et al., 2022). The development of thicker cell walls and increased production of root exudates can alter the rhizosphere's pH and redox state, reducing metal bioavailability. Furthermore, the formation of symbioses with rhizosphere microorganisms can enhance metal tolerance by promoting metal sequestration and reducing metal uptake (Tiwari and Lata, 2018; Skuza et al., 2022).

In summary, aquatic plants have evolved a range of physiological adaptations to tolerate heavy metal stress. These adaptations involve complex cellular mechanisms, biochemical pathways, and structural changes that work together to mitigate the toxic effects of heavy metals and ensure plant survival in contaminated environments.

3 Detoxification Strategies in Aquatic Plants

3.1 Chelation and sequestration mechanisms

Chelation and sequestration are primary detoxification strategies employed by aquatic plants to mitigate heavy metal toxicity. Chelation involves the binding of heavy metals to organic molecules, rendering them less toxic. Phytochelatins (PCs) and metallothioneins (MTs) are key chelators in plants. PCs are synthesized from glutathione and play a significant role in binding heavy metals and facilitating their sequestration into vacuoles (Kushwaha et al., 2016). Metallothioneins, on the other hand, are gene-encoded proteins that also bind heavy metals, aiding in their detoxification and homeostasis. Additionally, the compartmentalization of heavy metals within vacuoles is a critical sequestration mechanism that prevents the metals from interfering with cellular processes (Kushwaha et al., 2016).

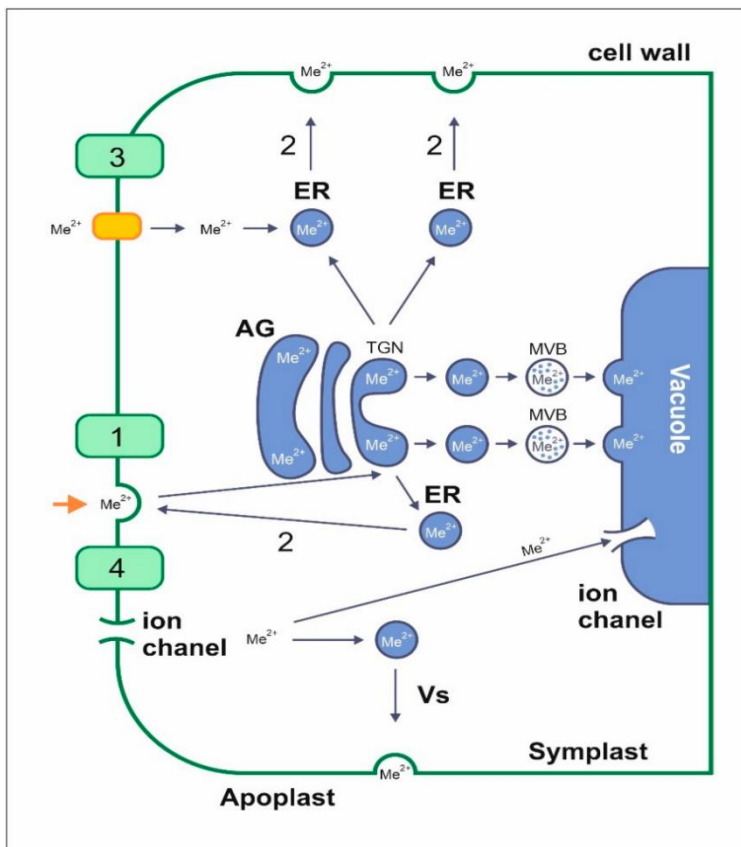


Figure 1 Cellular mechanisms of metal extraction/excretion and transportation through endocytosis - 1, exocytosis - 2, active transport - 3, diffusion - 4, and through ion channels (Photo credit: Skuza et al., 2022)

Image caption: MBV - multivesicular body, Me^{2+} - divalent metal, GA - Golgi apparatus, Vs - transport vesicles, TGN - early endosomes, RE - recycling endosomes (Adopted from Skuza et al., 2022)

3.2 Antioxidant defense systems

Heavy metal exposure often leads to the generation of reactive oxygen species (ROS), which can cause oxidative stress and damage cellular components. Aquatic plants have evolved robust antioxidant defense systems to counteract this oxidative stress. These systems include enzymes such as superoxide dismutase, catalase, and peroxidases, which neutralize ROS. The presence of antioxidants like glutathione and tocopherols further enhances the plant's ability to mitigate oxidative damage. The dynamic balance between ROS production and detoxification is crucial for maintaining cellular homeostasis and ensuring the plant's survival under heavy metal stress (Alsherif et al., 2021; Molina and Segura, 2021).

3.3 Role of phytochelatins and metallothioneins

Phytochelatins (PCs) and metallothioneins (MTs) are pivotal in the detoxification of heavy metals in aquatic plants. PCs are synthesized enzymatically from glutathione and are involved in the chelation and sequestration of heavy metals into vacuoles. The synthesis of PCs is regulated by the enzyme phytochelatin synthase, which is activated in response to heavy metal exposure (Yadav, 2010). Metallothioneins, being gene-encoded proteins, also play a significant role in binding heavy metals and facilitating their detoxification. The coordinated expression of genes encoding PCs and MTs is essential for the effective detoxification of heavy metals, as demonstrated in studies on various plant species. These molecules not only help in detoxification but also contribute to the overall metal homeostasis within the plant cells.

4 Molecular and Genetic Mechanisms

4.1 Gene expression and regulation

Plants have evolved various adaptive mechanisms to cope with heavy metal stress, including the regulation of gene expression. Key genes involved in heavy metal tolerance include those encoding for metallothioneins (MTs),

phytochelatins (PCs), and various transporters. Metallothioneins and phytochelatins play crucial roles in chelating heavy metals, thereby reducing their toxicity (Kosakivska et al., 2020). Genes such as the ZIP (ZRT IRT related proteins) family, natural resistance-associated macrophage proteins (Nramp), and P1B-type ATPase family have been identified and cloned, demonstrating their roles in heavy metal uptake and sequestration. Additionally, the expression of genes encoding γ -glutamyl-cysteine synthetase, which is involved in the synthesis of phytochelatins, has been shown to contribute to heavy metal tolerance.

4.2 Molecular markers for tolerance

Molecular markers are essential tools for identifying and breeding plants with enhanced heavy metal tolerance. These markers can be used to track the presence of specific genes associated with metal tolerance and accumulation. For instance, genes encoding ABC-type (ATP-binding cassette) transporters and cation diffusion facilitators (CDF) have been identified as key players in the sequestration of heavy metals in vacuoles (Kosakivska et al., 2020). The identification and use of these molecular markers can facilitate the development of plants with improved heavy metal tolerance through marker-assisted selection (Ovečka and Takáč, 2014).

4.3 Genetic engineering approaches

Genetic engineering offers a promising approach to enhance heavy metal tolerance in plants. By introducing genes that encode for metal-binding proteins or transporters, plants can be engineered to improve their capacity for heavy metal uptake, translocation, and detoxification. For example, the genetic modification of metallothioneins has been shown to enhance the tolerance and bioaccumulation of heavy metals in *Escherichia coli*, suggesting similar strategies could be applied to plants (Li et al., 2021). Additionally, the heterologous expression of genes involved in sulfur metabolism and metal transport has been demonstrated to improve the phytoremediation potential of plants (Fasani et al., 2018). Recent advancements in genome editing technologies, such as CRISPR/Cas9, provide further opportunities to precisely modify plant genomes for enhanced heavy metal tolerance (Khan et al., 2021).

5 Case Studies of Heavy Metal Tolerance

5.1 Tolerance in freshwater plants

Freshwater plants have evolved various mechanisms to tolerate and detoxify heavy metals, ensuring their survival in polluted environments. A notable example is Canadian waterweed (*Elodea canadensis*), which exhibits high tolerance to cadmium (Cd) by activating antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT). These enzymes mitigate oxidative stress caused by heavy metal accumulation. Additionally, the sequestration of Cd into vacuoles and binding to phytochelatins (PCs) further reduces its toxicity (Goyal et al., 2020).

Another significant case is duckweed (*Lemna minor*), known for its rapid growth and ability to accumulate heavy metals like lead (Pb) and zinc (Zn). Ubuza et al. (2019) found that the small duckweed can effectively remove Pb from water (Figure 1). The production of metal-binding proteins, such as metallothioneins (MTs), plays a crucial role in its detoxification strategy.

Figure from Ubuza et al. (2019) illustrates the findings on the use of duckweed for removing Pb from water. Panel B shows the highest bioaccumulation of 1.57 mg/L achieved at 3 d in the recirculated set-up. This result implies the efficient accumulation capabilities of duckweed as influenced by the recirculation mechanism. Panel C outlines the concentration of Pb in the effluent of 0.93 mg/L in the recirculated set-up with duckweed in 3 d was much lower compared to the initial concentration in the influent at 2.5 mg/L. This result underscores the potential of duckweed in phytoremediation, with recirculated systems enhancing metal removal efficiency.

Additionally, macrophytes such as *Pistia stratiotes*, *Eichhornia* spp., *Lemna* spp., and *Salvinia* spp. have been identified as effective hyper-accumulators, capable of phytofiltration to remove heavy metals from water. The role of phytohormones in enhancing the tolerance and detoxification mechanisms in these plants has also been highlighted, suggesting that hormonal regulation can mitigate metal toxicity (Nguyen et al., 2020).

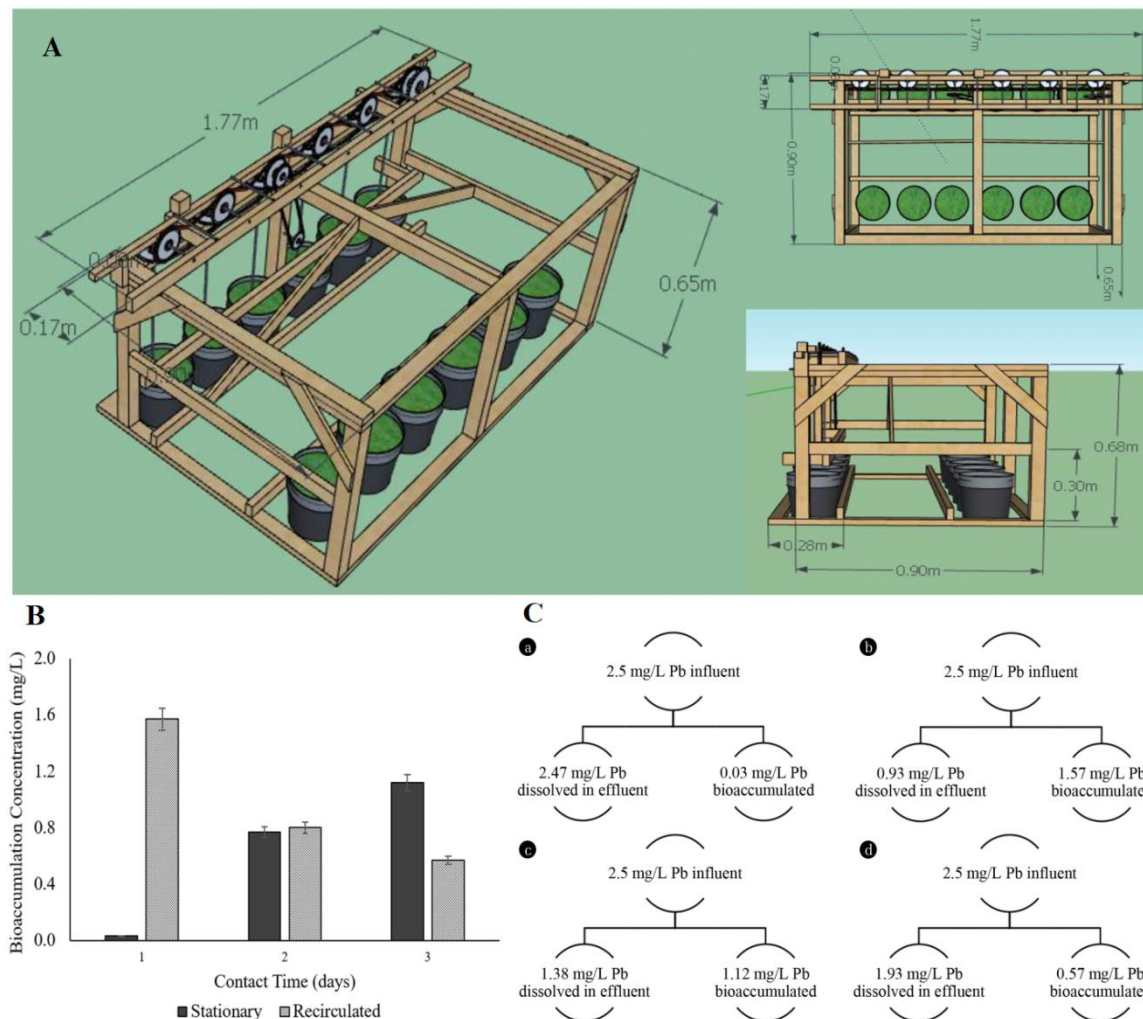


Figure 2 Experimental set-up and results of removing Pb from water by duckweed (Adapted from Ubuza et al., 2019)
 Image caption: (A) Isometric view, top view and front view of the experimental set-up showing; (B) The concentration of the accumulated Pb by duckweed in various contact times (3, 6, 9 d) both in the stationary and recirculated set-ups; (C) Mass balance of Pb at (a) 3 d stationary (b) 3 d recirculated (c) 9 d stationary (d) 9 d recirculated (Adapted from Ubuza et al., 2019)

5.2 Tolerance in marine plants

Marine plants, or macrophytes, also demonstrate remarkable heavy metal tolerance. *Posidonia oceanica*, a seagrass species, exhibits resilience to copper (Cu) contamination. It employs a combination of antioxidant defense mechanisms and metal-binding peptides to cope with Cu-induced stress. The presence of abundant sulfhydryl groups in its cells enhances its capacity to bind and detoxify heavy metals (Bertini et al., 2019).

Eelgrass (*Zostera marina*) is another marine plant that shows tolerance to heavy metals like mercury (Hg) and arsenic (As). Research indicates that *Zostera marina* utilizes a complex network of phytochelatin and metallothioneins to sequester and detoxify these metals. Additionally, its extensive root system aids in the immobilization of heavy metals, preventing their translocation to aerial parts (Greco et al., 2019).

5.3 Comparative analysis across species

A comparative analysis of heavy metal tolerance across freshwater and marine plants reveals distinct and shared strategies. Both *Elodea canadensis* and *Posidonia oceanica* exhibit strong antioxidant defenses, highlighting the universal importance of oxidative stress mitigation in heavy metal tolerance. However, freshwater plants like *Lemna minor* rely more on rapid growth and biomass accumulation to dilute metal concentrations, whereas marine plants like *Zostera marina* benefit from extensive root systems for metal immobilization.

Furthermore, the synthesis of metal-binding peptides such as phytochelatins and metallothioneins is a common strategy observed across species. The efficiency of these peptides in sequestering heavy metals is critical for both freshwater and marine plants. However, the expression levels and types of these peptides may vary, reflecting adaptations to specific environmental conditions.

6 Ecological and Environmental Implications

6.1 Role in phytoremediation

Aquatic plants play a crucial role in phytoremediation, a green technology that utilizes plants to remove contaminants from the environment. This method is particularly effective for heavy metal pollution in water bodies. Aquatic plants such as Canadian waterweed (*Elodea canadensis*), *Posidonia oceanica*, Eelgrass (*Zostera marina*) and duckweed (*Lemna minor*) have shown significant potential in accumulating heavy metals from polluted water, making them ideal candidates for phytoremediation (Souza and Silva, 2019; Ali et al., 2020; Pang et al., 2023). The ability of these plants to absorb and translocate heavy metals from water to their aerial parts enhances their phytoremediation efficiency (Pang et al., 2023). Moreover, the use of macrophytes in phytoremediation is cost-effective, environmentally friendly, and can be implemented on-site, reducing the logistical challenges associated with other remediation methods (Nguyen et al., 2020).

6.2 Impact on ecosystem health

The presence of heavy metals in aquatic ecosystems poses a severe threat to biodiversity and ecosystem health. Heavy metals can accumulate in the food chain, leading to toxic effects on aquatic organisms and humans. By employing aquatic plants for phytoremediation, the concentration of heavy metals in water bodies can be significantly reduced, thereby mitigating their harmful effects on the ecosystem. Aquatic macrophytes not only remove heavy metals but also improve water quality by reducing other pollutants, thus enhancing the overall health of the ecosystem (Obinna and Ebere, 2019; Souza and Silva, 2019). The use of aquatic plants in constructed wetlands has proven effective in treating industrial effluents and municipal wastewater, further contributing to ecosystem restoration.

6.3 Interaction with other pollutants

Aquatic plants used in phytoremediation can interact with a variety of pollutants, including organic contaminants. The ability of these plants to remove both heavy metals and organic pollutants makes them versatile tools for environmental cleanup (Christian and Beniah, 2019; Obinna and Ebere, 2019). Factors such as water pH, temperature, and the presence of other contaminants can influence the efficiency of pollutant removal by aquatic plants (Li et al., 2015; Christian and Beniah, 2019). For instance, acidic water conditions can enhance the uptake of heavy metals by plants (Li et al., 2015). Additionally, the interaction between heavy metals and organic pollutants can affect the bioavailability and toxicity of these contaminants, necessitating a comprehensive understanding of these interactions for effective phytoremediation (Christian and Beniah, 2019).

7 Challenges and Future Directions

7.1 Technical and methodological challenges

The study of heavy metal tolerance in aquatic plants faces several technical and methodological challenges. One significant challenge is the variability in heavy metal concentrations in natural environments, which complicates the standardization of experimental conditions and the reproducibility of results. Additionally, the complex interactions between different heavy metals and plant species require sophisticated analytical techniques to accurately measure and interpret the data. The heterogeneity of contaminated sites also poses a challenge, as it necessitates the development of site-specific remediation strategies. Furthermore, the long-term stability and effectiveness of phytoremediation techniques need to be evaluated under varying environmental conditions to ensure their practical applicability (Hasan et al., 2017; Nguyen et al., 2020).

7.2 Gaps in current knowledge

Despite significant advancements, there are still considerable gaps in our understanding of the mechanisms underlying heavy metal tolerance and detoxification in aquatic plants. One major gap is the limited knowledge of

the genetic and molecular basis of metal tolerance, which hinders the development of genetically engineered plants with enhanced phytoremediation capabilities. Additionally, the role of phytohormones and other signaling molecules in modulating plant responses to heavy metal stress is not fully understood and requires further investigation (Hasan et al., 2017; Nguyen et al., 2020). There is also a need for more comprehensive studies on the interactions between heavy metals and other environmental stressors, such as salinity and nutrient deficiency, to develop more robust phytoremediation strategies (Thakur et al., 2021).

7.3 Future research opportunities

Future research should focus on elucidating the genetic and molecular mechanisms of heavy metal tolerance in aquatic plants to facilitate the development of more effective phytoremediation technologies. Advanced biotechnological tools, such as CRISPR/Cas9, can be employed to create transgenic plants with enhanced metal uptake and detoxification capabilities. Additionally, exploring the role of microbial communities in the rhizosphere and their interactions with plant roots can provide new insights into improving phytoremediation efficiency. Research should also aim to develop integrated remediation approaches that combine phytoremediation with other bioremediation techniques to address the multifaceted nature of heavy metal contamination (Hasan et al., 2017). Finally, long-term field studies are essential to assess the sustainability and ecological impact of phytoremediation practices in diverse environmental settings (Nguyen et al., 2020).

8 Concluding Remarks

Aquatic plants exhibit a variety of physiological adaptations and detoxification strategies that enable them to tolerate and remediate heavy metal pollution in water bodies. Key findings highlight several mechanisms: Aquatic plants such as Canadian waterweed (*Elodea canadensis*), *Posidonia oceanica*, Eelgrass (*Zostera marina*) and duckweed (*Lemna minor*) are effective in removing heavy metals from water through phytofiltration and phytoaccumulation. These plants employ various cellular mechanisms for heavy metal detoxification, including binding to cell walls, chelation by phytochelatins and metallothioneins, and compartmentalization within vacuoles. Additionally, the association with arbuscular mycorrhizal fungi (AMF) can enhance plant growth and reduce heavy metal accumulation in edible parts by forming P-HM complexes.

Understanding the mechanisms of heavy metal tolerance in aquatic plants is crucial for several reasons. It plays a vital role in environmental protection by offering a sustainable and eco-friendly solution to mitigate heavy metal pollution, which poses severe threats to ecosystems and human health. Additionally, insights into the genetic and molecular mechanisms of metal tolerance can inform biotechnological applications, particularly in developing genetically engineered plants with enhanced phytoremediation capabilities. Furthermore, this knowledge has significant agricultural implications, aiding in managing crop safety and productivity in contaminated areas, thereby ensuring food security and reducing health risks.

Future research should focus on several key areas to enhance the effectiveness of phytoremediation and our understanding of heavy metal tolerance in aquatic plants. These include species-specific studies to investigate the heavy metal tolerance and accumulation capacities of a broader range of aquatic plant species, aiming to identify the most effective candidates for phytoremediation. Molecular and genetic engineering should be explored to enhance the metal tolerance and accumulation abilities of aquatic plants through genetic modifications and biotechnological approaches. Additionally, conducting large-scale field trials is essential to validate laboratory findings and develop practical guidelines for implementing phytoremediation technologies in diverse environmental settings. Understanding the interaction with microorganisms, particularly the synergistic effects of plant-microbe interactions and the role of mycorrhizal fungi, can further enhance heavy metal tolerance and accumulation. Finally, evaluating the long-term ecological and health impacts of using aquatic plants for heavy metal remediation is crucial to ensure the sustainability and safety of these practices. By addressing these research gaps, we can improve the efficacy of phytoremediation strategies and contribute to the sustainable management of heavy metal pollution in aquatic environments.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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