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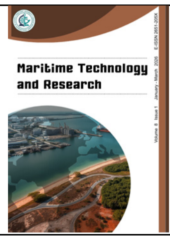

Review Article

Harnessing mangrove phytoremediation for coastal heavy metal pollution: A chemical environmental perspective

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Abstract
Mangrove ecosystems play a vital role in mitigating heavy metal (HM) contamination in coastal regions due to their unique biological and ecological characteristics. This review synthesizes current knowledge on the phytoremediation capacity of mangrove species, with a focus on their mechanisms of HM uptake, accumulation, and translocation. Various species, such as *Avicennia marina*, *Kandelia candel*, and *Rhizophora stylosa*, demonstrate notable bioconcentration factors (e.g., BCF_{root} up to 12.3 for Cd) and selective metal compartmentalization, particularly in roots, thereby minimizing translocation to aerial parts (e.g., TF as low as 0.05 for Pb). The analysis of metal concentrations across different mangrove sites worldwide reveals that sediment composition, sampling depth, and anthropogenic activities significantly influence HM distribution. Mechanistic processes including redox potential modulation, rhizosphere oxidation, and associations with microbial communities further enhance the immobilization and detoxification of metals such as Cd, Pb, Cr, Cu, and Hg. As a narrative review, this article consolidates global findings and highlights species-specific strategies (e.g., tolerance differences among Avicennia and Rhizophora) and ecological thresholds (e.g., salinity tolerance ranges of 10 - 35 PSU, optimal redox potential above –100 mV, and metal concentration limits beyond which growth declines). Future prospects include integrating molecular tools, designing engineered mangrove wetlands, and developing policy-driven restoration initiatives. Ultimately, mangrove-based phytoremediation contributes not only to coastal pollution control, but also to the achievement of Sustainable Development Goals (SDGs), particularly SDG 14 (Life Below Water) and SDG 13 (Climate Action), while supporting real-world applications, such as coastal restoration planning and nature-based solutions.

1. Introduction

Coastal pollution, caused by industrial and environmental discharges such as trace metals and toxic organics, poses a growing threat to aquatic ecosystems due to its persistence and wide dispersal via tidal action (Parvin et al., 2025). While some elements, like copper and iron, are essential at low levels, others, including cadmium, lead, mercury, and arsenic, are non-essential and toxic, leading to serious ecological and health consequences (Akbar et al., 2025). As contamination continues to rise from activities such as mining, brine discharge, fossil fuel combustion, and coastal development, there is an urgent need for environmentally friendly strategies to reduce exposure to toxic metals (Paul et al., 2024). Phytoremediation emerges as a sustainable and low-cost approach by using plants to absorb, stabilize, or detoxify harmful substances (Akbar & Khairunnisa, 2024; Ogunsola et al., 2025). Although several reviews have highlighted the ecological role of mangroves in metal retention, many of them remain descriptive in scope, focusing on either general ecological services or single-species case studies. What is still lacking is a comprehensive synthesis that integrates species-level comparisons with sediment geochemistry, particularly the interactions between root uptake, sediment redox conditions, and metal partitioning. Addressing this gap is essential to provide a mechanistic understanding of how different mangrove taxa function as phytoremediators under varying environmental contexts. In this context, mangroves offer a promising phytoremediation system. Similar to well-known terrestrial hyperaccumulators such as *Alyssum* species, which are capable of extracting nickel from serpentine soils, or vetiver grass (*Chrysopogon zizanioides*), widely applied for lead and arsenic removal in terrestrial settings, mangroves exhibit a comparable ability to tolerate and immobilize metals. However, they surpass terrestrial plants in one important aspect: their natural adaptation to saline and waterlogged coastal environments, where other hyperaccumulators cannot survive. This unique capacity, combined with their dense root networks, high biomass production, and specialized physiological mechanisms, makes mangroves particularly well suited for remediating polluted intertidal zones (Richter et al., 2016; Al-Solaimani et al., 2022). Utilizing mangrove-based phytoremediation not only reduces the ecological impact of heavy metals, but also supports long-term environmental restoration efforts in vulnerable shoreline regions.

Mangroves are vital components of coastal ecosystems, known for their ability to thrive in challenging saline environments while offering a wide range of ecological services (Yan et al., 2017). Beyond acting as natural buffers against storms and erosion, mangroves play a crucial role in filtering and immobilizing heavy metals (HMs) and other toxic pollutants from coastal waters and sediments (Yadav et al., 2023). Their dense root systems, along with specialized physiological traits, enable them to trap, accumulate, and detoxify harmful substances. However, long-term exposure to excessive HM concentrations can impair critical functions such as nutrient uptake, photosynthesis, and respiration, ultimately affecting mangrove health and survival (Nguyen et al., 2020). While mangroves possess internal defense mechanisms- including metal chelation, sequestration in vacuoles, and the activation of antioxidant systems- their tolerance has limits (Almahasheer et al., 2018). Alarmingly, mangrove habitats are rapidly declining due to coastal development, pollution, and climate-related stressors, weakening their natural capacity to buffer contaminants. If degradation continues unchecked, coastal ecosystems will lose an essential line of defense against toxic metal buildup, placing aquatic biodiversity at greater risk. To sustain mangrove-based phytoremediation, it is essential to implement conservation policies and support research on effective, plant-based remediation strategies tailored to coastal environments. Protecting mangroves means protecting the ecological health of our shorelines (Xie et al., 2022).

Mangrove plants exhibit remarkable adaptive strategies that enable them to cope with heavy metal toxicity, including avoidance, tolerance, and physiological adjustment through intricate biological and biochemical pathways. Recognizing their significant role in phytoremediation, particularly in the uptake and accumulation of heavy metals in coastal environments, this review aims to synthesize global research on their remediation potential. Specifically, the objectives of this review are to:

1) Identify the major sources contributing to heavy metal contamination in coastal zones.

2) Examine how mangroves absorb, transport, sequester, and eliminate various heavy metals under laboratory and field conditions.

3) Evaluate the adaptive capacities of different mangrove species in response to specific metal stress.

4) Clarify the underlying mechanisms that drive phytoremediation processes in mangrove systems.

5) Provide science-based recommendations to enhance future applications of mangrove-assisted green remediation in polluted coastal regions.

By consolidating these aspects, this review provides a framework for understanding the functional role of mangroves in mitigating heavy metal pollution and informs future strategies for sustainable coastal management.

2. Methods

2.1 Review approach

This article is a narrative review that synthesizes evidence on heavy metal (HM) dynamics in mangrove ecosystems, with emphasis on sources and distribution of HMs, uptake and translocation mechanisms, species-specific accumulation metrics, and physiological-biochemical stress responses. A narrative approach was selected to allow integration of heterogeneous study designs (field surveys, greenhouse experiments, laboratory trials, and prior reviews) and to contextualize findings across regions, metals, and taxa. To enhance transparency and rigor, the review process followed explicit steps for literature searching, study selection, data extraction, and qualitative synthesis; however, no meta-analysis or pooled effect estimation was attempted, due to variability in designs, units, and reporting standards.

2.2 Information sources and search strategy

Literature was retrieved from Scopus, Web of Science, ScienceDirect, PubMed/Medline, and Google Scholar. Searches covered inception to June 2025 and combined controlled terms and free text related to coastal contamination and mangroves. Representative query strings included combinations of the following concepts with Boolean operators: "mangrove*" AND ("heavy metal*" OR Cd OR Pb OR Zn OR Cu OR Cr OR Hg OR Mn) AND (phytoremediation OR uptake OR translocation OR bioaccumulation OR "bioconcentration factor" OR "translocation factor") AND (sediment* OR "coastal pollution" OR estuar*). Additional records were identified by backward and forward citation chasing of key papers. Only English-language, peer-reviewed literature was considered.

2.3 Eligibility and study selection

Records were screened at title-abstract level, followed by full-text assessment. Studies were eligible if they examined mangrove species in relation to HM contamination and reported at least one of the following: concentrations of metals in tissues or sediments; uptake/translocation pathways; species-specific accumulation metrics (e.g., BCF, TF, BAF); or physiological/biochemical responses to metal exposure. Field, greenhouse, and laboratory studies were included, as well as synthetic reviews that provided quantitative or mechanistic insights. Exclusions were applied to sources lacking explicit mangrove-metal linkage, non-peer-reviewed items, non-English texts, and duplicates.

2.4 Quality considerations and limitations

Methodological quality was appraised qualitatively, with attention given to sampling design, reporting of detection limits and QA/QC, clarity of exposure or depth strata, and consistency of units. Studies were not excluded solely on quality grounds but were weighted narratively when interpreting strength of evidence. The review was limited by geographic skew in available data, inconsistent reporting of contextual variables (e.g., pH, organic matter, redox), and incomplete availability of thresholds, such as EC_{50} across species. Foundational, earlier studies were retained when they provided unique species- or site-specific data not updated in recent literature, ensuring completeness while maintaining an up-to-date synthesis.

3. Distribution and impact of heavy metals in mangrove habitats

Mangrove ecosystems, situated at the interface between terrestrial and marine environments, are highly vulnerable to heavy metal (HM) pollution due to their proximity to urban, industrial, and agricultural sources (Dai et al., 2018; Ma et al., 2025) (**Figure 1**). As transitional ecosystems, mangroves are exposed to regular tidal flooding and drainage that generate fluctuating redox conditions in their sediments. During inundation, reduced and anoxic states prevail, favoring the precipitation of insoluble metal sulfides that immobilize contaminants. Conversely, when sediments are exposed during low tide or aeration, oxidized conditions can promote the dissolution of these sulfides, altering metal speciation and increasing the mobility of certain elements such as Fe, Mn, and Cd. This dynamic redox cycling determines whether mangrove sediments function primarily as sinks or as potential sources of heavy metals. Runoff carrying metal contaminants, such as cadmium (Cd), lead (Pb), mercury (Hg), and copper (Cu), often accumulates in estuarine sediments where mangroves thrive. These contaminants originate from multiple anthropogenic activities, including mining, shipping, pesticide use, oil refining, and untreated sewage discharge (Ma et al., 2025; Zhang et al., 2007). Once deposited, metals interact with sulfides, carbonates, and organic matter, undergoing complex geochemical processes influenced by pH, redox potential, and salinity (Cheng & Yap, 2015). Importantly, different metals show contrasting behaviors in these sediments; for example, Pb tends to adsorb strongly to organic matter and mineral surfaces, leading to lower mobility, whereas Cr often remains more soluble under oxidizing conditions, thereby increasing its potential bioavailability. Such differences highlight the need to consider individual metal characteristics when assessing contamination risks in mangrove habitats (Huang & Wang, 2010). Despite partial immobilization in sediments, heavy metals are not permanently sequestered. Tidal pumping, organic matter decomposition, and microbial activity can remobilize metals, making them bioavailable for uptake by mangrove plants and benthic fauna. Additionally, environmental disturbances such as dredging, storm surges, or mangrove deforestation can resuspend sediments and release stored metals back into the water column. This reintroduction exacerbates exposure risks for estuarine organisms and may trigger bioaccumulation across trophic levels. Notably, fine-grained sediments and high organic content in mangrove soils tend to retain more metals, making them effective sinks under stable conditions, but also latent sources of contamination when disturbed.

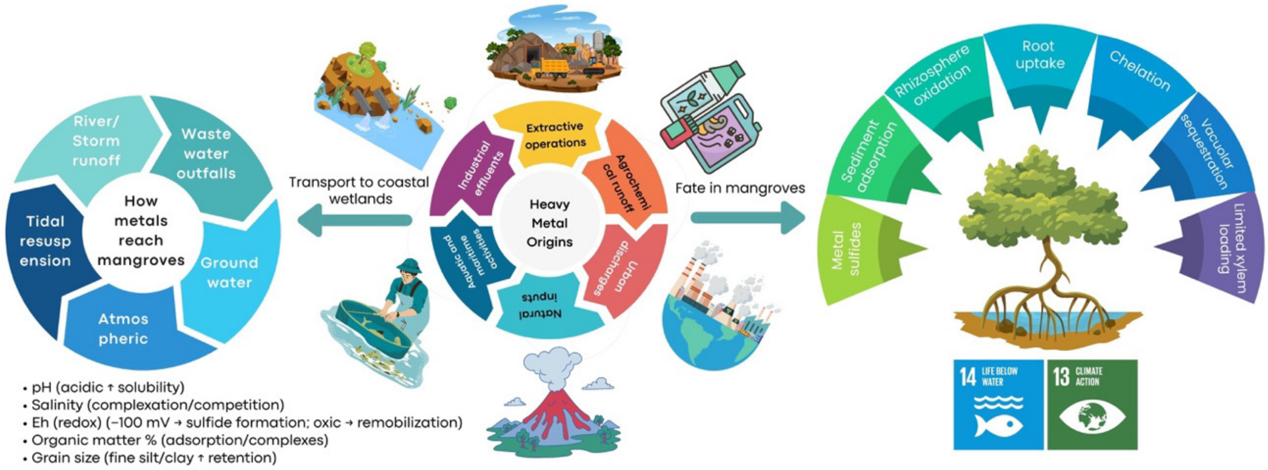

Figure 1 Distribution and impact of heavy metals in mangrove habitats.

Heavy metal pollution poses substantial ecological threats to mangrove ecosystems by impairing physiological functions, altering microbial communities, and reducing biodiversity (Sari & & Din, 2012). Prolonged exposure to elevated concentrations of metals like Cr, Zn, and Hg can disrupt photosynthesis, enzyme activity, and nutrient transport in mangrove species, resulting in stunted growth and premature senescence (Al-Solaimani et al., 2022). However, mangroves exhibit remarkable resilience through various tolerance mechanisms such as metal sequestration in roots, chelation, and compartmentalization within vacuoles. These adaptations allow mangroves to function as natural biofilters, significantly reducing the mobility and toxicity of metals in coastal systems. Additionally, mangrove sediments act as long-term reservoirs for HMs, contributing to sediment stabilization and contaminant immobilization. Nonetheless, environmental disturbances, such as deforestation, dredging, or climate-driven sea-level rise, can reintroduce stored metals into the aquatic column, heightening exposure risk for estuarine organisms (Nath et al., 2013; Rath & Das, 2023). Monitoring metal concentrations in mangrove tissues and sediments provides valuable insight into contamination trends and ecosystem health. Therefore, mangroves not only serve as critical buffers against coastal metal pollution, but also act as early-warning bioindicators for environmental management. Their conservation is essential, not just for biodiversity, but also for the ecosystem services they provide in mitigating toxic metal contamination in vulnerable coastal zones.

4. Key drivers influencing metal mobilization from sediment

The mobility and transfer of heavy metals (HMs) in mangrove ecosystems are intricately governed by sediment physicochemical properties such as organic content, redox potential, pH, and mineral composition. Fine-textured sediments with organic matter content exceeding ~5 - 7 % typically provide strong adsorption sites for metals like Fe, Zn, and Cu, enhancing their retention capacity (**Table 1**). In the Mahanadi Delta, India, Fe concentrations ranged between 3,489.87 and 63,247.85 μg g^{-1}, indicating strong metal retention capacity within high-organic, clay-dominated substrates (Swain et al., 2021). However, once redox potential (Eh) declines below approximately –100 to –150 mV, common in waterlogged mangrove soils, metals bound to iron or manganese oxides become destabilized and mobilized, thereby increasing their bioavailability. In Shenzhen Bay, China, Zn reached 296.30 μg g^{-1}, and Pb was as high as 47.80 μg g^{-1}, likely influenced by redox-mediated transformations and variable pH affecting desorption and solubility (Li et al., 2015). Additionally, salinity and sulfate-reducing conditions promote metal sulfide formation, reducing mobility, particularly for Cd and Pb. Such conditions were observed in Pichavaram, India, where Cd ranged from 0.30 to 0.87 μg g^{-1} and Pb from 11 to 26 μg g^{-1} (Dhananjayan et al., 2025).

Heavy metal accumulation in mangrove sediments is strongly affected by anthropogenic pressures, including urban runoff, industrial effluents, aquaculture, and maritime activities. Spatial variation in HM concentrations reflects different intensities of these inputs across geographical locations. For instance, high Cu (112.00 μg g^{-1}) and Zn (57.20 μg g^{-1}) levels were recorded on Farasan Island, Saudi Arabia, a region influenced by port and desalination activities (Usman et al., 2013). In contrast, areas like Angke Kapuk, Indonesia- situated within a dense metropolitan region- reported lower but concerning levels of Cu (8.80 μg g^{-1}) and Pb (0.96 μg g^{-1}), indicating diffuse pollution sources (Jaya et al., 2022). Meanwhile, industrial expansion in Guangdong, China, likely contributes to high Pb (86.40 μg g^{-1}), Zn (87.00 μg g^{-1}), and Cr (87.60 μg g^{-1}) levels in MNRs (Liu et al., 2014). These findings highlight how specific land-use practices leave distinct heavy metal signatures: aquaculture operations often elevate Cu due to feed additives and antifouling paints; vehicular traffic and urban runoff are strongly associated with Pb accumulation; textile and tanning industries contribute Cr and Zn; and port or shipping activities increase Cu and Zn inputs. Such associations demonstrate that waste disposal, catchment-scale development, and resource exploitation are not only linked to overall pollution intensity, but also to the characteristic metal profiles found in mangrove sediments. The variability also underscores the potential for long-range transport and deposition of

HMs via riverine or estuarine flows, as seen in Jiulong River Estuary, where Mn reached 583.00 µg g⁻¹ (Yadav et al., 2023). Monitoring such spatial trends is crucial for targeted mitigation efforts.

Table 1 Summary of different heavy metal concentrations in different mangrove coastal sediments worldwide.

Mangrove Forest Location	Heavy metals concentrations (µg g⁻¹ dry wt)										Sampling depth (cm)	References
	Zn	Pb	Ni	Mn	Hg	Fe	Cu	Cr	Cd	As		
Angke Kapuk, Jakarta, Indonesia	14.79	0.96	–	–	–	–	8.80	–	–	–	±30	(Jaya et al., 2022)
Conception Bay, Newfoundland, New Caledonia	1.35	–	1.12	2.90		22.64 - 721.69	0.22	1.22	–	–	0 - 50	(Marchand et al., 2011a)
Exotic Futian Island, Zhejiang, China	252.00	77.00	45.00	–	0.17	–	93.00	81.00	2.96	150.00	0 - 30	(He et al., 2014)
Fadiouth, Southeast of Dakar, Senegal	5.40	2.40	2.50	21.00	–	–	3.50	28.80	0.03	–	0 - 20	(Bodin et al., 2013)
Farasan Island, Jazan city, Saudi Arabia	57.20	7.20	8.48	–	–	–	112.00	9.61	1.23	–	0 - 20	(Usman et al., 2013)
Farasan Islands, Saudi Arabia	2.8 - 25.0	0.9 - 6.1	2.1 - 18.4	–	–	–	1.3 - 13.5	4.6 - 23.7	0.02 - 0.20	–	0 - 10	(Alnasser et al., 2024)
Jeddah, Saudi Arabia	6.2 - 43.2	1.6 - 12.9	4.6 - 29.5	–	–	–	2.9 - 30.4	9.9 - 43.1	0.06 - 0.28	–	0 - 10	(Alnasser et al., 2024)
Jiulong River Estuary, Fujian, China	111.00	18.30	16.90	583.00	–	–	29.70	4.73	0.09	–	0 - 30	(Yadav et al., 2023)
Kuantan, Kuantan city, Malaysia	–	44.41	–	117.73	–	–	32.79	–	–	–	0 - 30	(Yunus et al., 2020)
Lantebung, Makassar, Indonesia	–	3.77 - 10.52	–	–	–	–	1.28 - 6.11	–	–	–	0 - 10	(Setiawan, 2013)
Mahanadi Delta, Odisha, India	4.29 - 16.47	9.5 - 27.29	0.04 - 7.57	–	–	3,489.87 - 63,247.85	0.93 - 6.44	2.98 - 26.56	0.01 - 1.88	0.00 - 0.03	0 - 30	(Swain et al., 2021)
Malaysian Peninsula, Northern Borneo, Malaysia	4.30	83.10	–	–	–	–	31.90	6.00	0.80	–	0 - 10	(Cheng & Yap, 2015)
Mediterranean coastal lagoon, Across Atlantic Sea, Morocco	88.6	25.5	25.9	–	–	–	28.8	–	0.38	–	0 - 30	(Xie et al., 2022)
Merak Besar, Banten, Indonesia	0.41 - 1.59	1.04 - 2.34	–	–	–	–	0.16 - 2.18	–	0.08	–	0 - 20	(Heriyanto & Suharti, 2019)

Table 1 (continued) Summary of different heavy metal concentrations in different mangrove coastal sediments worldwide.

Mangrove Forest Location	Heavy metals concentrations (µg g^{-1} dry wt)										Sampling depth (cm)	References
	Zn	Pb	Ni	Mn	Hg	Fe	Cu	Cr	Cd	As		
MNRs of South China, Guangdong, China	24.80 - 87.00	25.60 - 86.40	–	–	0.061 - 0.24	–	10.00 - 31.00	28.50 - 87.60	0.07 - 0.39	2.44 - 20.10	0 - 50	(Liu et al., 2014)
Nansha Mangrove, Guangdong, China	159.00	55.30	48.40	880.00	–	–	113.00	155.00	0.78	–	0 - 30	(Wu et al., 2014)
Native Futian Island, Guangdong, China	258.50	72.00	44.60	–	0.14	–	88.80	96.20	0.94	171.7	0 - 30	(He et al., 2014)
North-west Coast of South America, Ecuador, USA	678.30	81.30	82.20	469.00	–	16,471.1 - 45,423.1	253.80	94.50	1.90	12.20	0 - 30	(Fernández-Cadena et al., 2014)
Pichavaram, Tamil Nadu, India	27 - 109	11 - 26	bdl - 119	94 - 471	–	–	bdl - 31	25 - 120	0.30 - 0.87	68 - 140	0 - 20	(Dhananjayan et al., 2025)
Red Sea, Cairo, Egypt	–	25.00	22.00	16.10	–	–	108.00	–	1.80	–	0 - 30	(El-Said & Youssef, 2013)
Shenzhen Bay, Guangdong, China	296.30	47.80	62.80	–	–	–	31.70	55.40	2.30	–	0 - 20	(Li et al., 2015)
South East Coast, Tamil Nadu, India	126.80	32.36	38.61	373.00	–	–	506.20	194.83	6.58	–	0 - 30	(Yadav et al., 2023)
Sundarbans, West Bengal, India	65.59	22.18	30.17	579.44	–	–	25.74	55.98	0.15	–	0 - 30	(Chowdhury et al., 2015)
Thi Vai Estuary and Can Gio, Ho Chi Minh city, Vietnam	92	21	53	–	–	–	27	99	0.1	–	0 - 20	(Xie et al., 2022)
Yanbu Bay, Yanbu city, Saudi Arabia	48.8 - 511.5	11.5 - 111.3	27.3 - 241.8	–	–	–	17.2 - 217.2	14.9 - 289	–	–	0 - 30	(Alharbi et al., 2019)
Yanbu, Saudi Arabia	8.4 - 68.1	3.4 - 17.6	9.1 - 45.5	–	–	–	5.01 - 48.1	16.3 - 68.3	0.13 - 0.41	–	0 - 10	(Alnasser et al., 2024)
Yingluo Bay and Dandou Bay, Guangxi, China	56.44	25.97	27.13	–	–	–	14.95	61.88	0.11	7.67	0 - 20	(Xie et al., 2022)
Zhanjiang, China	6.84 - 144.98	0.03 - 2.16	–	–	0.001 - 0.072	–	–	0.41 - 51.58	0.001 - 0.158	0.03 - 9.3	0 - 5	(Ma et al., 2025)

Beyond environmental conditions, the transfer of HMs from sediment to mangrove biota is influenced by species-specific root uptake mechanisms and biological activity. Some mangrove species possess well-developed aerenchyma that facilitates radial oxygen loss (ROL), altering sediment redox conditions and affecting HM speciation. For example, in Nansha Mangrove, Guangdong, China, high Mn (880.00 µg g^{-1}) and Cr (155.00 µg g^{-1}) concentrations suggest active metal cycling likely enhanced by biological oxygenation zones (Wu et al., 2014). Furthermore, root exudates such as organic acids may chelate metals like Zn or Cu, increasing their solubility and bioavailability. This could explain the elevated Zn (252.00 µg g^{-1}) and Cu (93.00 µg g^{-1}) found in Exotic Futian Island, Zhejiang, China (He et al., 2014). Microbial processes in the rhizosphere also play a crucial role, with sulfate-reducing bacteria promoting metal sulfide precipitation, as seen in the Jiulong Estuary (Yadav et al., 2023). Meanwhile, symplastic versus apoplastic pathways in root transport can regulate internal metal translocation. The variability in biological uptake is reflected in the wide Pb range in Yanbu Bay, Saudi Arabia (11.5 - 111.3 µg g^{-1}) despite similar sediment matrices (Alharbi et al., 2019). These findings highlight the complex, biologically mediated controls on metal fluxes in mangrove ecosystems.

5. Absorption pathways and translocation processes of metals in mangroves

Mangroves absorb heavy metals primarily through root-soil interfaces, where both apoplastic and symplastic pathways mediate the initial uptake process (**Figure 2**). The root epidermis and exodermis act as the first barrier, allowing passive movement of metal ions (e.g., Zn^{2+}, Cd^{2+}, Pb^{2+}) via the apoplastic route until reaching the endodermis, where the Casparian strip forces selective ion entry through the symplastic pathway (Alharbi et al., 2019). The binding of metals to root cell wall pectins and mucilage, or their complexation with exudates, may prevent translocation and contribute to metal sequestration in the rhizosphere (Yunus et al., 2020). Additionally, the rhizosphere's redox conditions and pH, influenced by root activity, significantly determine the bioavailability and speciation of metals (Meera et al., 2023). For instance, Fe and Mn are more mobile under reducing conditions, whereas Pb and Cr tend to precipitate. Through fine regulation of root permeability, transporter expression, and mycorrhizal associations, mangroves minimize metal toxicity at the entry point, establishing an essential barrier for heavy metal homeostasis in saline and contaminated sediments (Zhou et al., 2021).

Once inside root cells, metal ions are either transported symplastically toward the stele for upward movement or retained within cortical cells through intracellular detoxification mechanisms. Cytosolic chelators such as phytochelatins (PCs) and metallothioneins (MTs) bind toxic metals like Cd, Hg, and As, forming non-toxic complexes that are either sequestered into vacuoles or trafficked through vesicular transport pathways (Yan et al., 2017). Vacuolar compartmentalization serves as a major detoxification strategy, especially in mangrove species such as *Avicennia marina* and *Kandelia candel*, where Cd and Zn are predominantly localized in root vacuoles ((Huang & Wang, 2010; Nath et al., 2014). Additionally, ATP-binding cassette (ABC) transporters and natural resistance-associated macrophage proteins (NRAMPs) mediate intracellular movement across membranes, aiding in ion detoxification and redistribution (Wang et al., 2019). The regulation of redox-sensitive elements like Fe and Mn involves coordination with ROS-scavenging systems to avoid oxidative damage. This intracellular orchestration ensures that only minimal amounts of metals reach the xylem, reducing the risk of translocation to sensitive aerial tissues like leaves.

The translocation of heavy metals from roots to shoots in mangroves is tightly regulated to avoid physiological impairment in aerial organs. Metals that escape root sequestration enter the xylem, where loading is mediated by specific metal transporters, such as ZIP (ZRT-IRT-like proteins) and HMA (heavy metal ATPases) (Marchand et al., 2011b). However, translocation factors (TFs) for many metals remain low in most mangrove species, indicating efficient root-level retention. For metals that do reach the leaves, further detoxification is achieved via redistribution into less metabolically active tissues, binding to the cell wall, or vacuolar storage (Rath & Das, 2023). Additionally, phloem recirculation mechanisms may play a role in redistributing excess metals back toward stem or root tissues, contributing to homeostasis. In *Aegiceras corniculatum*, leaf tissues show preferential sequestration of Zn and Mn, while toxic metals like Pb and Cd exhibit minimal accumulation. This controlled long-distance transport, combined with spatial detoxification, enables mangroves to thrive in metal-polluted coastal environments without compromising essential physiological functions such as photosynthesis or transpiration (Huang et al., 2024).

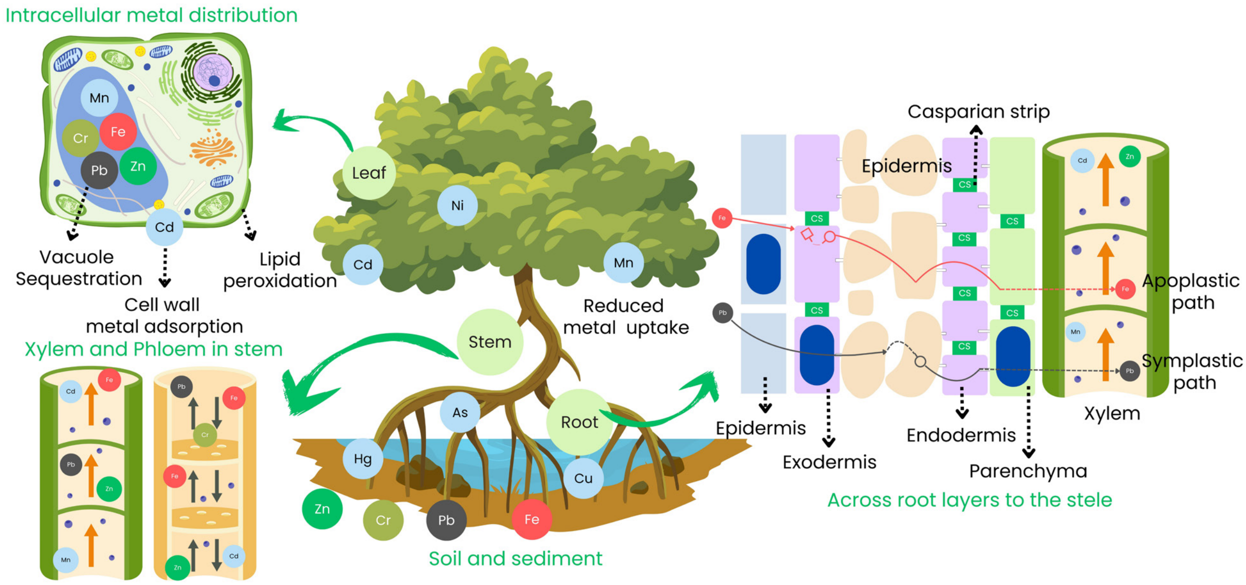

Figure 2 Heavy metal uptake and transport in mangroves.

At the molecular scale, metal fluxes in mangroves follow a conserved plant transport cascade. Uptake at the root epidermis is mediated largely by ZIP/IRT-like transporters (e.g., ZIP1/ZIP4/IRT1-type) for divalent cations such as Zn^{2+}, Mn^{2+}, and Cd^{2+}, after which ions move symplastically across the cortex to the endodermis. Xylem loading at the stele is primarily driven by P1B-type ATPases (HMA2/HMA4), enabling long-distance ascent to shoots. During this journey, metals are buffered by cytosolic chelators (phytochelatins, metallothioneins) and are shuttled across membranes by ABCC transporters as PC-metal complexes or partitioned by MTP/CDF carriers into vacuoles and the apoplast. In leaves, unloading and redistribution of metal-chelate complexes are facilitated by YSL proteins, while NRAMP1/NRAMP3 and tonoplast MTP1/MTP3 coordinate vacuolar import-export to maintain cellular homeostasis. Functionally, this sequence can be read as a flow: epidermal uptake (ZIP/IRT) → symplastic transfer → xylem loading (HMA2/HMA4) → leaf unloading (YSL) → vacuolar sequestration (ABCC–PC, MTP; with NRAMP-mediated recycling). Consistent with their roles as essential micronutrients, Zn and Mn commonly accumulate to higher levels in leaves, compared with Pb or Cd, which are largely retained in roots due to strong cell-wall binding, iron-plaque adsorption, and rapid chelation-vacuolar sequestration. In some halophytic mangroves (e.g., Avicennia), limited Cu/Zn can also be excreted via salt glands, further constraining leaf burdens. This transporter-based framework clarifies why mangroves display low translocation factors for toxic metals (Pb, Cd) yet tolerate and compartmentalize physiologically required metals (Zn, Mn) in aerial tissues.

6. Physiological and biochemical strategies of metal tolerance in mangroves

6.1 Ionic, osmotic, and oxidative stress responses

Mangrove plants exhibit remarkable adaptive mechanisms to cope with diverse heavy metal-induced stresses, particularly ionic, osmotic, and oxidative stress (**Table 2**). Ionic stress arises when excessive metal ions, such as Cd^{2+} or Pb^{2+}, interfere with essential ion transport, disrupting electrochemical gradients across the plasma membrane and inhibiting key enzymatic activities, which in turn suppresses cellular growth (Zhou et al., 2021). In response, mangroves employ strategies like ion exclusion at the root-soil interface and intracellular compartmentalization to isolate toxic ions. Osmotic stress, often triggered by heavy metal-induced disruption of water balance, leads to turgor loss and tissue dehydration. Mangroves counteract this by accumulating compatible solutes, such as proline and glycine betaine, which restore osmotic balance and preserve cellular integrity within the vacuole and cell wall (Meera et al., 2023). Simultaneously, oxidative stress, a hallmark of heavy metal toxicity, results from overproduction of reactive oxygen species (ROS), causing lipid peroxidation and structural damage in organelles like chloroplasts and mitochondria. To combat this, mangroves enhance both enzymatic antioxidants (e.g., superoxide dismutase, catalase) and non-enzymatic antioxidants (e.g., ascorbate, glutathione), effectively mitigating oxidative damage and sustaining metabolic homeostasis (Meera et al., 2023). These synergistic responses highlight the biochemical resilience of mangroves under metal stress.

Table 2 Mechanistic overview of mangrove responses to heavy metal-induced stress.

Stress Type	Primary Trigger	Physiological Impact	Biochemical Consequence	Target Cellular Site	Downstream Effect	Tolerance Strategy in Mangroves	Reference
Ionic stress	Excess metal ions (e.g., Cd^{2+}, Pb^{2+})	Ion transport disruption	Enzyme inhibition	Plasma membrane	Growth inhibition	Ion exclusion, compartmentalization	(Zhou et al., 2021)
Osmotic stress	Disrupted water balance	Turgor loss	Accumulation of osmolytes	Vacuole/cell wall	Leaf wilting, tissue dehydration	Osmotic adjustment through compatible solutes	(Meera et al., 2023)
Oxidative stress	ROS overproduction	Lipid peroxidation	Antioxidant enzyme activation	Chloroplast, mitochondria	Cell damage, necrosis	Activation of enzymatic/non-enzymatic defense systems	(Meera et al., 2023)
Nutrient imbalance	Competitive metal uptake	Nutrient deficiency	Altered nutrient transport	Xylem/phloem pathways	Chlorosis, reduced photosynthesis	Nutrient reallocation, mycorrhizal association	(Yan et al., 2017)
Water stress	Limited water uptake	Reduced transpiration	Increased ABA levels	Stomata, xylem	Stomatal closure, reduced biomass	Leaf succulence, stomatal regulation	(Wang et al., 2019)
Salinity stress	Salt-metal synergism	Ion toxicity	Na^{+}/K^{+} imbalance	Root cortex	Reduced root elongation	Salt secretion through glands, selective ion uptake	(Das et al., 2016)
Metal-specific toxicity	Unique metal binding	Specific metabolic disruption	DNA/protein interaction	Nucleus, ribosome	Protein malfunction, DNA breaks	Chelation and vacuolar sequestration of metals	(Puthusseri et al., 2021)
Redox imbalance	Altered redox status	Redox potential shift	GSH depletion, NAD(P)H changes	Cytosol	Loss of redox homeostasis	Redox homeostasis via antioxidant network	(Marchand et al., 2011b)
pH fluctuation stress	Soil acidification/alkalinity	Disrupted ion availability	Precipitation or mobilization of metals	Rhizosphere	Metal solubility change	Rhizosphere pH regulation via exudates	(Rath & Das, 2023)
Membrane instability	ROS, lipid degradation	Permeability alteration	Phospholipid breakdown	Cell membrane	Electrolyte leakage	Stabilization via lipid remodeling and Ca^{2+} signaling	(Huang et al., 2024)

6.2 Nutrient imbalance, water stress, and cellular stability

Mangroves face multifaceted physiological challenges under heavy metal exposure, including nutrient imbalance, water stress, salinity stress, and metal-specific toxicity. Nutrient imbalance occurs when heavy metals compete with essential nutrients, disrupting their uptake and transport through xylem and phloem, leading to deficiencies that manifest as chlorosis and diminished photosynthesis. Mangroves respond by reallocating nutrients and forming symbiotic relationships with mycorrhizal fungi to enhance nutrient absorption (Yan et al., 2017). Water stress, often linked to reduced root water uptake in contaminated environments, triggers decreased transpiration and elevated abscisic acid (ABA) levels, prompting stomatal closure and reduced biomass. Adaptive features, such as leaf succulence and regulated stomatal behavior, help maintain water balance (Wang et al., 2019). Salinity stress is amplified by the synergistic effects of salt and metal toxicity, resulting in Na^+/K^+ imbalance within root cortical cells, impairing root elongation. Mangroves mitigate this through selective ion uptake and active salt excretion via glands (Das et al., 2016). In natural field settings, salinity stress rarely occurs in isolation, but is often compounded by simultaneous exposure to heavy metals. Such combined stress amplifies ionic disequilibria, enhances oxidative damage, and reduces overall plant vigor compared to single-stressor scenarios. Field observations suggest that mangrove tolerance under these dual pressures depends on synergistic defense strategies, including salt-gland excretion coupled with vacuolar sequestration of metals, highlighting the ecological relevance of integrated stress responses. Furthermore, metal-specific toxicity targets vital cellular components, where metals bind directly to DNA or proteins, disrupting metabolic functions. To limit this, mangroves employ chelation and sequestration of metals into vacuoles, reducing cytosolic toxicity (Puthusseri et al., 2021).

In mangrove ecosystems exposed to heavy metals, several stressors further challenge cellular stability, including redox imbalance, pH fluctuation, and membrane instability. Redox imbalance, caused by shifts in redox potential and depletion of antioxidants like glutathione (GSH), disrupts redox homeostasis in the cytosol. Mangroves counteract this through an antioxidant network that stabilizes reactive oxygen species (Marchand et al., 2011b). pH fluctuation in the rhizosphere, driven by acidification or alkalinity, affects metal solubility and ion availability, either enhancing metal mobility or causing precipitation. To adapt, mangrove roots regulate rhizosphere pH via exudate secretion (Rath & Das, 2023). Membrane instability occurs under oxidative stress as lipids degrade, altering membrane permeability and causing electrolyte leakage. Mangroves stabilize membranes through lipid remodeling and calcium-mediated signaling pathways, ensuring cellular integrity under heavy metal toxicity (Huang et al., 2024).

7. Mangroves as effective bioaccumulators of heavy metals

Mangrove species exhibit remarkable abilities to accumulate heavy metals such as cadmium (Cd) and chromium (Cr), particularly in their root systems, demonstrating their strong potential for phytostabilization in contaminated coastal areas (**Table 3**). For cadmium, species like *Kandelia candel* show exceptional root accumulation (55.2 μg g^{-1}) with a high root bioconcentration factor (BCF_{root} = 27.65), indicating strong retention in below-ground tissues and limited translocation to shoots (TF = 0.015) (Wang et al., 2013). Similarly, *Avicennia marina* accumulates Cd significantly in roots (1.5 μg g^{-1}) with a high BCF_{root} (2.54) but minimal translocation (TF = 0.01) (Nath et al., 2013). In contrast, chromium uptake varies widely among species. *Bruguiera gymnorrhiza* and *Kandelia candel* exhibit high root Cr accumulation (25.61 and 21.4 μg g^{-1}, respectively) and BCF_{root} values over 18, suggesting effective metal sequestration (Wang et al., 2013). Interestingly, *Acanthus ilicifolius* shows higher translocation for Cr (TF = 0.21), implying differential partitioning (Yan et al., 2017). Overall, mangroves maintain metal homeostasis by sequestering metals in roots while minimizing transport to aerial tissues, making them excellent candidates for mitigating heavy metal pollution in coastal zones.

Mangroves exhibit a substantial ability to accumulate copper (Cu) and mercury (Hg), contributing to their role as natural phytoremediators in polluted coastal zones. For copper, *Acanthus ilicifolius* and *Bruguiera gymnorrhiza* show high root accumulation (105.99 and 60.5 µg g^{-1}, respectively) and root bioconcentration factors (BCF_{root} = 2.6 and 3.4), suggesting efficient uptake and below-ground sequestration (Wang et al., 2013). In contrast, *Kandelia candel* displays a unique pattern with relatively high leaf accumulation (11 µg g^{-1}) and a high translocation factor (TF = 0.9), indicating greater shoot transport. For mercury, *Rhizophora apiculata* exhibits the most impressive root accumulation (4.3 µg g^{-1}) and BCF_{root} (25.3), reflecting its exceptional retention capacity (Ding et al., 2011). Similarly, *Rhizophora stylosa* shows a high BCF_{root} of 5.39 and TF of 0.74, emphasizing its dual capability in uptake and translocation. These patterns underscore the species-specific differences in heavy metal handling, with some mangroves favoring root sequestration, and others capable of moderate aerial transport, making them suitable for targeted phytoremediation strategies depending on site contamination profiles.

A cross-study comparison further reinforces the importance of standardized metrics, such as translocation factor (TF), bioconcentration factor (BCF), and bioaccumulation factor (BAF), for evaluating phytoremediation potential in mangroves. When expressed in these terms, species-specific strategies become clearer. For cadmium (Cd), *Kandelia candel* consistently demonstrates very high root BCF values (>27) coupled with extremely low TF (<0.02), underscoring its efficiency for root-level phytostabilization. In contrast, *Acanthus ilicifolius* and *Sonneratia apetala* show higher TF values (0.3 - 0.4), suggesting greater potential for limited phytoextraction. For chromium (Cr), *Bruguiera gymnorrhiza* and *Kandelia candel* exhibit strong root sequestration (BCFroot >18), whereas *Acanthus ilicifolius* displays a relatively higher TF (0.21), indicating differential partitioning to shoots. In the case of copper (Cu), *Acanthus ilicifolius* and *Bruguiera gymnorrhiza* are effective accumulators with BCFroot >2.5, while *Kandelia candel* is unique for its high shoot translocation (TF ≈ 0.9), making it a candidate for phytoextraction applications. For mercury (Hg), *Rhizophora apiculata* exhibits exceptional retention capacity (BCFroot >25), whereas *Rhizophora stylosa* combines uptake with moderate translocation (TF = 0.74), balancing stabilization and aerial transport. Finally, for lead (Pb) and zinc (Zn), *Avicennia marina* and *Kandelia candel* demonstrate robust root accumulation (BCFroot >1.9), while *Kandelia candel* again stands out for its relatively higher TF in Zn (0.8), offering versatility depending on remediation goals. These patterns highlight that targeted phytoremediation strategies can be developed by matching contaminant profiles with species-specific accumulation traits, ensuring that management interventions are both site-appropriate and metal-specific.

Extending the evidence of metal accumulation capacity among mangrove species, manganese (Mn), lead (Pb), and zinc (Zn) also demonstrate differential uptake and storage behavior. *Avicennia marina* consistently shows substantial Mn accumulation in both leaves and roots, reaching up to 544 µg g^{-1} in roots, with moderate translocation factors (TF = 0.64), suggesting dual uptake and sequestration potential (Yadav et al., 2023). For lead (Pb), species like *Kandelia candel* and *Avicennia marina* stand out with high root concentrations (up to 189 µg g^{-1}) and BCF_{root} > 1.9, highlighting their phytostabilization efficacy (Nath et al., 2013). However, low TF values across most species suggest Pb is primarily retained in roots. In the case of Zn, *Sonneratia apetala* and *Avicennia marina* exhibit remarkable root accumulation (up to 378 µg g^{-1}), with *Kandelia candel* showing a relatively high TF (0.8), indicating notable shoot transport (Yan et al., 2017). These data emphasize species-specific metal handling strategies, reaffirming mangroves' vital role in coastal phytoremediation across a wide spectrum of heavy metals.

Table 3 Heavy metal accumulation, translocation, and bioconcentration in mangrove species.

Heavy metals	Mangrove species	Leaf (μg g^{-1})	Root (μg g^{-1})	TF	$BCF_{shoot/leaf}$	BCF_{root}	References
Cd	*Avicennia marina*	0.01	1.5	0.01	0.02	2.54	(Nath et al., 2013)
Cd	*Aegiceras corniculatum*	0.15	0.35	0.33	0.37	1.08	(Wang et al., 2013)
Cd	*Avicennia marina*	0.09	0.36	0.25	0.23	0.9	(Wang et al., 2013)
Cd	*Acanthus ilicifolius*	0.09	0.2	0.41	0.22	0.51	(Wang et al., 2013)
Cd	*Kandelia candel*	0.83	55.2	0.015	0.04	27.65	(Wang et al., 2013)
Cd	*Sonneratia apetala*	0.15	0.41a	0.37	0.39	1.05	(Wang et al., 2013)
Cd	*Bruguiera gymnorrhiza*	0.14	0.25	0.56	0.55	0.98	(Yan et al., 2017)
Cr	*Avicennia marina*	6.95	15.6	0.45	0.02	0.05	(Yadav et al., 2015)
Cr	*Avicennia marina*	0.49	21	0.02	0.02	0.68	(Nath et al., 2013)
Cr	*Aegiceras corniculatum*	0.3	11.2	0.01	0.05	3.1	(Wang et al., 2013)
Cr	*Bruguiera gymnorrhiza*	0.59	25.61	0.02	0.7	29.3	(Wang et al., 2013)
Cr	*Kandelia candel*	3.3	21.4	0.15	2.85	18.44	(Wang et al., 2013)
Cr	*Sonneratia apetala*	1	12.3a	0.08	0.5	6.15	(Wang et al., 2013)
Cr	*Acanthus ilicifolius*	2.99	13.1	0.21	1.61	7.3	(Yan et al., 2017)
Cu	*Acanthus ilicifolius*	17	105.99	0.171	0.41	2.6	(Wang et al., 2013)
Cu	*Sonneratia apetala*	8	153a	0.05	0.09	1.64	(Wang et al., 2013)
Cu	*Avicennia marina*	5	14	0.36	0.14	0.39	(Yan et al., 2017)
Cu	*Avicennia marina*	15	62	0.24	0.03	0.12	(Yan et al., 2017)
Cu	*Bruguiera gymnorrhiza*	11.99	60.5	0.21	0.68	3.4	(Yan et al., 2017)
Cu	*Kandelia candel*	11	1.2	0.9	1.2	1.33	(Yan et al., 2017)
Hg	*Aegiceras corniculatum*	0.97	1.44	0.67	2.21	3.32	(Ding et al., 2011)
Hg	*Avicennia marina*	0.6	0.699	0.85	1.89	2.25	(Ding et al., 2011)
Hg	*Kandelia candel*	0.66	2.17	0.3	1.5	4.93	(Ding et al., 2011)
Hg	*Rhizophora apiculata*	1.4	4.3	0.33	8.24	25.3	(Ding et al., 2011)
Hg	*Rhizophora stylosa*	1.76	2.38	0.74	3.99	5.39	(Ding et al., 2011)
Mn	*Rhizophora mucronata*	6.8	N/A	N/A	0.99	N/A	(Yadav et al., 2015)
Mn	*Avicennia marina*	348	544	0.64	0.23	0.35	(Yadav et al., 2023)

Table 3 (continued) Heavy metal accumulation, translocation, and bioconcentration in mangrove species.

Heavy metals	Mangrove species	Leaf (μg g^{-1})	Root (μg g^{-1})	TF	$BCF_{shoot/leaf}$	BCF_{root}	References
Mn	*Acanthus ilicifolius*	6.2	N/A	N/A	0.6	N/A	(Yadav et al., 2023)
Mn	*Avicennia marina*	39	105	0.37	0.65	1.75	(Nath et al., 2013)
Pb	*Rhizophora mangle*	0.01	0.2	0.07	N/A	0.02	(Fernández-Cadena et al., 2014)
Pb	*Avicennia marina*	0.74	189	0.004	0.01	1.98	(Nath et al., 2013)
Pb	*Aegiceras corniculatum*	0.88	19.9	N/A	0.21	0.33	(Wang et al., 2013)
Pb	*Acanthus ilicifolius*	1.65	18.21	0.091	0.029	0.33	(Wang et al., 2013)
Pb	*Bruguiera gymnorrhiza*	1.71	21.98	0.08	0.039	0.55	(Wang et al., 2013)
Pb	*Sonneratia apetala*	0.7	22.1a	0.03	0.01	0.31	(Wang et al., 2013)
Pb	*Avicennia alba*	3.9	4	0.975	0.06	0.07	(Yan et al., 2017)
Pb	*Avicennia marina*	8	15	0.55	0.24	0.44	(Yan et al., 2017)
Pb	*Kandelia candel*	11	28	0.39	0.37	0.95	(Yan et al., 2017)
Zn	*Avicennia marina*	14	378	0.04	0.09	2.42	(Nath et al., 2013)
Zn	*Bruguiera gymnorrhiza*	12	47.01	0.26	0.11	0.45	(Wang et al., 2013)
Zn	*Sonneratia apetala*	40	108a	0.37	0.17	0.45	(Wang et al., 2013)
Zn	*Aegiceras corniculatum*	11.91	99.05	0.125	0.07	0.55	(Yan et al., 2017)
Zn	*Kandelia candel*	23	29	0.8	0.49	0.61	(Yan et al., 2017)

8. Phytotoxicity and stress responses of mangroves to metal exposure

Heavy metal exposure significantly affects the underground parts of mangrove plants, particularly the root system, which acts as the primary barrier for metal uptake from the environment (**Table 4**). Studies have shown that exposure to Cd^{2+}, Cu^{2+}, and Zn^{2+} leads to reduced root biomass, diameter, and length. For instance, *Kandelia obovata* treated with Cd and Zn for six months experienced severe reductions in root growth parameters (Du et al., 2013). Similarly, *Avicennia marina* exposed to Cu^{2+}, Zn^{2+}, Pb^{2+}, and Hg^{2+} for 12 months displayed decreased root biomass, height, and diameter (MacFarlane & Burchett, 2002). Cd^{2+} exposure also inhibited root catalase isoenzymes in *Bruguiera gymnorrhiza* within just 60 days (Yi-ming et al., 2008), highlighting the biochemical sensitivity of mangrove roots. Moreover, zinc exposure caused structural changes such as thickening of the outer cortex and increased lignification in roots of multiple species, including *Aegiceras corniculatum* and *Rhizophora stylosa* (Cheng et al., 2010). These findings suggest that mangrove roots exhibit both morphological and biochemical responses under heavy metal stress, playing a crucial role in initial metal sequestration and stress mitigation.

Mangroves possess adaptive mechanisms to counteract oxidative stress caused by heavy metals, primarily through the activation of antioxidant enzymes. *Aegiceras corniculatum*, when exposed to low concentrations of Cd^{2+} (0.5 μg/L), showed increased activities of peroxidase (POD) and superoxide dismutase (SOD), suggesting an upregulated detoxification response (Shengchang &

Qi, 2003). In combined metal treatments involving Pb^{2+}, Cd^{2+}, and Hg^{2+}, *Kandelia candel* and *Bruguiera gymnorrhiza* displayed elevated concentrations of SOD, POD, CAT, and malondialdehyde (MDA) in root tissues (Zhang et al., 2007). Notably, *Rhizophora stylosa* under Cd^{2+} stress showed high protein accumulation and moderate MDA levels but relatively low antioxidant enzyme activity, indicating species-specific oxidative stress tolerance (Zhou et al., 2021). Furthermore, a gradient toxicity study involving Cu, Pb, Cd, and Hg showed that *R. stylosa* exhibited the strongest enzymatic antioxidant response at moderate toxicity (T3), compared to other mangroves such as *Ceriops tagal* (Yong & Youshao, 2022). These enzymatic profiles reveal not only the biochemical capacity of mangroves to mitigate metal-induced stress, but also highlight the differential sensitivity and resilience mechanisms among species in contaminated habitats.

Table 4 Experimental evidence of heavy metal toxicity in mangrove roots and shoots.

Mangrove species	Treatment duration	Concentrations	Heavy metals	Experimental layout	HMs effects on underground parts	References
Aegiceras corniculatum	60 days	0.05, 0.5, 5, 50, 100 µg/L	Cd^{2+}	Sand culture with constant flooding	Growth, POD, SOD promoted at 0.5 µg/L Cd	(Shengchang & Qi, 2003)
Aegiceras corniculatum	28 days (measured at 0, 3, 7, 14, 28 days)	Cu: 5 - 75 mg/L, Pb: 1 - 15 mg/L, Cd: 0.2 - 3 mg/L	Cu^{2+}, Pb^{2+}, Cd^{2+}	Pot experiment in sand with Cu^{2+}, Pb^{2+}, Cd^{2+} and mixture	High POD response under all metals; rapid protein increase; sensitive but responsive enzymatically	(Zhou et al., 2021)
Aegiceras corniculatum	6 months	0, 5, 10, 20, 30 mg/L for each metal	Cu^{2+}, Zn^{2+}, Cd^{2+}	Greenhouse pot experiment with Hoagland medium and sandy soil, treated with $CuCl_2$, $ZnCl_2$, $CdCl_2$	Heavy metals reduced biomass and altered carbohydrate metabolism: increased soluble sugar, decreased starch. TP and CT levels significantly increased, especially extractable and protein-bound CT fractions	(Guangqiu et al., 2007)
Aegiceras corniculatum, *Bruguiera gymnorrhiza*, *Rhizophora stylosa*	120 days	200, 400, 600, 800 mg/kg DW	Zn^{2+}	Sand culture with constant flooding	Zn inhibited root permeability, thickened outer cortex, and increased cell wall lignification	(Cheng et al., 2010)
Avicennia alba and Rhizophora apiculata	3 months	Pb (0, 0.03, 0.3 and 3 mg L^{-1}) and Cd (0, 0.005; 0.05 and 0.5 mg L^{-1})	Pb^{2+} and Cd^{2+}	Hydroponic setting	Inhibited root elongation and reduced root thickness	(Sari & and Din, 2012)
Avicennia germinans	Natural field exposure (sampling of soil and leaf tissue)	Sediment: Zn > Cu > Cr > Pb > As > Cd > Hg (exact values in ppm on Fig. 6); leaf BCFs: Cd up to 30, Hg < 5	Zn, Pb, Hg, Cu, Cr, Cd, As	Field study at 3 sites (A: urban, B: park, C: island)	Highest BCFs for Pb and Hg in senescent leaves; consistently **negative RT% for Hg** across all sites → indicates active phytoextraction	(Maldonado-Román et al., 2016)
Avicennia marina	12 months	Hg^{2+}, Pb^{2+}, Zn^{2+}, and Cu^{2+} (40, 80, 120, and 160 mg kg^{-1} DW)	Cu^{2+}, Zn^{2+}, Pb^{2+}, and Hg^{2+}	Soil medium formulated commercially and subjected to intermittent inundation.	Decreased biomass, length, and thickness of roots	(MacFarlane & Burchett, 2002)

Table 4 (continued) Experimental evidence of heavy metal toxicity in mangrove roots and shoots.

Mangrove species	Treatment duration	Concentrations	Heavy metals	Experimental layout	HMs effects on underground parts	References
Avicennia marina	12 months	40, 80, 120, 160 mg/kg DW	Cu^{2+}, Zn^{2+}, Pb^{2+}, Hg^{2+}	Composed soil culture with constant flooding	Root and leaf biomass, chlorophyll, CO_2 exchange, and photosystem II yield declined with higher metal doses; Cu and Zn excreted via salt glands; Hg and Pb not detected	(Naidoo et al., 2014)
Avicennia marina	50 days	250, 500, 1000 mg/L	Pb^{2+}	Sand culture with constant flooding	Biomass of leaf and root decreased significantly at 500 mg/L Pb; roots only affected at 1000 mg/L	(Yan et al., 2015)
Avicennia marina	50 days	250, 500, and 1000 mg L^{-1}	Pb^{2+}	Sand culture with periodic flooding	Decreased root biomass was observed at 1000 mg/L Pb exposure, along with elevated levels of MDA, and enhanced activities of SOD and POD enzymes	(Yan et al., 2010)
Avicennia marina	Natural condition, sampled over 60 points (no artificial duration)	Sediment: Pb (4.9 - 534 mg/kg), Zn (9.3 - 668 mg/kg), Cu (1 - 206 mg/kg), Cr (1.3 - 199 mg/kg), others: see full data	As, Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb, Zn	Field study (water and sediment exposure)	Fine roots stored more metals than sediment, with low leaf transfer (TF < 0.13) and root BCF up to 3.5, mainly for Mn, Fe, Cu, and Zn	(Nath et al., 2014)
Avicennia marina	28 days (measured at 0, 3, 7, 14, 28 days)	Cu: 5 - 75 mg/L, Pb: 1 - 15 mg/L, Cd: 0.2 - 3 mg/L	Cu^{2+}, Pb^{2+}, Cd^{2+}	Pot experiment in sand with Cu^{2+}, Pb^{2+}, Cd^{2+} and mixture	Highest SOD, CAT, and POD activities among species; MDA content significantly increased under Cd and mixed metals; strong tolerance to oxidative stress	(Zhou et al., 2021)
Avicennia marina	0, 1, 2, 4, 8, 12, 16, 20 weeks	Sediment: Zn (75.1), Cr (66.6), Ni (65.5), Pb (55.2), Cu (17.8), Cd (0.21) mg/kg Leaf: varies by stage, e.g., Pb in senescent leaf = 2.04 mg/kg	Cu, Zn, Cr, Ni, Cd, Pb	Field collection of leaves (young, mature, senescent) + litterbag decomposition (0 - 20 weeks) in estuary	Cu & Zn decreased with leaf age; Pb increased with age; all metals increased during decomposition; Cu, Zn, Cd in litter ≈ sediment; Cr, Ni, Pb < sediment	(Lang et al., 2023)
Avicennia marina	Not specified (natural aging)	Leaf: Cu = 2 - 3 mg/kg DW; Fe = 262 - 555 mg/kg; Pb = 8.6 - 8.7 mg/kg Soil (top 30 cm): Fe = 2,740 - 10,500 mg/kg, Pb = 1 - 2.5 mg/kg	Al, As, Cd, Cr, Cu, Fe, Mn, Mo, Ni, Pb, Sr, V, Zn	Field sampling of leaves and soils at 4 sites in the Central Red Sea (KSA): 91 leaves and 26 soil cores analyzed	V, Cd, and As rose with leaf age, showing remobilization; only Cu reabsorbed (~51 %) before senescence. Mangroves transferred metals to surface via litter	(Almahasheer et al., 2018)

Table 4 (continued) Experimental evidence of heavy metal toxicity in mangrove roots and shoots.

Mangrove species	Treatment duration	Concentrations	Heavy metals	Experimental layout	HMs effects on underground parts	References
Avicennia marina and Kandelia obovata	9 days	P (0, 30, 90) mg kg^{-1} as KH_2PO_4 and Cd (0, 0.5, 5) as $CdCl_2 \cdot 2.5H_2O$	Cd^{2+} and P^{3+}	Hydroponic culture	Higher root permeability with reduced biomass and smaller diameter	(Dai et al., 2018)
Avicennia sp., *Rhizophora sp.*	Not a time-course treatment; field inventory and risk assessment study	As: 3.33 - 21.15 mg/kg; Pb: 7.61 - 22.75 mg/kg; Zn: 39.67 - 122.52 mg/kg (others also quantified)	As, Pb, Zn, Fe, Al, Mn, Ni, Cr, Cu	Sediment core sampling from Puzi River mouth wetland (active vs partial tidal zones), Taiwan	Arsenic was the main contaminant; Pb and Zn were moderate. Rhizospheric PGPR bacteria showed arsenic resistance and PGP traits, aiding in metal stress reduction and root health	(Dey et al., 2022)
Bruguiera gymnorrhiza	60 days	1, 10, 20, 30 mM	Cd^{2+}	Sand culture with constant flooding	1 mM Cd significantly inhibited CAT isoenzymes in root	(Yi-ming et al., 2008)
Bruguiera gymnorrhiza	28 days (measured at 0, 3, 7, 14, 28 days)	Cu: 5 - 75 mg/L, Pb: 1 - 15 mg/L, Cd: 0.2 - 3 mg/L	Cu^{2+}, Pb^{2+}, Cd^{2+}	Pot experiment in sand with Cu^{2+}, Pb^{2+}, Cd^{2+} and mixture	Highest protein content under Cu^{2+}; low MDA; CAT and POD increased moderately	(Zhou et al., 2021)
Kandelia candel	90 days	Cu^{2+}: 0.1, 1, 5, 10 mg/L; Zn^{2+}: 1, 5, 25, 50, 125 mg/L	Cu^{2+}, Zn^{2+}	Water culture	EC_{50} for Cu: 3.8 mg/L; EC_{50} for Zn: 46.3 mg/L	(Chiu et al., 1995)
Kandelia candel	90 days	Cr^{3+}(1, 1.5, 2, 2.5, and 3 mg L^{-1})	Cr^{3+}	Sand culture with periodic flooding	Decreased root biomass by 60.65 % and inhibited root development	(Rahman et al., 2009)
Kandelia candel	90 days	25 mg L^{-1}	Cd^{2+}	Hydroponic setting	Suppressed root lengthening, thickness, and overall mass	(Rahman et al., 2011)
Kandelia candel and *Bruguiera gymnarrhiza*	60 days	Hg^{2+} (0.2, 1, 2, and 3 mg L^{-1}), Cd^{2+} (0.2, 1, 2, and 3 mg L^{-1}), and Pb^{2+} (1, 5, 10, and 15 mg L^{-1})	Pb^{2+}, Cd^{2+}, and Hg^{2+}	Sand culture with periodic flooding	Elevated levels of CAT, POD, SOD, and MDA were detected in roots under combined exposure to Pb, Cd, and Hg	(Zhang et al., 2007)
Kandelia candel and *Bruguiera gymnorrhiza*	30 days	Hg (0.1 and 1.5 mg L^{-1}), Pb (1 and 10 mg L^{-1}), and Cd (0.1 and 0.5 mg L^{-1})	Cd^{2+}, Pb^{2+}, and Hg^{2+}	Hydroponic setting	Concentrations >T1 caused breakdown of leaf chlorophylls, elevated proline, GSH, and PC-SH levels in leaves under stress	(Huang & Wang, 2010)
Kandelia obovata	30 days	Zn (500, 100, 0) mg/kg dry wt. and Cd (5, 2.5, 0) mg/kg dry wt.	Cd^{2+} and Zn^{2+}	Pot culture experiments	Cd and Zn notably inhibited root elongation, whereas the presence of phenolic acids enhanced root tolerance to these metals	(Chen et al., 2020)
Kandelia obovata	60 days	Cd-contaminated soil (3.99 mg kg^{-1}), Zn (0, 80,300, and 400 mg kg^{-1})	Cd^{2+} and Zn^{2+}	Pot experiment	N/A	(Chen, 2022)

Table 4 (continued) Experimental evidence of heavy metal toxicity in mangrove roots and shoots.

Mangrove species	Treatment duration	Concentrations	Heavy metals	Experimental layout	HMs effects on underground parts	References
Kandelia obovata	6 months	0, 2.5, 5, 10, 20, 40 mg Cd kg^{-1} dry weight	Cd^{2+}	Pot and hydroponic setting	Decreased root mass, thickness, elongation, and overall dry weight	(Du et al., 2013)
Kandelia obovata	3 months	Cd (0, 2.5, 5, 10, 20, and 40 mg L^{-1})	Cd^{2+}	Pot experiment	Elevated LMWOAs and amino acids; reduced GSH and protein in roots	(Xie et al., 2013)
Kandelia obovata	28 days (measured at 0, 3, 7, 14, 28 days)	Cu: 5 - 75 mg/L, Pb: 1 - 15 mg/L, Cd: 0.2 - 3 mg/L	Cu^{2+}, Pb^{2+}, Cd^{2+}	Pot experiment in sand with Cu^{2+}, Pb^{2+}, Cd^{2+} and mixture	High protein accumulation and antioxidant enzyme activity under Pb^{2+}; moderate MDA increase	(Zhou et al., 2021)
Kandelia obovata	Same	Similar pattern; e.g., Cu in young leaf = 0.34 mg/kg, increases linearly over 20 weeks to ~13.7 mg/kg	Cu, Zn, Cr, Ni, Cd, Pb	Same as above	Cu, Zn, Cd showed strong accumulation; Ni, Pb levels stayed low in decomposition; tannins affected metal migration and binding	(Lang et al., 2023)
Laguncularia racemosa	30 days	0.05, 0.5 mg/L	Cr^{3+}	Water culture	Growth, pigments, gas exchange unaffected by Cr levels	(Rocha et al., 2009)
Laguncularia racemosa	Natural field exposure (sampling of soil and leaf tissue)	BCFs for Cd < 30, others < 5 (varied by site)	As, Cd, Cr, Cu, Hg, Pb, Zn	Field study at 3 sites (A: urban, B: park, C: island)	Positive RT% for Cu, Pb (Site C), negative for As and Zn; anatomical root changes suggest suitability as bioindicator species	(Maldonado-Román et al., 2016)
Rhizophora apiculata	6 months	500, 1,000 mg/L	Cr^{3+}	Soil culture with periodic flooding	Stomatal density increased under Cr stress, especially in salty conditions	(Nguyen et al., 2017)
Rhizophora apiculata	42 years (1978 - 2020)	Soil: Cu = 60.4 - 134.0 mg/kg; Cr = 3.76 - 21.14 mg/kg; Ni = 2.63 - 12.01 mg/kg Roots: Cu = 0.21 - 8.17; Cr = 0.26 - 11.7; Ni = 0.11 - 8.54 mg/kg	Cu, Cr, Ni	Field study at 208 plots in Can Gio Mangrove Forest (Vietnam); 11 plots sampled for HM analysis; scenario simulations for 42 years	HMs accumulated in root and leaf tissues; root Cr > Cu > Ni. High root HM levels (>20 mg/kg total) led to reduced growth rates. Retention confirmed via long-term tissue accumulation and EF values	(Nguyen et al., 2020)
Rhizophora mangle	21 days	Pb^{2+}: 62.5, 125, 250 µg/g DW; Cd^{2+}: 25, 250, 500 µg/g DW; Hg^{2+}: 10, 100, 500 µg/g DW	Pb^{2+}, Cd^{2+}, Hg^{2+}	Waterlogged muddy sand medium under continuous inundation.	No effect of Pb up to 250 µg/g; survival affected by 500 µg/g Hg	(Walsh et al., 1979)
Rhizophora mangle	Natural field exposure (sampling of soil and leaf tissue)	Highest metal in sediment: Zn (up to 87.6 ppm), Cu (up to 53.9 ppm), As (up to 23.5 ppm)	As, Cd, Cr, Cu, Hg, Pb, Zn	Field study at 3 sites (A: urban, B: park, C: island)	Root exclusion likely via iron plaque; positive RT% for Cu (Site A), for As, Cd, Pb (Site C); low leaf accumulation; may immobilize metals at root-sediment interface	(Maldonado-Román et al., 2016)

Table 4 (continued) Experimental evidence of heavy metal toxicity in mangrove roots and shoots.

Mangrove species	Treatment duration	Concentrations	Heavy metals	Experimental layout	HMs effects on underground parts	References
Rhizophora stylosa	28 days (measured at 0, 3, 7, 14, 28 days)	Cu: 5 - 75 mg/L, Pb: 1 - 15 mg/L, Cd: 0.2 - 3 mg/L	Cu^{2+}, Pb^{2+}, Cd^{2+}	Pot experiment in sand with Cu^{2+}, Pb^{2+}, Cd^{2+} and mixture	High protein content under Cd^{2+}; moderate MDA; lower antioxidant enzyme response	(Zhou et al., 2021)
Rhizophora stylosa, *Kandelia obovata*, *Bruguiera gymnorhiza*, *Ceriops tagal*	28 days	Cu: 0 - 112.5 mg/L; Pb: 0 - 22.5 mg/L; Cd: 0 - 4.5 mg/L; Hg: 0 - 4.5 mg/L	Cu^{2+}, Pb^{2+}, Cd^{2+}, Hg^{2+}	Seedlings in pot trials exposed to Cu, Pb, Cd, Hg at five levels (CK–T4); assessed enzyme activity and stress markers	SOD and POD peaked then declined; R. stylosa (T3) showed best antioxidant defense, C. tagal (T1) the weakest. MDA rose with dose	(Yong & Youshao, 2022)
Sonneratia apetala	4.5 months (May - Oct 2005)	CK: Cu 0.0057; Pb 0.0024; Zn 0.197; Cd 0.0002 mg/L SW: Cu 2; Pb 1; Zn 5; Cd 0.1 FW: Cu 10; Pb 5; Zn 25; Cd 0.5 TW: Cu 20; Pb 10; Zn 50; Cd 1	Cu^{2+}, Pb^{2+}, Zn^{2+}, Cd^{2+}	Greenhouse pot test with 4 treatments: control, standard, 5×, and 10× wastewater, enriched with nutrients and metals	Root vitality and CAT unchanged; POD and SOD rose with metal levels	(Zhang et al., 2011)

Field-based observations further illustrate mangroves' capacity to accumulate and regulate heavy metals, which varies depending on species and site conditions. *Avicennia germinans* showed high bio-concentration factors (BCFs) for Pb and Hg in senescent leaves, with consistently negative translocation rates for Hg across urban and park environments, indicating active root-level retention and selective exclusion (Maldonado-Román et al., 2016). Similarly, *Avicennia marina* sampled across 60 locations revealed that fine roots accumulated heavy metals more intensely than surrounding sediment, with BCFs up to 3.5 for Mn and Fe, and minimal upward translocation (TF < 0.13) for most metals (Nath et al., 2014). Moreover, leaf aging influences metal accumulation patterns; for example, Pb concentration increased with leaf senescence, while Cu was partially reabsorbed before leaf drop, reflecting a regulatory strategy (Almahasheer et al., 2018). These physiological behaviors demonstrate the mangrove's complex internal detoxification and recycling mechanisms. Coupled with structural root modifications- such as iron plaque formation in *Rhizophora mangle*- these traits enable mangroves to immobilize or remobilize metals efficiently, making them effective biofilters and potential candidates for phytoremediation in metal-polluted coastal ecosystems.

A comparative view of root and shoot responses reveals that underground tissues are generally more sensitive to heavy metal exposure than aerial parts. Root biomass and elongation often declined by more than 50 % under high Cd or Pb concentrations, while shoot parameters, such as leaf chlorophyll or photosystem II efficiency, tended to show more gradual reductions, often below 30 % until prolonged exposure was reached. Biochemically, roots exhibited rapid antioxidant responses, with sharp increases in catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) activities within weeks of exposure, whereas shoots displayed delayed or lower enzymatic activation. This contrast highlights the role of roots as the primary barrier and first line of detoxification in mangroves.

While EC_{50} values or precise tolerance thresholds were not consistently reported across studies, and are therefore not included in **Table 4**, available dose–response evidence indicates that *Kandelia candel* tolerates moderate Zn and Cu levels (EC_{50} for Zn ≈ 46.3 mg/L; Cu ≈ 3.8 mg/L), whereas *Rhizophora stylosa* maintains antioxidant defenses longer under multi-metal treatments, compared to *Ceriops tagal* and *Bruguiera gymnorrhiza*. Overall, *Rhizophora stylosa* and *Avicennia marina* emerge as promising candidates for phytoremediation, due to their ability to sustain growth and activate stress enzymes under combined metal exposures, making them suitable for application in contaminated coastal zones.

9. Conclusions and future prospects

This review consolidates current evidence that mangrove ecosystems play a pivotal role in regulating and mitigating heavy metal contamination within coastal landscapes. Their natural adaptations, including the development of specialized root systems, rhizosphere oxidation, and selective metal sequestration in belowground tissues, allow them to function as highly effective phytoremediators. Numerous studies have demonstrated that mangroves can act both as sinks and regulators of heavy metals, with sediment organic content, salinity, and redox potential shaping the balance between immobilization and release. The consistent accumulation of cadmium, lead, chromium, and mercury across regions such as Southeast Asia, the Middle East, and South Asia highlights their global ecological significance. However, efficiency is not uniform across taxa; species such as *Avicennia marina*, *Kandelia candel*, and *Rhizophora stylosa* display variable bioaccumulation factors and translocation efficiencies depending on sediment chemistry and hydrological conditions. This emphasizes the necessity of localized management strategies that consider both species-specific physiology and site-level geochemistry. Land-use practices also contribute unique metal signatures, with aquaculture often linked to copper enrichment, traffic and urban runoff associated with lead, and industrial development contributing chromium and zinc. Recognizing these patterns is essential to design monitoring programs that capture spatial heterogeneity and inform pollution source attribution. A clearer understanding of these ecological and geochemical interactions can provide a stronger foundation for applying mangroves as part of holistic, ecosystem-based strategies for coastal restoration and pollution control.

Future directions in mangrove phytoremediation research must move beyond descriptive surveys toward mechanistic and technology-driven approaches. Omics-based tools, such as transcriptomics, metabolomics, and proteomics, can identify tolerance genes and molecular pathways responsible for heavy metal detoxification and adaptive responses. Integrating such knowledge with transgenic approaches could enhance stress resilience under severe contamination, while microbial enhancement through inoculation with beneficial rhizosphere consortia has potential to improve both metal immobilization and plant health. These innovations highlight opportunities for synergy between ecological science and applied biotechnology in addressing one of the most pressing coastal challenges. At the policy level, mangrove phytoremediation can be embedded into ecosystem-based restoration initiatives and urban coastal planning frameworks as a nature-based solution that delivers multiple co-benefits. This approach aligns directly with global sustainability agendas, contributing to SDG 13 (Climate Action) by strengthening resilience against climate-related hazards, SDG 14 (Life Below Water) through improved water quality, SDG 15 (Life on Land) via biodiversity conservation, and SDG 11 (Sustainable Cities and Communities) by supporting safer coastal settlements. Long-term monitoring programs and standardized metrics of phytoremediation success will be critical to assess progress and inform adaptive management. Ultimately, leveraging mangroves as green infrastructure integrates pollution control with shoreline stabilization, carbon sequestration, and livelihood protection. Such a comprehensive strategy requires sustained interdisciplinary collaboration among ecologists, engineers, biotechnologists, and policymakers to ensure that the scientific potential of mangrove phytoremediation is fully realized in practice and translated into durable coastal sustainability outcomes.

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CRediT author statement

Said Ali Akbar: Conceptualization; Methodology; Formal analysis; Writing - Original Draft; Visualization. **Zulkarnain Jalil:** Supervision; Validation; Project administration; Writing - Review & Editing. **Chitra Octavina:** Data Curation; Investigation; Resources. **Ichsan Setiawan:** Methodology; Software; Validation. **Maria Ulfah:** Formal analysis; Data Curation; Writing - Review & Editing. **Teuku Haris Iqbal:** Investigation; Resources; Visualization. **Edy Miswar:** Funding acquisition; Project administration.

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