

# Bioremediation of mercury contaminated soil and water: A review

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## Abstract

Mercury (Hg) pollution of soil and water environments is a major global threat to human health, agri-food systems and ecosystems and industrial activities mainly coal combustion augmented their content in different environmental media. Bioremediation is a nature-based solution involving microbial- and plant-based (phytoremediation) technologies that clean-up Hg contaminated sites. Here, we review Hg-resistant bacteria and how latest insights in our understanding of the cellular and biochemical mechanisms of the mer operon genes responsible for Hg resistance and transformation have facilitated developments in microbial Hg-bioremediation. We also review the phytoremediation mechanisms, including those of bacterial- and fungi-assisted phytoremediation processes, which have shown promising results in reducing Hg<sup>2+</sup> to Hg<sup>0</sup>. This review provides a detailed knowledge of novel Hg bioremediation mechanisms and methods. Consequently, microbial- and phyto-based bioremediation technologies have a critical role in the reclamation of Hg-contaminated environments and the protection of human health and ecosystems.

## KEYWORDS

bacteria, bioremediation, fungi, mer operon, mercury, microbes

## 1 | INTRODUCTION

Mercury (Hg) is a pervasive environmental pollutant that poses an imperative peril to human health and ecosystems (J. Chen et al., 2018). Hg is emitted to the natural environment through innumerable anthropogenic activities, including Hg mining and processing, artisanal gold mining, fossil fuel burning, waste burning or various other polluting activities, as well as natural processes, such

as forest fires and volcanic eruptions (Beckers & Rinklebe, 2017; Joy & Qureshi, 2023; O'Connor et al., 2019; Q. Yang et al., 2021). The emitted inorganic Hg (IHg) species, including Hg<sup>2+</sup> and Hg<sup>0</sup>, neutral Hg sulphides and Hg thiols, can be converted to the more toxic and bioavailable form of methylmercury (MeHg) by anaerobic microorganisms (Lyu et al., 2020; Xiang et al., 2022; J. Zhang, Li, et al., 2023; C. J. Zhang, Liu, et al., 2023; Z. Zhang, Zhao, et al., 2023).

Since the study of the Minamata disease in the 1950s, there has been growing concern about the accrual of Hg, mainly MeHg, in food and its potential influence on human health and the milieu. For example, studies have shown that MeHg can accrue in fish and other marine organisms, posing a risk to seafood consumers (Barst et al., 2022; Issifu et al., 2022; McKinney et al., 2022; Motta et al., 2022; Riesgo et al., 2023; Zampetti & Brandt, 2023), and MeHg is also found in elevated concentrations in rice, which threaten food security (Aslam et al., 2022; Hu et al., 2023; Y. Huang et al., 2023; Xie et al., 2023). Application of nano activated carbon and rice hull biochar decreases the uptake of Hg in rice plants (L. Wang, Hou, et al., 2020; J. Wang, Shaheen, et al., 2020; Xing et al., 2020).

Various remediation technologies have been developed for the removal of Hg from the environment (Inobeme et al., 2023; Teng et al., 2020). The goal of these methods is to either separate Hg from the environment or convert it to less harmful forms (Lewis et al., 2016; A. D. Singh et al., 2023). Among these methods, phytoremediation and microbial bioremediation are particularly promising with the characteristics of being environmentally friendly, easy to operate, cost-effective and favourable for maintaining soil health (Y. Guo, Sommer, et al., 2023; K. Guo, Yan, et al., 2023; Wani et al., 2023). The Hg toxicity is menacing diverse life forms, application of chemical agents for their remediation leading to more load on the environment is not an efficient solution. To conquer the limitations of conventional approaches, numerous eco-friendly methods are used. The application of microbe- and plant-dependent methods has got more consideration (Rahman & Singh, 2020). Large-scale application of Hg-volatilising bacteria is employed to clean Hg-polluted water and soils. There are several examples in which these are employed for removal of Hg from contaminated media (Mahbub et al., 2017; Velázquez-Riaño & Benavides-Otaya, 2016; Wagner-Döbler, 2013). In this review, we focus on bioremediation approaches for Hg remediation. Microbial bioremediation involves the use of living microorganisms to degrade or eliminate pollutants or unwanted substances from soil or water (El Moukhtari et al., 2023), whereas phytoremediation is a form of bioremediation that uses plants to degrade or uptake heavy metals in soil. Both approaches have been shown to be effective in removing Hg from the environment. The objective of this review was to provide latest information on promising materials and innovative methods in Hg removal from soil and water. This review provides comprehensive overview of phytoremediation approaches, and different bioremediation techniques and their mechanisms in Hg removal from the environment, and highlights their potential for application in sustainable Hg remediation.

## 2 | MICROBIAL BIOREMEDIATION

The use of microbial bioremediation for the cleanup of mercury contaminated water was first demonstrated by Williams and Silver (1984), who assessed bacterial resistance and detoxification of heavy metals (Ustiatik et al., 2022). Since then, the application of this process has been made easier by the transgenic approach (Saravanan

et al., 2022). For example, Hg-declining bacterial strains of *Escherichia coli* have been modified by mer operon clone establishment and other recombinant DNA methods for bioremediation (Maqsood et al., 2022; Rafeeq et al., 2023; Sone et al., 2017).

Microbial bioremediation is an effective alternative to traditional remediation processes because it is sustainable, eco-friendly, cost-effective, reduces the chances of producing secondary pollutants and requires less energy than chemical methods (Hou et al., 2023). Moreover, it can be useful to the polluted area itself and has great potential for pollutant removal (Ustiatik et al., 2022). Table 1 lists microbes used in bioremediation of Hg.

### 2.1 | Microbial bioremediation

The removal of Hg(II) from aqueous environments can be difficult due to its properties like high reactivity and low vapour pressure (Mukherjee & Bordoloi, 2011). Solar-driven reduction of Hg(II) to Hg(0) further complicates its removal (Qiu et al., 2022). Natural microbial communities frequently include innate Hg resistance mechanisms that help them survive in Hg(II) contaminated aquatic environments (Y. Chen et al., 2023; Choudhury & Chatterjee, 2022). MeHg represents 2% of total concentration of Hg in soils, and this form is preferred in biomagnifications (Xu et al., 2015). As human beings existed at the top of the food chain, and highly represented to biomagnification of Hg in consecutive tropic levels, and food is the major source of Hg intake by humans (Priyadarshane et al., 2022). Likewise, sulphate-reducing bacteria species have been exploited for the removal of Hg from wetlands via adsorption mechanisms, however, the reported removal efficiency is relatively low (Diao et al., 2023). Transgenic bacteria with modified genetic mechanisms for Hg resistance and efflux processes have been developed, resulting in greater resistance to Hg in the transgenic strains (J. Zhang, Li, et al., 2023; C. J. Zhang, Liu, et al., 2023; Z. Zhang, Zhao, et al., 2023). Table 2 summarises the transgenic microbes used in Hg remediation processes described in the literature.

### 2.2 | Intrinsic and engineered microbial bioremediation

The process of in situ bioremediation refers to the treatment of contaminants without extraction by stimulating microorganisms in the ground to detoxify Hg/contaminant ions (Cameselle & Reddy, 2022; Koul et al., 2022). However, the effectiveness of the process is affected by temperature, electron acceptor availability and nutrient content (Bwapwa, 2022). Intrinsic bioremediation processes harness naturally occurring microbes, which have inherent potential to detoxify contaminants without external assistance but require a sufficient supply of nutrients and aerobic conditions to stimulate metabolic process. However, engineered in situ bioremediation involves the introduction of specific microorganisms, including genetically engineered microbes, to enhance the bioremediation process (S. Hussain, Jianjun,

TABLE 1 Microbes used in bioremediation of Hg.

Organism type	Organism	Efficiency of Hg removal	References
Gram-negative bacteria	<i>Vibrio parahaemolyticus</i> (PG02)	90 mg g <sup>-1</sup> of Hg	Jafari et al. (2015)
	<i>Vibriofluviialis</i>	63 mg g <sup>-1</sup> of Hg	Saranya et al. (2017)
	<i>Escherichia coli</i>	~95 mg g <sup>-1</sup> of Hg	X. Wang et al. (2018)
	<i>Alcanivorax xenomutans</i> (NIOT-EQR_J7)	Can reduce up to 70% of Hg(II)	Joshi et al. (2022)
	<i>Halomonas</i> sp. (NIOT-EQR_J248 and NIOT-EQR_J251)		
	<i>Marinobacter hydrocarbonoclasticus</i> (NIOT-EQR_J258)		
	<i>Herbispirillum huttiense</i> TL36, <i>Klebsiella oxytoca</i> TL49 and <i>Rhizobium radiobacter</i> TL52	Tolerated high levels of HgCl <sub>2</sub> concentrations	Rojas-Solis et al. (2023)
	<i>Brevundimonas</i> (MH885484)	96.31% and 99.72% at 24 and 48 h	M. M. Zhao et al. (2021)
	<i>Pseudomonas</i> (MH885475)		
	<i>Pseudomonas</i> (MH885482)		
	Purple nonsulfur bacteria ( <i>Rhodovulum sulfidophilum</i> SRW1-5, and <i>Affifella marina</i> strains SSS2-1 and SSW15-1)	87%-95%	
	<i>Burkholderia contaminans</i> TR100	Tolerated up to 60 mg L <sup>-1</sup> HgCl <sub>2</sub>	Cardona et al. (2022)
	<i>Pseudomonas</i> sp. TP30	Tolerated up to 60 mg L <sup>-1</sup> HgCl <sub>2</sub>	
	<i>Stenotrophomonas maltophilia</i> ADW10	99.9%	Naguib et al. (2019)
	<i>Klebsiellapneumoniae</i> strain FY2, <i>Klebsiellapneumoniae</i> isolate 23	Can grow in 700 ppm mercury and could also tolerate a high salinity of 35 ppt of NaCl	Pushkar et al. (2019)
	<i>Enterobacter</i> sp. strain Amic_7, <i>Enterobacter</i> sp. strain 08		
	<i>Acinetobacterseohaensis</i> strain S34		
	<i>Acinetobacter</i> sp. 815B5_12ER2A		
	Mercury-resistant bacteria KX832953.1	90%	
	<i>Pseudomonas aeruginosa</i>		K. Yin et al. (2016)
<i>Cupriavidus metallidurans</i> MSR33	Removed 82% mercury	Bravo et al. (2020)	
Algae	<i>Phormidium ambiguum</i>	97%	Shanab et al. (2012)
Algae	<i>Ulva lactuca</i>	99 mg g <sup>-1</sup> of Hg	Henriques et al. (2017)
	<i>Chlorella vulgaris</i>	94.6 mg g <sup>-1</sup> of Hg	Y. Peng et al. (2017), Solisio et al. (2019)
	<i>Scenedesmus obtusus</i>		R. Huang et al. (2019)
	<i>Skeletonema costatum</i>	~80%	Soedarti et al. (2017)
	<i>Pseudochlorococcum typicum</i>	97%	Shanab et al. (2012)
Gram-negative	<i>Pseudomonas putida</i>	100% mercury and reduce Hg(II) to Hg <sup>0</sup> vapour	W. Zhang et al. (2012)
Gram-positive	<i>Bacillus cereus</i> (AZ-1, AZ-2, AZ-3)	83, 76, 76 mg g <sup>-1</sup> of Hg	Amin and Latif (2017)
	<i>Fictibacillus nanhainensis</i> (SKT-B)	82.25%	Nurfitriani et al. (2020)
	<i>Bacillus toyonensis</i> (PJM-F1)	81.21%	Nurfitriani et al. (2020)
	<i>Bacillus thuringiensis</i> PW-05	90%	Dash and Das (2016b)
	Sulphate-reducing bacteria H1, H8, and H10	-	M. Ma et al. (2017), M. M. Zhao et al. (2021)
	<i>Bacillus megaterium</i> LBA119	62%-97.36%	H. Wang et al. (2022)
	<i>Bacillus</i> sp. strain CSB_B078	Can grow in 700 ppm mercury and could also tolerate a high salinity of 35 ppt of NaCl	Pushkar et al. (2019)
	<i>Bacillus cereus</i> AA-18 (OK562834)	Remediate 86% Hg of industrial wastewater up to 72 h at large scale	Amin et al. (2022)

(Continues)

TABLE 1 (Continued)

Organism type	Organism	Efficiency of Hg removal	References
Yeast	<i>Yarrowia</i> spp. ( <i>ltd1</i> and <i>ltd2</i> )	-	Oyetibo et al. (2016)
Symbiotic fungi	<i>Metarhizium robertsii</i>	-	Wu et al. (2022)
Fungi	<i>Penicillium</i> spp. DC-F11	-	

TABLE 2 Transgenic microbes used in Hg remediation.

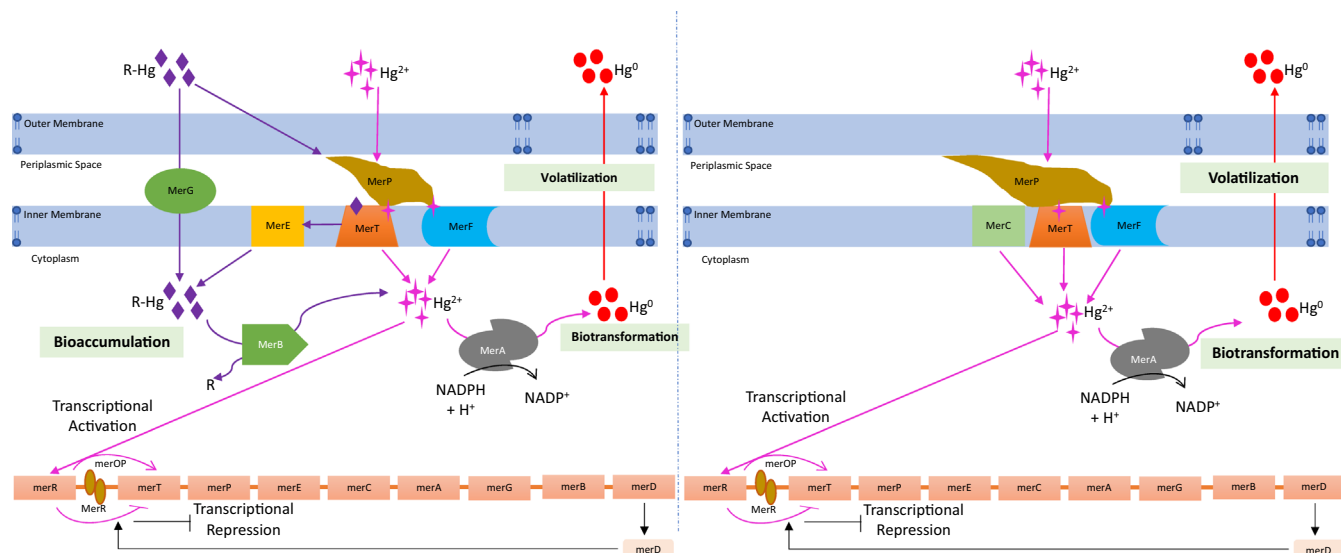
Organism	Transgenic and genes involved	Hg concentration	References	
Transgenic strain in bioremediation of mercury	<i>Escherichia coli</i> (ppk gene)	Recombinant <i>E. coli</i> /pBSK-P16S-mt1-rpsT and pBSK-P16S-g10-ppk-rpsT, and mt-1 gene (metallothionein) and ppk gene (polyphosphate kinase)	120 and 80 $\mu\text{mol}$	Ruiz-Díez et al. (2012)
	Mouse (mt-1 gene)	<i>Bacillus cereus</i> BW-03 (pPW-05), and <i>merA</i> gene	5–50 ppm	Dash and Das (2015)
	<i>Bacillus thuringiensis</i> PW-05			
	Rice metallothionein (MT) isoforms	Recombinant <i>E. coli</i> GST-OsMTs, and Glutathione-S-transferase (GST), OsMT1, OsMT2, OsMT3 and OsMT4	20, 13.7, 10 and 7 $\text{nmol Hg}^{2+}/\text{mg}$ (dry weight of culture)	Shahpiri and Mohammadzadeh (2018)
	<i>Pseudomonas pseudoalcaligenes</i> S1	<i>merT</i> , <i>merP</i> and <i>merA</i>	60, 40, and 20 $\text{mg L}^{-1}$	J. Zhang et al. (2020)
	<i>Deinococcus radiodurans</i>	MerH; Produce resistance against mercury and degrades marinum strain	-	Meruvu (2021)
	<i>Acidithiobacillus ferrooxidans</i>	MerC via mercury degradation	-	Arshadi et al. (2020)
	<i>Rhodopseudomonas palustris</i>	Mercury transporting system expression		
	<i>Pseudomonas putida</i> KT2440		98% $\text{Hg}^{2+}$ adsorbed	Xue et al. (2022)
	<i>Pseudomonas</i> K-62	Exhibit expression of organomercurial lyase and Hg degradation	-	Sharma and Kumar (2020)
	<i>Escherichia coli</i> (DH5 $\alpha$ J23106)	Overexpressing <i>merB</i> gene	Degrade MeHg to more than 81.6% in a culture medium under anoxic and oxic conditions	Q. Yang et al. (2023)

et al., 2022; A. Hussain, Rehman, et al., 2022). Bacteria, macrophytes, algae and fungi have all been used for remediating Hg polluted sites by alteration via bioaccumulation and biosorption processes (Arunraja et al., 2023; Chugh et al., 2022; Kristanti & Hadibarata, 2023; Rani et al., 2021; Saha et al., 2022; Tan et al., 2023).

Mercury-resistant bacteria can be used to either remove Hg or transform toxic forms of Hg into less toxic ones depending on the level of Hg pollution at the affected site (N. Gupta et al., 2022). Several mechanisms have been identified for Hg resistant bacteria to eliminate Hg from the surroundings, which include (a) thiol group binding with different oxidative states of Hg, (b) formation of a permeability barrier that prevents Hg from entering the cell and thus lowering its toxicity and (c) the mer operon (He et al., 2023; Nivetha et al., 2022; A. Pal et al., 2022).

In recent years, bioremediation has become increasingly favoured for cleaning up of Hg polluted environments (Ghosh et al., 2023). Mercury-resistant bacteria harbouring mer genes have been used for the detoxification of mercuric compounds via reduction and adsorption processes (Krout et al., 2022). These microorganisms possess the mer operon, which consist of *merA*, *merR*, *merP*, *merD*, *merC*, *merT*, *merG*, *merE* and *merF* genes. Among these genes, *merA*, *merR*, *merC*, *merP*, *merE* and *merT* are involved in the reduction of Hg (Kumari et al., 2020).

The promoter gene (*merR*) of the mer operon is activated by Hg(II) and induces the production of downstream genes (Hui et al., 2022). Organomercury lyase, encoded by *merB*, catalyses protolytic breakdown of C-Hg bonds in organo Hg compounds. Encoded by periplasmic protein (*merP*), *merA* and *merB*, as well as several inner



**FIGURE 1** (A and B) Diagrammatic representation of *mer* operon and associated genes in broad and narrow range Gram-negative mercury-resistant bacteria, respectively. MerG and merP along with merT and merE facilitate the entry of organic R-Hg, and merP through merF and merT aids in the transportation of inorganic Hg in the cell. And merF (merF). Both organic and inorganic Hg undergo subsequent enzymatic transformation by merB and merA, respectively for conversion into volatile Hg, which escapes out of the cell. The accumulated organomercurials are digested by MerB lyase enzyme to convert into mercuric ions, which are then reduced to free form by merA, reductase. The mechanisms conferring resistance are named in green boxes. The specific function of genes involved in the functioning of mer operon are: merA (Mercuric ion reductase; Conversion of  $\text{Hg}^{2+}$  to  $\text{Hg}^0$ ), merB (Organomercuriallyase; Lysis of C-Hg bond), merP (Periplasmic mercuric ion binding protein; Transfer of  $\text{Hg}^{2+}$  to integral membrane proteins), merT (Mercuric ion transport protein; Transport of mercuric ion), merD and merR (Regulator proteins; negative and positive operon regulators, respectively). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

membrane proteins such as merT, merC, merE, merF and merG, aid in transporting  $\text{Hg(II)}$  into or out of the cytoplasmic membrane (Amin et al., 2022; Amin & Latif, 2017). The mercury transporter proteins (merC, merP, merE and merT) are responsible for the transportation of  $\text{Hg(II)}$ , whereas the cytoplasmic reductase encoded by the merA gene is accountable for the conversion of  $\text{Hg(II)}$  into  $\text{Hg(0)}$  (Giri et al., 2014). Consequently, the presence of the merA gene is an essential factor in defining the presence of the Hg reduction route in bacteria (D. Li, Li, et al., 2022; X. Li, Yang, et al., 2022).

Mercury-resistant bacteria possessing mer-induced resistance have been isolated (Joshi et al., 2021). The mer operon genes, which are typically found on genomic DNA (R. Zheng et al., 2018), plasmids (D. Li, Li, et al., 2022; X. Li, Yang, et al., 2022), the components of the Tn21 transposon in plastids (Dhir, 2019) and integrons (Dunon et al., 2022) are all variable in their number and characters. The mer genes are not limited to bacteria, having also been discovered in archaeobacteria including *Sulfolobus solfataricus*, *Halobacterium*, *Halococcus* strain, and Asgard archaea (Artz et al., 2015; J. Zhang, Li, et al., 2023; C. J. Zhang, Liu, et al., 2023; Z. Zhang, Zhao, et al., 2023). They function as promoters, regulators or operators as well as functional genes. There are two subcategories of the mer factors: broad-spectrum mer and narrow-spectrum mer types. Only the broad-spectrum type exhibits resistance to both the organomercurials (i.e., methylmercury) and inorganic Hg salts (Cardona et al., 2022).

Microbial bioremediation of inorganic Hg polluted environments is an energy dependent process that involves the donation of

electrons during NADPH conversion to  $\text{NADP}^+$  that causes  $\text{Hg(II)}$  to convert  $\text{Hg(0)}$ , which is then released out of the bacterial cell, thus conferring resistance. The mer operon is a conserved positive operon (Boyd & Barkay, 2012) consisting of operator, promoter and regulatory genes (merR) along with functional genes comprising merT, merP, merD, merF, merC, merA (Figure 1). MerA encodes flavin-dependent disulfide oxidoreductase mercuric reductase, merB encodes organomercury lyase, merP is a periplasmic  $\text{Hg(II)}$  scavenger protein and merE, merT, merG, merC, merF are membrane spanning proteins, which can transport  $\text{Hg(II)}$  in the cytoplasm, which is abridged by merA, merG and merD (regulatory proteins). Alternatively, merB is specific to broad range operons (Dash & Das, 2012). The biochemical method of inorganic Hg resistance is similar across a diverse group of bacteria. In narrow range mer-dependent resistant bacteria, the biochemical route for inorganic Hg resistance involves the conversion of  $\text{Hg(II)}$  to  $\text{Hg(0)}$  via enzyme mercuric reductase, which is produced by gene merA. Since  $\text{Hg(0)}$  is characterised by high vapour pressure, it is easily volatilised and released.

Bacteria that are resistant to broad range kinds employ different resistance mechanisms. Organomercurial complexes are carried into the cytoplasm and the bond between carbon and Hg is broken by organomercurial lyase encoded by merB to generate  $\text{Hg(II)}$  ions. The  $\text{Hg(II)}$  ions are later transformed to  $\text{Hg(0)}$  by mercuric ion reductase, encoded by merA, utilising the NADPH-based mechanism described above (Sharma et al., 2021). Inorganic Hg acts as an inducer and amplifies the activity of the functional genes (Mishra et al., 2021). Following external Hg depletion, the secondary regulator merD switches

**TABLE 3** Resistance mechanisms of microbes towards mercury ions.

Microorganism	Resistance mechanisms	Reference
<i>Ochrobactrum</i> sp. HG16, <i>Klebsiella rosea</i> EP1 and <i>Lysinibacillus</i> sp., <i>Serratia marcescens</i> HG19 and <i>Bacillus</i> sp. CM111	Extracellular sequestration	François et al. (2012)
<i>Ulva lactuca</i>	Biosorption and bioaccumulation	Shanab et al. (2012)
<i>Bacillus cereus</i> BW-03	Bioaccumulation	De et al. (2014)
<i>Escherichia coli</i>	Active export (ABC transporters)	Lerebours et al. (2016)
<i>Bacillusthuringiensis</i> PW-05	Extracellular sequestration (thermodynamically favourable interaction)	Dash and Das (2016a)
<i>Yarrowia</i> spp. (Idd1 and Idd2)	Passive adsorption	Oyetibo et al. (2016)
<i>Pseudomonas</i> sp.	Enzymatic detoxification (mercuric reductase)	Giovannella et al. (2016)
<i>Bacillus firmus</i>	Enzymatic detoxification (mercuric reductase)	Noroozi et al. (2017)
<i>Phormidium ambiguum</i>	Biosorption and bioaccumulation	Henriques et al. (2017)
<i>Bacillus cereus</i> BW-201B	Extracellular sequestration (trapped by bacterial EPS and subsequently released by mer operon)	Dash, Basu, and Das (2017)
<i>Pseudomonas pseudoalcaligenes</i> S1	Bioaccumulation	J. Zhang et al. (2020)
<i>Fictibacillus nanhainensis</i> (SKT-B) and <i>Bacillus toyonensis</i> (PJM-F1)	Bioaccumulation	Nurfitriani et al. (2020)

off in many Proteobacteria, which inhibits the mer operon (A. D. Singh et al., 2023). Table 3 presents an overview of the various Hg resistance mechanisms of microbes.

In addition to the mer operon, bioremediation can involve alternative mechanisms. For example, iron oxidising acidophilic Hg-sensitive bacteria, such as *Shewanella oneidensis* MR-1 and *Geobacter metallireducens* GS-15, have been found to reduce Hg(II) when augmented ferrous ions involving the action of cytochrome c oxidase to produce volatile Hg(0) without mercuric reductase (Wiatrowski et al., 2006). Bacterial strain RS3 (*Marinomonas* sp.), which was isolated from the Red Sea, was observed to remove most Hg(II) ions (78% removed) from a contaminated water (50 mg L<sup>-1</sup> HgCl<sub>2</sub>) within 3 days (Al-Ansari, 2022). In both nutrient poor and rich environments,

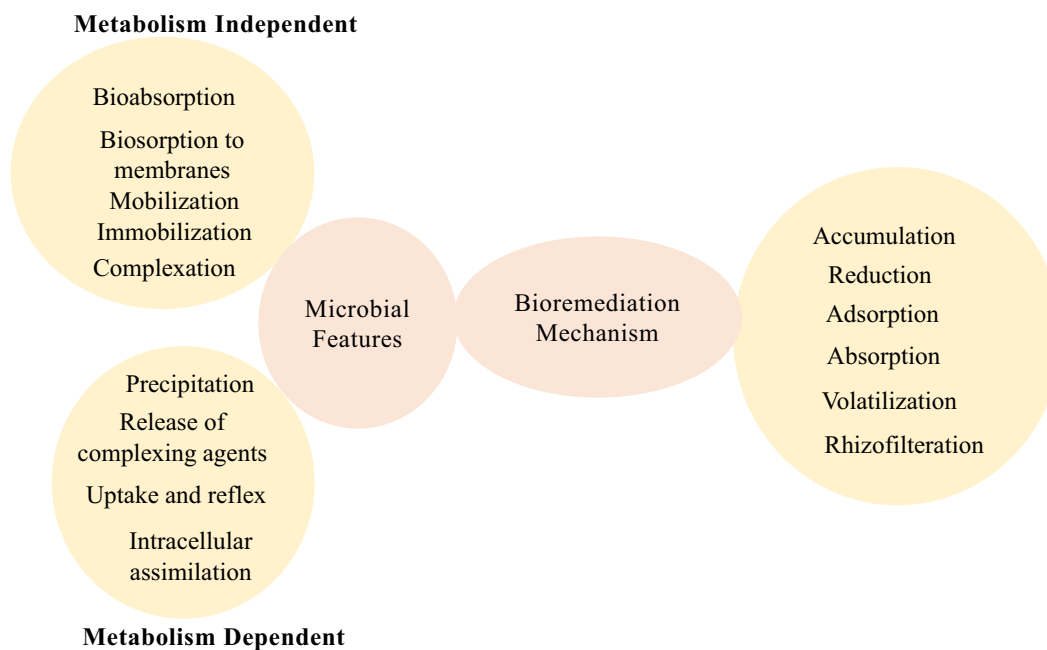
*Pseudomonas* sp. strain AN-B15 has been observed to efficiently remove Hg(II) by converting it to Hg(0) and by converting Hg(II) to Hg sulfide and Hg-sulfhydryl (Chang et al., 2022). These bacteria can function efficiently in anoxic conditions where levels of Hg(II) are low (Ali et al., 2022). Moreover, these bacteria have developed mechanisms for sequestering heavy metals ligands that are toxic to other organisms (Sharma et al., 2022; Thathapudi et al., 2023). Beckers et al. (2019) discovered that, regardless of soil treatment, Hg mobilisation was greater at low redox potentials (EH) and declined with increasing EH. In addition, the use of biochar and sugar beet factory lime decreased the Hg outflow, but not their ethylation and methylation. Figure 1 indicates the representation of mer operon and allied genes in broad and narrow range Gram-negative mercury-resistant bacteria.

## 2.3 | Cellular and genetic mechanisms of mercury removal by mercury-resistant bacteria

The mechanisms responsible for the survival of bacteria species at Hg contaminated sites, making those efficient candidates for bioremediation, are discussed below. Figure 2 illustrates the bacterial characteristics associated with Hg bioremediation processes and mechanisms involved.

### 2.3.1 | Biosorption (extracellular)

Biosorption is a process by which Hg ions are captured on the cell wall, whether the biomass is living or not (Ugya et al., 2021). With living cells, microbial secretion of negatively charged extracellular polymeric substances (EPS) fix Hg ions in a nonspecific manner. Volatile organosulfur by-products can aid Hg tolerance through extracellular sequestration (Demarco et al., 2023; Zeng et al., 2020). It is well acknowledged that EPS is secreted by different microbes under heavy metal stress (Mukkata et al., 2019). Bacterial species *Bacillus thuringiensis* PW-05 (Dash & Das, 2016a) and *Bacillus cereus* BW-201B (Dash, Basu, & Das, 2017) have been shown to use EPS as mode of Hg tolerance. It is vital to note that the pH of the system influences the binding of metals to the EPS matrix, with adsorption capacity increasing at lower pH levels owing to greater Hg chelating (P. Gupta & Diwan, 2017). Microbial adsorption processes involve EPS binding and immobilizing Hg, which have been observed for *B. cereus* MM8, *Bacillus* sp. CM111, *Kocuria rosea* EP1, *Ochrobactrum* sp. HG16 and *Lysinibacillus* sp. HG17 (François et al., 2012) and *Bacillus* sp. S3 (Zeng et al., 2020). An assessment of the biosorption of Hg by purple non-sulfur bacteria (PNSB) showed that dead PNSB cells were more effective for removing Hg(II) than living cells, with the *Affella marina* strain SSS2-1 being the most effective PNSB strain. It was shown that for dead cells the sorption process fitted the Langmuir model whereas live cells fitted the Freundlich model (Mukkata et al., 2019). While various bacterial species have shown potential for bioremediation through Hg sequestration, further research is needed to optimise the process.



**FIGURE 2** List of the bacterial features utilised in mercury bioremediation processes and mechanism that take place for conversion into nonlethal form. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 2.3.2 | Bioaccumulation (intracellular)

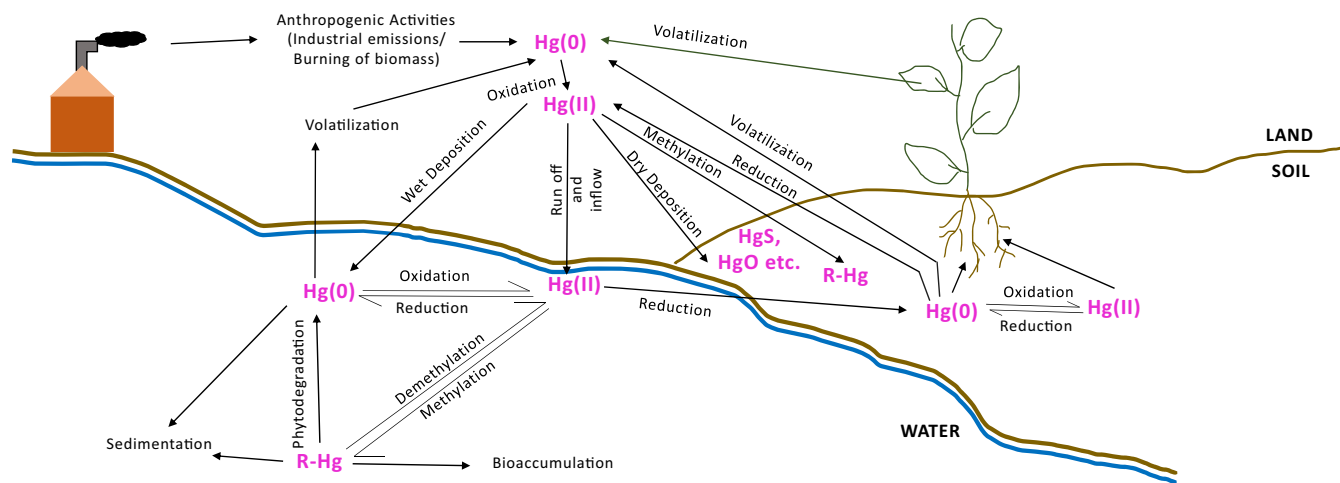
Bioaccumulation is a process by which microbes uptake and sequester metal ions within their intracellular space. Certain metal-binding peptides, such as metallothioneins and phytochelatins, play an imperative role in microbial bioaccumulation of Hg contaminants in bacterial cells (Balzano et al., 2020; K. Yin et al., 2019). Microbial intracellular absorption of Hg can involve the use of enzymes that directly absorb Hg, with one known example being *Bacillus* sp. (Alotaibi et al., 2021). Many marine bacterial strains that exhibit Hg resistance (31.5%) will involve a bioaccumulation process (Dash & Das, 2016b). For example, *Pseudomonas pseudoalcaligenes* S1 was observed to bioaccumulate as much as 133 mg g<sup>-1</sup> of Hg (J. Zhang et al., 2020) and *Bacillus toyonensis* (PJM-F1) removed 81% of Hg from a contaminated water by bio accretion (Nurfitrani et al., 2020). The competence of bacteria to tolerate Hg and operate at low concentrations makes them promising candidates for Hg bioremediation.

### 2.3.3 | Reduction of Hg(II) to Hg(0)

Some microbes bring about the reduction of Hg(II) to Hg(0) by enzymatic reduction, which is facilitated by cytoplasmic flavoenzyme mercuric reductase (Rani et al., 2021). Narrow-spectrum Hg resistance microbes have been observed to reduce inorganic Hg(II) salts as well as some organomercurial derivatives. The process involves passive diffusion of Hg(0) from the cell under common functional conditions (S. Singh & Kumar, 2020) and the transportation of Hg(II) inside the cytoplasm via MerT along with MerC and MerF transporters, where Hg(II) is volatilised by reduction to Hg(0) (He et al., 2023).

### 2.3.4 | Reduced uptake

Various processes can reduce the uptake of different types of heavy metals including efflux-mediated mechanisms, the association of certain proteins involved in metal resistance or by mer operon regulating uptake in the cell. This often serves as the first line of defence for prokaryotic cells to survive under contaminated conditions (Benmalek & Fardeau, 2016; Capdevila et al., 2016). Although efflux-induced processes have not yet been found to cause microbial resistance to Hg, it cannot be completely considered off given that it is widely acknowledged that numerous microbial species are still unknown. Research has shown analogous efflux-induced resistance to numerous potentially toxic elements in microbes secluded from the aquatic environment (Chenia & Jacobs, 2017). It is quite likely that the resistance mechanism for other potentially toxic elements in microbes would result in the co-occurrence of genetic apparatus for Hg resistance and efflux processes, leading to Hg-resistant strains (Bombaywala et al., 2021; Fang et al., 2016; C. Pal et al., 2015; Saravanakumar et al., 2023). Pushkar et al. (2019) in their studies reported several Hg-resistant bacteria (Enterobacter, Klebsiella and Acinetobacter) in Mithi River, which are used for bioremediation of Hg, and they have the ability to endure high content of Hg. Bacteria existed everywhere and can bioremediate Hg employing their integral processes (Mahbub et al., 2016). Bacteria also work in coordination with other microbes for efficient Hg removal (Santos-Gandelman et al., 2014). Figure 3 depicts different bioremediation strategies applied for remediation of Hg in soil and water.



**FIGURE 3** Depicts the bioremediation mechanism of Hg removal from soil and water. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/ldr.4989)]

## 2.4 | Horizontal gene transfer (in situ molecular breeding)

Horizontal gene transfer (HGT) is a recent development in bioremediation, where a donor vector carrying Hg resistance genes exchanges genetic material with a recipient bacteria. The process relies on transformation, transduction and conjugation processes, with the latter being most important (Ali et al., 2022). Nutrient supply is essential for the transfer process, and works best by targeting receiver bacteria in their indigenous environment that are prevalent and robust (Matsui & Endo, 2018). The necessary factors for successful HGT include genes with the required transposons, plasmids with conjugable properties, exclusion of transposons from the plasmid and further amalgamation with the genomic DNA in the recipient with the possibility of conjugation between donor and recipient (Kohler et al., 2019). However, this approach requires more research and a more comprehensive understanding of the soil microbes involved before it is fully commercialised.

## 2.5 | Alternative microorganisms used for bioremediation

### 2.5.1 | Yeast

Recent research has revealed the ability of yeast species, such as *Saccharomyces cerevisiae*, *Schizosaccharomyces pombe* and *Candida* sp., to acclimate to Hg contaminated environments and remediate Hg contaminants (Anaemene, 2012; Leong & Chang, 2020). This offers a novel route for rapid Hg bioremediation by acting, with greater growth rates and superior cell wall organisation for biosorption than bacterial strains (Bahafid et al., 2017). The presence of negative surface functional groups (e.g., carboxyl and phosphates) on yeast can aid binding with metal cations (S. Singh et al., 2020) and the net-structured floc facilitates oxygen diffusion and decreases energy consumption (Kumar et al., 2020).

### 2.5.2 | Fungi

A promising solution to remediate Hg-polluted environments is to use Hg-resistant fungi to break down toxic forms of Hg into less toxic forms. Fungi isolated from the rhizosphere of plants grown at contaminated sites are often of interest for bioremediation purposes (Vaksmas et al., 2023). Biochemical assays have shown that plant symbiotic fungus, *Metarhizium robertsii*, can degrade methylmercury and decrease Hg(II) in soil and water. In one study, Wu et al. (2022) described the process, which involves demethylation of organomercury by methylmercury demethylase (MMD) and subsequent reduction to  $Hg^+$  by mercury ion reductase. This bioremediation process was revealed to improve plant growth under mercury stress, and over expressing the enzymes involved by genetic manipulation further improved plant growth. This finding suggests the prospective to develop sustainable fungi-based bioremediation technologies to clean up Hg pollution, though further research is needed before it can be fully commercialised.

### 2.5.3 | Algae

Algae-based bioremediation (phycoremediation) is the use of algae (e.g., cyanobacteria, microalgae and macroalgae) for Hg removal, which offers several advantages such as low odour and toxicity, remediation of co-contaminants and producing a biomass product that can be harvested as a valuable product (Dubey et al., 2022), thus making it a sustainable bioremediation approach (Chugh et al., 2022). The application of marine macroalgae, such as Phaeophyta, Rhodophyta and Chlorophyta, is beneficial due to their specific binding preferences to different metals, which is attributed to differences in their cell wall (Ashokkumar et al., 2022; Z. Peng et al., 2022). The green alga, *Ulva lactuca*, which is characterised by several surface functional groups including hydroxyl, amino, sulphate and carbonyl groups, has shown good promise for Hg removal (Henriques et al., 2017). Moreover,



**TABLE 4** Hg phytoremediation potential and toxicity of Hg promising species.

Plant species	Growth parameters (phytotoxic conc.)	Hg accumulation	References
<i>Boehmeria nivea</i>	Poly-γ-glutamic acid	Leaf increased by 4.4-fold, and the translocation factor increase; root > stem > leaf	J. Xu et al. (2023)
<i>Cardamine violifolia</i>	-	Roots and above parts 6000 μg g <sup>-1</sup> ; Bioaccumulation factor high; TF ~ 1.5	Cui et al. (2023)
<i>Clidemia sericea</i>	Biomass reduction	Root > Leaves > Stem; Bioconcentration factor > 1; Translocation > 1	Durante-Yáñez et al. (2022)
<i>Medicago sativa</i>	nZVI and organic fertilisers; Increase Biomass	Decrease of Oxidative stress; H <sub>2</sub> O <sub>2</sub> and MDA reduction; Higher proline content.	Baragaño et al. (2022)
<i>Lupinus albus</i>	-	Nodules 600 μg Hg g <sup>-1</sup> dw Roots 1400 μg Hg g <sup>-1</sup> dw Cluster roots 2550 μg Hg g <sup>-1</sup> dw Bioaccumulation factor high	Quiñones et al. (2021)
<i>Brassica juncea</i>	Plant showed better efficiency	Hg content values ranging from 0.11 to 0.80 mg kg <sup>-1</sup> . Root > Shoot > Leaves.	Raj and Maiti (2021)
<i>Vigna unguiculata</i>	Negligible biomass decrease with Hg	Root > leaf > stem; Bioconcentration Factor < 1 (all genotypes); TF < 1 for native genotype 2. translocation factor ~1.5 (for 0.2 mg Hg kg <sup>-1</sup> dw) for both commercial lines	Marrugo-Negrete et al. (2020)
<i>Brassica juncea</i>	Plant showed better efficiency up to the concentration level of 500 mg Hg kg <sup>-1</sup> soil	Metal Concentration: 10, 50, 100, 500 and 1000 mg Hg kg <sup>-1</sup> soil root > leaf > stem	Raj et al. (2020)
<i>Phragmites australis</i>	-	Root (Hg)—806 μg kg <sup>-1</sup> dw stem (Hg)—495 μg kg <sup>-1</sup> dw leaves (Hg)—833 μg kg <sup>-1</sup> dw translocation factor—0.57/1.99	Mbanga et al. (2019)
<i>Jatropha curcas</i>	Accumulator	Concentration: 1, 5 and 10 μg Hg g <sup>-1</sup>	Álvarez-Mateos et al. (2019)
<i>Lathyrus pratensis</i>	-	Shoot (Hg)—0.108 mg kg <sup>-1</sup> dw	Umlaufová et al. (2018)
<i>Epipactis</i> sp.	-	Shoot (Hg)—0.152 mg kg <sup>-1</sup> dw	
<i>Cyrtomium macrophyllum</i>	20.6% biomass reduction	Shoot (Hg)—36.44 mg kg <sup>-1</sup> dw root (Hg)—13.90 mg kg <sup>-1</sup> dw Bioconcentration Factor—0.061; translocation factor—2.62	Xun et al. (2017)
<i>Manihot esculenta</i>	Significant root biomass decrease	Hg is not determined in plants; root (Hg)—6.836 and 12.13 g kg <sup>-1</sup> dw) (50 and 100 μM Hg)	Alcantara et al. (2017)
<i>Sesbania grandiflora</i>	56% growth decrease 19% biomass reduction (60 mg Hg L <sup>-1</sup> )	Mostly in roots	Malar et al. (2015)
<i>Jatropha curcas</i>	-	Plant (Hg)—max. 7.25 mg kg <sup>-1</sup> dw) (for 10 mg Hg kg <sup>-1</sup> soil) Bioconcentration factor—good, with increased exposure (4th month); translocation factor ~1 (after 2 months, then decreased)	Marrugo-Negrete et al. (2015)
<i>Lepidium sativum</i>	27% decrease in shoot length; 53% decrease in the root (10 mg Hg kg <sup>-1</sup> )	Mostly in roots; add compost accumulation; Bioconcentration factor—high for 10 mg Hg kg <sup>-1</sup> dw in 2/1 compost	Smolinska and Rowe (2015)
<i>Atriplex conodocarpa</i>	Biomass, leaf area and the number remained unchanged (in regard to unspiked soil)	Shoot (Hg)—1.09 mg kg <sup>-1</sup> dw translocation %—19%	Lomonte et al. (2010)
<i>Chilopsis linearis</i>	49% decrease in root length	Root (Hg) with Hg concentration; translocation factor—low	E. Rodríguez et al. (2009)
<i>Brassica juncea</i>	5.1-fold reduced transpiration rates	Shoots (Hg)/root (Hg)—0.3–0.76	Moreno et al. (2008)

(Continues)

TABLE 4 (Continued)

Plant species	Growth parameters (phytotoxic conc.)	Hg accumulation	References
<i>Cucumis sativus</i>	96% root length reduction (10 days old seedlings) 98% root length reduction (15 days old seedlings)	Root (Hg)—sevenfold and 5.6-fold > cotyledons (after 10 and 15 days)	Cargnelutti et al. (2006)
<i>Oryza sativa</i>	50% shoot biomass reduction	Root (Hg) > shoot (Hg)	Du et al. (2005)

transgenic *Chlorella* has been developed that expresses *merA* gene from *Bacillus megaterium* strain MB1, resulting in higher Hg removal rates, higher Hg tolerance (40  $\mu$ M HgCl<sub>2</sub>) and faster growth rates than wild-type *Chlorella* (C. C. Huang et al., 2010). By the mechanism of bioaccumulation, Hg strongly binds in macroalgae tissues without being converted to more toxic methylmercury (Henriques et al., 2017). Hg is transported within the algal cell, and in detoxification, phycochelators produced by algae aid the conversion of harmful Hg into less harmful forms (Chugh et al., 2022).

### 3 | PHYTOREMEDIATION

Phytoremediation involves the use of plants to clean up soil by taking up, adsorbing or decomposing pollutants (Bhat et al., 2022) without the need for excavation. Phytoremediation is considered a sustainable remediation technique (Cristaldi et al., 2017; Derakhshan Nejad et al., 2018; L. Wang, Hou, et al., 2020; J. Wang, Shaheen, et al., 2020). The mobility of Hg is imperative for their providence in the environment and appraised the accomplishment of this method. These are complex and leads to unforeseen mechanism. There are diverse inferences of soils with greater Hg content, and plants growing on these are moderately to hardly control (Antoniadis et al., 2017). Remediation of soils contaminated with Hg can be accomplished with *Artemisia vulgaris*, *Galium mollugo* and *Stellaria holostea* hyperaccumulator plants (Antoniadis et al., 2021). The alteration of gene expression may enhance the sustainability of plants in altering climatic conditions. The enhanced phytoremediation of Hg employing CRISPR-Cas9 method in genome editing might be a prospective and suitable response with respect to climatic variations. The competence of hyperaccumulators can be enhanced through this technique (Sarma et al., 2021). Phytoremediation processes comprise of phytoextraction, phytostabilisation, rhizofiltration and rhizodegradation mechanisms through different plant species (see Table 4).

#### 3.1 | Hg phytoremediation plant species

There has been relatively limited literature published regarding Hg hyperaccumulation by phytoremediation plants, and a widely accepted definition of an 'Hg hyperaccumulator' species is not yet established (Qian et al., 2018). However, this is a growing area of research interest with more than 200 plants having been studied to determine their ability to remediate Hg pollution. Some plants have

shown good potential as candidates for Hg bioremediation. The fern *Eremochloa ciliaris* was determined to be an 'Hg hyperaccumulator' by Qian et al. (2018). *Erato polymnioides* found in Ecuadorian rainforest acid soils with prospective of microbe-allied phytoremediation also shows promise as an Hg hyperaccumulator species (Chamba et al., 2017). Further research is needed on limitations to this approach, particularly its suitability to severely polluted soils and the Hg removal rate (Lin et al., 2012; L. Wang, Hou, et al., 2020; J. Wang, Shaheen, et al., 2020). Alternative plant species for Hg phytoremediation are those that grow well in severely Hg-contaminated environments. The phytoavailability of Hg in floodplain soils was small owing to great mean pH values (6.2–6.8) (Overesch et al., 2007). Correspondingly, the Hg uptake by floodplain grassland herbage was relatively small too in comparison to the corresponding stocks in soil, and augmenting soil acidity increases phytoavailability and appears to considerably stimulate soil–plant mobility of Hg. Grave accumulation in green fodder and plants cultivated on wet soils accrue more Hg.

#### 3.2 | Phytoremediation mechanisms

##### 3.2.1 | Phytoextraction

Phytoextraction is the process of contaminants being taken up through plant roots into their biomass (Karalija et al., 2022). Chemically enhanced phytoextraction increases the bioavailability of target contaminants, leading to greater extraction rates (M. Kumar, Bolan, et al., 2022; K. Kumar, Shinde, et al., 2022). For instance, amino polycarboxylic acid increases the bioavailability of Hg in the soils and enhances transport to aerial parts of plant (Makarova et al., 2022). Makarova et al. (2021) used S-containing chelate and P-containing chelate to enhance the phytoextraction of Hg by *Trifolium repens* L., with both constituents increasing Hg absorption by the plant. A study by Amir et al. (2020) on *Typha latifolia* L. showed that the application of citric acid (CA) with different concentrations of Hg (1, 2.5, 5 mM) decreased the plant's agronomic characters, but the application of CA improved the plant physiology and increased the activity of antioxidant enzymes, mitigating Hg-mediated oxidative damage and electrolyte leakage after 4 weeks. Y. Guo, Sommer, et al. (2023) and K. Guo, Yan, et al. (2023) performed study on *Medicago truncatula*, finding that *Rhizophagus irregularis* played a vital function in Hg tolerance of this plant, indicating its potential use in the phytoremediation of Hg pollution. Additionally, the addition of thiosulphate to soil can increase the quantity of Hg bound to the

Fe/Mn oxide fraction, which enhances Hg bioavailability (Ranieri et al., 2020).

### 3.2.2 | Phytostabilisation

Phytostabilisation decreases the bioavailability of Hg by immobilising it in the rhizosphere, reducing uptake by plant roots and avoiding accumulation in the aboveground parts of plants (Farooqi et al., 2022). However, while reducing the amount of bioavailable Hg, the contamination remains in the ground, requiring long-term monitoring. A study of Hg species in soil treated by phytostabilisation showed that only 0.1% of Hg was water soluble (i.e., highly bioavailable), 1.1% Hg was associated with humic and fulvic acids, while the remaining Hg was associated with stable complexes. The *Salix* species used proved effective for the immobilisation of Hg in contaminated soil (Tiodar et al., 2021).

### 3.2.3 | Rhizoremediation

Rhizoremediation entails the removal of contaminants by filtration of polluted groundwater or surface water by plant roots. During this process, the contaminants are both absorbed and adsorbed onto the roots. The selection of suitable plants is based on several traits such as tolerance to Hg and a large surface area for absorption (Cristaldi et al., 2017). Terrestrial plants are preferred for Rhizoremediation as they possess well-developed roots with a fibrous structure that provides a large surface area for absorption. It should be noted that, when the root adsorption efficiency exceeds its maximum, the plants employed for rhizofiltration must be harvested and discarded (Pérez-Palacios et al., 2017). *Phaseolus vulgaris* and *Helianthus annuus* have been identified as suitable used extract Hg from contaminated groundwater, with Hg accumulating in the root (Malik et al., 2023). *Bidens pilosa* and *Heliocarpus americanus* have also been identified as potential candidates by Kalinhoff and Calderón (2022). They reported that *Bidens pilosa* functioned well at Hg levels below  $2 \text{ mg L}^{-1}$ , whereas *Heliocarpus americanus* can endure higher levels ( $<4 \text{ mg L}^{-1}$ ) and is also a good candidate plant due to its fast growth.

### 3.2.4 | Phytovolatilisation

Phytovolatilisation is feasible for the small group of volatile metals, including Hg. In this process, Hg is absorbed by plant roots, transported via the xylem and discharged to the atmosphere via cellular tissues (Tiodar et al., 2021). Insertion of genes from other organisms into phytovolatilisation plants by genetic engineering can improve their Hg removal capabilities. The direction of the Hg transporter, encoded by the mer determinant, distinguishes it from other known bacterial Hg resistance mechanisms (Pathak et al., 2020). The merA gene encodes a protein called mercuric reductase, which converts Hg(II) to elemental Hg(0) (M. Ma et al., 2019). The merA gene has been modified in plants

using genetic engineering to remove Hg (Krout et al., 2022; K. Kumar, Shinde, et al., 2022). For organomercury, the enzyme organomercurial lyase (MerB) catalyses the protonolysis of the carbon-mercury bond, producing an inorganic species (Barkay & Gu, 2021). Cells must have both the merA and merB genes to remediate organomercury (Sharma et al., 2021). Phytovolatilisation raises some concern due to secondary pollution of the atmosphere by volatilised elemental Hg (L. Wang et al., 2021). Therefore, the expression of additional mer genes has been conducted to create plants that accumulate Hg without discharging Hg(0) to the atmosphere (S. Singh & Kumar, 2020). MerC, merF and merT are known as membrane transporter genes that function in translocating Hg(II) into the cell, in addition to the genes merA and merB (Guha et al., 2022). These genes provide plants with the ability to gather more Hg in their tissues than wild type. The merP encodes a periplasmic protein that facilitates the absorption of  $\text{Hg}^{2+}$  and is physically linked to merT (Hwang et al., 2020).

Natural plants have limited phytovolatilisation potential for Hg and thus the research in this topic is mainly focused on transgenic approaches by inducing merA/merB genes in plants like tobacco, rice and *Arabidopsis* (R. Li et al., 2020). Phytoremediation approaches depend on various gene combinations to improve absorption, translocation or detoxification as well as regulate the emission of Hg into the air through plants (D. Yin et al., 2022). A possible weakness of the method is the ability of the gene-modified plant to adapt to the surroundings (Yaashikaa et al., 2022). Figure 4 represents the different phytoremediation mechanisms involved in remediation of Hg. Tables 5 and 6 differentiates literature of Hg phytoremediation in water and soil.

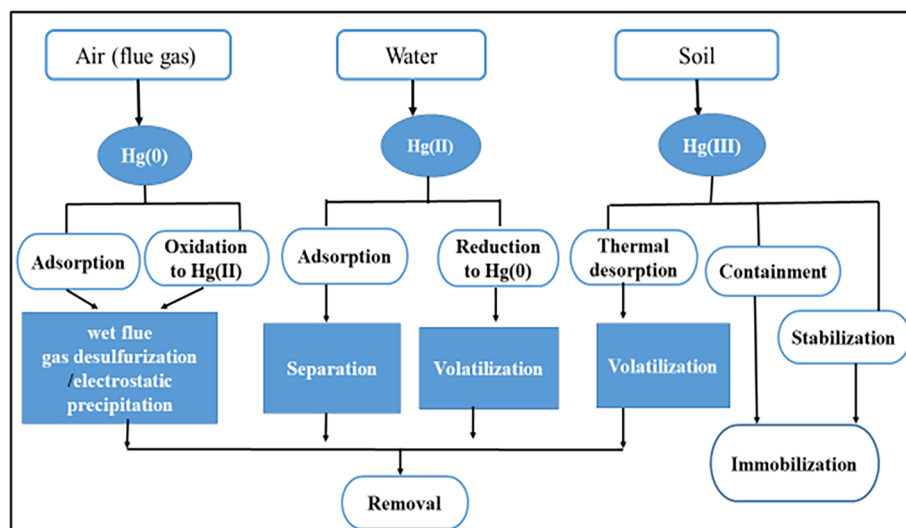
## 3.3 | Enhanced phytoremediation

### 3.3.1 | Applying exogenous chemicals or substances

Phytoremediation processes can be improved by applying exogenous chemicals or substances. For example, ammonium sulphate can be applied to the roots of *Brassica juncea* in low pH soil (J. Wang et al., 2017). Ammonium chloride, sodium nitrate and ethylenediaminetetraacetic acid can mitigate Hg stress in *B. juncea*, while ammonium thiosulphate and sodium sulphite considerably increase Hg uptake (J. Wang et al., 2017). Furthermore, results exhibited that organic matter (OM) can play an imperative role in phytoremediation by influencing Hg in the rhizosphere, which helps limit the transport of Hg cations to plant roots (C. L. Guo et al., 2019; S. Hussain, Jianjun, et al., 2022; A. Hussain, Rehman, et al., 2022).

### 3.3.2 | Bacteria-assisted phytoremediation

Plant growth-promoting bacteria (PGPB) comprise a varied collection of prokaryotes found in the rhizosphere (known as rhizobacteria), occupying root nodules (known as rhizobia), or residing inside the



**FIGURE 4** Phyto remediation mechanisms of Hg removal in soil and water. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/ldr.4989)]

tissues of plants (known as endophytes) (Y. Ma et al., 2016; Narayanan & Glick, 2022). These bacterial systems are numerous and often inadequately characterised, but they have been shown to enhance plant growth and provide protection against phytopathogens. PGPB typically supply beneficial nutrients, such as fixed N, Fe and P, as well as signals that initiate systemic resistance, hormones, enzymes, antibiotics or siderophores (K. Naik et al., 2019). The Hg-plants-bacteria triad has been the focus of many studies related to the removal of Hg from polluted environments and symbiotic bacteria. For example, exploiting natural legume–rhizobia relationships for Hg phyto remediation. These relationships are well-established, and as rhizobia enhance plant growth, they can lower Hg stress in plants (Tiodar et al., 2021).

In addition, the application of Hg-resistant endophytic bacteria to maize plants has revealed increased growth on Hg-polluted substrates, enhanced total uptake of Hg and mitigated its phytotoxicity by mediating its bioaccumulation (Mello et al., 2020). While many bacterial isolates display significant phenotypic variability in respect to tolerance (to Hg, pH and salt) and phosphate solubilisation, none have been observed to synthesise siderophores. These studies highlight the taxonomic precision that plants use to establish microbial interactions, but also highlight the absence of strains that are Hg-tolerant (Tiodar et al., 2021).

In comparison to an untreated control, roots of *Vigna unguiculata* ssp. *sesquipedalis* growing in soil contaminated with Hg ( $27 \text{ mg kg}^{-1}$ ) grew longer (11%), absorbed more Hg (25%) and had lower Hg concentrations in aerial portions (–55%) (Mathew et al., 2015). In another study, *Brevundimonas diminuta* SF-S1-5 and *Alcaligenes faecalis* SF-S1-60, two heavy metal-resistant rhizobacteria, significantly assisted *Scirpus mucronatus* growth in sand soil contaminated by a mixture of Pb ( $100 \text{ mg kg}^{-1}$ ) and Hg ( $1 \text{ mg kg}^{-1}$ ). Hamzah et al. (2015) found that the presence of bacteria increased phytoaccumulation of Hg in shoots (by up to  $7.5 \text{ mg kg}^{-1}$ ) in comparison to uninoculated plants. Sitarska et al. (2016) reported on enhanced growth and  $\text{Hg}^{2+}$  absorption capabilities of *Salvinia natans* and *Lemna minor* cultivated in a water

solution comprising  $0.3 \text{ mg L}^{-1} \text{ Hg}(\text{NO}_3)$  by three strains of epiphytic bacteria. Franchi et al. (2017) examined a group of five Hg/As-resistant bacteria in conjunction with thiosulphate, a fertiliser that acts as a metal mobilising agent. The bacteria species were selected based on their ability to produce IAA, ammonia, exopolysaccharide, biofilm or fix  $\text{N}_2$ . It was reported that the combined treatment of thiosulphate and bacteria synergistically increased the Hg phytoaccumulation level by 36% and 45% in *Lupinus albus* and *B. juncea* plants, respectively.

### 3.3.3 | Fungi-assisted phyto remediation

Mycorrhizal fungi (MF) can colonise the plant root cortex, on their surface, or nearby the epidermal root cells. These fungi provide plants with phosphates, nitrates or other inaccessible nutrients; they also facilitate the exchange of carbohydrates (Genre et al., 2020) and the formation of relationships through the hyphal network, enabling the transmission of resources and chemical signals between plants (Boyno & Demir, 2022). Cozzolino et al. (2016) reported that a commercial (arbuscular mycorrhizal fungi) AMF formula of humic acid with *R. irregularis* and *Funneliformis mosseae* propagules decreased Hg uptake and translocation while promoting plant growth and phosphorus uptake in *Lactuca sativa* at Hg pollution levels below  $10 \text{ mg kg}^{-1}$ . Similarly, Wu et al. (2022) found that *Metarhizium robertsii* fungus helped break down methylmercury, thereby reducing its accumulation in plants and significantly enhancing their growth in polluted soils. According to this study, fungi utilise MMD to demethylate methylmercury and Hg reductase to convert Hg to volatile elemental Hg, demonstrating the mechanism for Hg tolerance in fungi. These findings imply that environmentally benign techniques to Hg pollution remediation can be developed based on these mechanisms.

According to Aguirre et al. (2018), commercial AMF formula with *Glomus*, *Entrophospora* and *Scutellospora* genera increased *L. sativa* seedling growth and stimulated root elongation in comparison to non-inoculated control seedlings, even at  $100 \text{ mg kg}^{-1}$  Hg. In soil

TABLE 5 Phytoremediation studies of Hg on soil.

Plant species	Results	References
<i>Clidemia sericea</i>	The results obtained for the tissues differed in order of metal accumulation, with the root showing the highest concentration of metals. The highest values of bioconcentration (BCF > 1) were presented for Hg at T3 and of translocation (TF > 1) for Hg. Thus, <i>C. sericea</i> demonstrated its potential as a phytostabiliser of Hg in mining soils, strengthening as a wild species with results of resistance to the stress of the PTEs evaluated, presenting similar behaviour and little phytotoxic affection on the growth and development of each of the plants in the different treatments.	Durante-Yáñez et al. (2022)
<i>Miscanthus sinensis</i>	The soil mercury concentration from 1.48 to 706 mg kg <sup>-1</sup> . The changes in biomass yield in dry mass, chlorophyll content and SOD activity indicated <i>M. sinensis</i> was tolerant to higher levels of soil mercury exposure, and could grow even if at soil mercury up to 706 mg kg <sup>-1</sup> . Mercury bioconcentration and translocation factors were close to or greater than 1 when exposed to soil mercury up to 183 mg kg <sup>-1</sup> .	A. Zhao et al. (2019)
<i>Triticum aestivum</i> , <i>Hordeum vulgare</i> , <i>Lupinus luteus</i>	The decrease Hg concentration from 29.17 µg g <sup>-1</sup> at 0–10 cm horizon to 20.32 µg g <sup>-1</sup> at 10–40 cm horizon demonstrated the anthropogenic origin of the mercury in the soil. The mercury concentration in the plants accounted for less than 3% of mercury concentration in the soil. The Hg concentrations in the plants were similar or even higher than that of the bioavailable Hg in the soils. Mercury extraction yields reached up to 719 mg ha <sup>-1</sup> for barley.	Tangahu et al. (2011)
<i>Poa annua</i>	The increase in the Hg accumulation in shoots and roots 2.66 and 236.39 mg kg <sup>-1</sup>	Pedron et al. (2013)
<i>Chenopodium glaucum</i>	Higher Hg accumulation in roots, stems and leaves 1100%, 600% and 200%	J. Wang, Feng, Anderson, Qiu, et al. (2011), J. Wang, Feng, Anderson, Zhu, et al. (2011)
<i>Lupinus albus</i>	Higher the Hg accumulation in plants 1.94–2.47 µg plant <sup>-1</sup>	L. Rodríguez et al. (2016)
<i>Cyrtomium macrophyllum</i>	exhibited high levels of biomass production in contaminated soils with 5, 10, 20, 50, 100, 200 and 500 mg kg <sup>-1</sup> Hg, however, slight toxic effects such as chlorosis and necrosis were observed in contaminated soils with 1000 mg kg <sup>-1</sup> Hg	Xun et al. (2017)
<i>Jatropha curcas</i>	Study reported that reduction existed in the development of plant planted in 5, 10, 20, 40 and 80 µg mL <sup>-1</sup> Hg(NO <sub>3</sub> ) <sub>2</sub> -containing solution, and the leaf area decreased as the dosage of Hg increased	Marrugo-Negrete et al. (2016)
<i>Oryza sativa</i>	The result exhibited that the increase in the MeHg accumulation in grains 3.59–31.43 µg kg <sup>-1</sup> , and also rise in IHg accumulation in grains, straw and roots, that is, 4–15 µg kg <sup>-1</sup> ; 0.3–1 mg kg <sup>-1</sup> about 10–28 µg kg <sup>-1</sup>	Y. Li et al. (2019)
<i>Festuc arubra</i> , <i>Poa pratensis</i> , <i>Armoracia lapathifolia</i> , <i>Helianthus tuberosus</i> , <i>Salix viminalis</i>	The highest concentrations of mercury were found at the roots, but translocation to the aerial part also occurred. Most of the plant species tested displayed good growth on mercury contaminated soil and sustained a rich microbial population in the rhizosphere. These results indicate the potential for using some species of plants to treat mercury-contaminated soil through stabilisation rather than extraction.	Sas-Nowosielska et al. (2008)
<i>Opuntia stricta</i> , <i>Aloe vera</i> , <i>Setcreasea purpurea</i> , <i>Chlorophytum comosum</i> and <i>Oxalis corniculata</i>	The results demonstrated that the effect of different concentrations of mercury on the accumulation condition of roots was greater than that of shoots. There was an ideal Hg concentration for transfer by each plant species. <i>Oxalis corniculata</i> was the most suitable for transferring Hg and was more suitable for repairing soils with Hg at concentrations of less than 500 µg L <sup>-1</sup> .	Z. Liu et al. (2017)

TABLE 6 Phytoremediation studies of Hg on water.

Plant species	Results	References
<i>Brassica juncea</i>	Roots-concentrated Hg 100–270 times (on a dry weight basis). The plants translocated little Hg to the shoots, which accounted for just 0.7%–2% of the total Hg in the plants.	Moreno et al. (2008)
<i>Chilopsis linearis</i>	The concentration of Hg in shoots indicated that <i>C. linearis</i> absorbed and translocated Hg at higher concentrations, compared to reported data. At the highest concentration, Hg produced a breakdown of the spongy parenchyma	E. Rodríguez et al. (2009)
<i>Eichornia crassipes</i> , <i>Pistia stratiotes</i> , <i>Scirpus tabernaemontani</i> , <i>Colocasi aesculenta</i>	The higher the Hg concentration, the greater the amount of mercury removed by the plants. The largest uptake and accumulation capability is for water lettuce, followed by water hyacinth, taro and rush, respectively.	Tangahu et al. (2011)
<i>Azolla pinnata</i>	Metal content decreased to 70%–94%	Delgado-González et al. (2021)
<i>Eichornia crassipes</i>	Accumulation from 26 to 327 mg kg <sup>-1</sup> in dry weight	Odjegba and Fasidi (2007)
<i>Oenanthe javanica</i>	More than 1 mg kg <sup>-1</sup> remediated and 807 of BCF value	Furong et al. (2021)
<i>Pistia stratiotes</i>	Accumulation of Hg concentrations from 1 to 15 mg kg <sup>-1</sup> DW	V. Kumar et al. (2019)
<i>Typhadomin-gensis</i>	Reduces 99.6 ± 0.4% of the mercury in contaminated water	Gomes et al. (2014)
<i>Lemna minor</i> and <i>Salvinia natans</i>	The efficiency of mercury removal from the substrate in the phytoremediation process was 96%. The total protein was increased for <i>L. minor</i> by 34%, <i>S. natans</i> by 84%, and in mixed culture by up to 99%. Also, the total chlorophyll increased	Sitarska et al. (2023)

(Continues)

TABLE 6 (Continued)

Plant species	Results	References
	for <i>L. minor</i> by 14% and for the mixed culture by up to 60%. For <i>S. natans</i> , the total chlorophyll decreased by 53%.	

containing 1 mg kg<sup>-1</sup> of Hg, commercial AMF formulas combined with *Lolium perenne* led to greater root uptake (0.49 vs. 0.12 mg kg<sup>-1</sup> of Hg), less translocation (0.28 vs. 0.75 mg kg<sup>-1</sup> of Hg) in contrast with the non-inoculated control (Leudo et al., 2020). It should be noted that although non-native AMF inocula promote plant growth and protect against Hg toxicity by reducing its bioavailability, they do not eliminate Hg from the contaminated site, thus requiring long-term monitoring. Hg-tolerant arbuscular mycorrhizal strains may be useful for phytostabilisation. Kodre et al. (2017) found that *Zea mays* inoculated with *Glomus* sp. isolated from a Hg contaminated site accumulated significantly more Hg (reaching 439 mg kg<sup>-1</sup>) than plants treated with a commercial inoculum. Hg tetra-thiolate complexes were detected in arbuscular mycorrhizal roots, showing AMF's ability to modify Hg soil-to-root mobility. Debeljak et al. (2018) reported AMF's potential role in Hg cycling. Putative Hg-hyperaccumulator plants may be colonised with AMF for phytoremediation purposes. *E. polymnioides* showed the highest Hg accumulation in roots among plant species collected from gold mine soils, attributed to high AMF colonisation (Chamba et al., 2017). *Chrysopogon zizanioides* inoculated with commercial AMF had enhanced growth and Hg accumulation, but only in highly contaminated soil (6 mg kg<sup>-1</sup>) (Bretaña et al., 2019). Hg-tolerant fungal root endophytes *Aspergillus* sp., *Curvularia geniculata* P1, *Lindgomycetaceae* P87 and *Westerdykella* sp. P71 increased dry weight and Hg(II) deposition in *Aeschynomene fluminensis* and *Z. mays* by reducing Hg(II) translocation (Aguirre et al., 2018). The addition of mycorrhizae to *L. perenne* L. improved Hg absorption and distribution in roots and shoots and increased Hg elimination from soil, enhancing the diversity of soil microbe families (Saldarriaga et al., 2023).

#### 4 | CONCLUSIONS AND RECOMMENDATIONS

Mercury is a highly toxic metal whose production sources are both natural and human based. Hg contaminating feats on soil and its capability to extend marine ecosystem represents peril to human and environmental health, owing to its bio accrual and biomagnification ability in the food chain. Because of this reason there is increasing scientific concern for decreasing the Hg content in the soil and water environments. Bioremediation based on application of various microbial and phytoremediation approaches can be employed to remove or transform mercury into a less harmful form. Mercury-resistant bacteria

with the mer operon in their genome survive in the presence of Hg (Hg resistance) and can convert harmful forms of Hg to less toxic forms. Bacteria containing the merB gene and genetically modified organisms with the mer operon, including merB and other useful genes that provide resistance to other metals, tolerance to changes in pH and endurance in extreme environments, are considered appropriate for use in bioremediation. In phytoremediation, plants with high biomass are commonly used, however, the disposal of harvested plants containing Hg must be carefully considered. In addition, the emission of Hg(0) to the atmosphere from various phytoremediation plant species, particularly transgenic plants, needs to be evaluated further. In conclusion, contaminated soil health can be improved through phytoremediation and bioremediation approaches, offering an environmentally friendly, long-lasting and cost-effective remediation method with great efficiency.

### CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

### DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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