Applied Microbiology and Biotechnology (2018) 102:5437–5444
https://doi.org/10.1007/s00253-018-8969-6

MINI-REVIEW

Lead absorption mechanisms in bacteria as strategies for lead bioremediation

Sonia M. Tiquia-Arashiro[1]

Received: 21 February 2018 / Revised: 23 March 2018 / Accepted: 24 March 2018 / Published online: 8 May 2018

Abstract

Bacteria exhibit a number of metabolism-dependent and metabolism-independent processes for the uptake and accumulation of toxic metals. The removal of these metals from environmental sources such as soil, sludge, and wastewaters using microbe-based technologies provide an alternative for their recovery and remediation. Lead (Pb) is a pervasive metal in the environment that adversely affects all living organisms. Many aspects of metal-microbe interactions remain unexploited in biotechnology and further development and application is necessary, particularly to the problem of Pb release into the environment. Thus, this review provides a synopsis of the most important bacterial phenotypes and biochemical attributes that are instrumental in lead bioremediation, along with what is known of their genetic background that can be exploited or improved through genetic engineering. This review also highlights the potential of Pb-resistant bacteria in bringing about detoxification of Pb-contaminated terrestrial and aquatic systems in a highly sustainable and environmental friendly manner, and the existing challenges that still lie in the path to in situ and large-scale bioremediation.

Keywords Bioremediation · Lead resistance · Metallothionein · Lead bioabsorption · Lead bioaccumulation

Introduction

Lead is widely recognized as one of the most pervasive metal that has caused extensive health problems and environmental contamination in many parts of the world. Lead poisoning is common among children and leads to mental retardation in children (Boeckx 1986; Moncrieff et al. 1964). Lead affects both the male and female reproductive systems. In men, lead reduces sperm count when blood lead levels exceed 40 μg $dL^{-1}$of blood (Grant 2009). Elevated blood lead levels in pregnant women lead to miscarriage, prematurity, and low birth weight (Cleveland et al. 2008). Lead also is toxic to natural biota including microorganisms by inhibiting enzyme activity, damaging DNA, and disrupting cell membrane permeability (Nies 1999; Jaishankar et al. 2014). Industrial activities, such as the manufacture of batteries, pigments, lead arsenate insecticides, or lead water pipes, are the main sources of lead in the environment (Tong et al. 2000). In industrial areas, total lead concentration can reach up to 10,000 mg kg^{-1}, which is 100 to 1000 times higher that of soil (Schwab et al. 2005; Akmal and Jianming 2009). In aquatic ecosystems, lead tends to settle at the bottom of the water where it concentrates and is capable of accumulating in the tissues of aquatic biota (Bowman et al. 2018). Due to extensive anthropogenic activities, lead has increased significantly, which led to biomagnifications at different tropic levels in the food chain (Kundu et al. 2016; Lombardi et al. 2010). Despite the fact that lead is the most common metal found in Superfund sites (Enger and Smith 1992), it is less commonly studied compared to other metals. Lead not only needs to be remediated from the ecosystem, it is also requires to be recovered from every possible source given its importance in commercial and industrial applications.

The impact of metals on biological processes has led to the emergence of a variety of resistance mechanisms. Bacterial metal resistance mechanisms include precipitation of metals as phosphates, carbonates, and sulfides, intracellular accumulation with low molecular weight, cysteine-rich proteins, extracellular sequestration in biopolymers, energy-dependent efflux mechanisms, and alteration of cell morphology (Higham et al. 1984; Taghavi et al. 2009; Roanne 1999; Naik and Dubey 2011; Naik et al. 2012a; Jarosławiecka and Piotrowska-Seget 2014). Interestingly, it is precisely the study

✉ Sonia M. Tiquia-Arashiro
smtiquia@umich.edu

[1] Department of Natural Sciences, University of Michigan-Dearborn, Dearborn, MI 49128, USA

of these adaptation to metal tolerance that is providing the tools to carry out bioremediation. Bacterial strains that possess these unique capabilities prove to be valuable for the recovery or removal of metals from contaminated sites.

Over the last several decades, studies on the use of bacterial strains for environmental restoration have primarily focused on exploiting their potential for heavy metal remediation both in terrestrial and aquatic ecosystems mainly because remediation processes with microorganisms are cost effective and are highly efficient as compared to conventional methods (physicochemical methods). Conventional methods generally utilize non-regenerable materials, which in turn increases the cost of the remediation process. Furthermore, these methods accumulate substantial secondary waste and are therefore not environmental friendly. Tapping any of the resistance mechanisms mentioned above has significant potential for the development of environmentally friendly and cost-effective process for heavy metal decontamination.

Overall, microbes play an important role in the process of lead mobilization and transformation in the environment and the investigation on Pb bioremediation mechanisms is of practical significance. Despite the many interesting metal-related properties of other biological agents (e.g., fungi/yeasts, algae and plants), this review focuses on bacterial systems, particularly on current knowledge of several lead resistance mechanisms in bacteria and the approaches and strategies for lead removal from the environment. In general, bacteria are more resistant to metals than eukaryotic organisms and are therefore excellent players in bioremediation of metals. Moreover, bacteria are excellent biosorbents owing to their surface to volume ratio, and due to high number of potentially active sorption sites (Veglio et al. 1997; Pagnanelli et al. 2000). Emerging technologies in this arena rely on enhancing the biosorption of metals into biomass, or the precipitation and transformation of ions by exploiting some metal-related facet of bacterial metabolism. This review also highlights bacterial systems that are amenable to genetic analysis and, eventually, to genetic engineering for the enhancement of their lead-associated abilities. Figure 1 illustrates a schematic diagram summarizing the features and differences of each adsorption mechanism.

Biosorption of lead on cell surface

The cell wall is a natural barrier for toxic metals since the functional groups of several macromolecules in the cell wall are involved in metal binding (Fomina and Gadd 2014). The cell walls of both Gram-positive and Gram-negative bacteria naturally carry a negative charge, which bind to metal cations and regulate movement of metals across the membrane. Carboxyl groups in Gram-positive bacterial cell walls are the key binding sites for metal cations, whereas phosphate groups contribute significantly to metal binding in Gram-negative species (Gadd 2009). Carbonyl, phosphate, hydroxyl, and amino groups in the cell wall of *Pseudomonas aeruginosa* ASU6a (Gabr et al. 2008) are recognized to participate in binding Pb^{2+}, while molecules with amide, amino, hydroxyl, or carboxyl groups participate in the binding of Pb^{2+} *Synecochoccus* sp. cell wall (Shen et al. 2008). Interestingly, in *E. coli*, almost 97% of Pb^{2+} is bound in the cell membrane, while almost no Pb^{2+} is detected in peptidoglycan (Kumar and Upreti 2000). The adsorption capacity of Pb^{2+} on the cell surface is strongly affected by pH and the initial lead concentration. The study of pH effect on metal removal (e.g., lead) by *Pseudomonas pseudoalcaligenes* and *Micrococcus luteus* by indicates that the metal biosorption increased with increasing pH from 2 to 6 (Leung et al. 2000), with a maximum absorption capacity achieved at pH 5 and initial metal concentration of 100 mg L^{-1} (Leung et al. 2000).

Biosorption of lead on extracellular polymeric substances (EPS)

Another mechanism that many metal-tolerant bacteria possess involves absorption of metals by secreting extracellular polymeric substances (EPS). These EPS are of particular relevance to the bioremediation process because of their involvement in the flocculation process and binding of metal ions from solutions (Salehizadeh and Shojaosadati 2003). EPS are such complex blend of high molecular weight polyanionic polymers, such as proteins, humic acids, polysaccharides and nucleic acids that bind cationic metals with different degrees of specificity and affinity (Bhaskar and Bhosle 2006; Pal and Paul 2008). Several lead-resistant bacteria including *Klebsiella michiganensis* R19, *Providencia rettgeri* L2, *Raoultella planticola* R3, and *Serratia* sp. L30 have been found to absorb lead in mono- and mixed metal solutions (Bowman et al. 2018). These bacterial strains can grow at 1.25 or 1.5 g L^{-1} of Pb $(NO_3)_2$. In mono-metal (lead only) solutions, the Pb^{2+} removal is highest for *K. michiganensis* R19. In the multiple metal solutions containing eight metals (As, Pb, Cu, Mn, Zn, Cd, Cr, and Ni), the highest Pb^{2+} removal is recorded for *K. michiganensis* (297 mg Pb g^{-1}), followed by *R. planticola* R3 (102 mg Pb g^{-1}) and *P. rettgeri* L2 (0.11 mg Pb g^{-1}). The highly selective affinity towards Pb^{2+} observed for strain *K. michiganensis* R19 suggests its use for the recovery of Pb^{2+} from multiple-metal solutions (Bowman et al. 2018).

The binding process results in metal immobilization, preventing toxic cationic metals from entering the cell. EPS binding of Pb^{2+} has been observed in several lead-resistant bacteria (Roanne 1999; Salehizadeh and Shojaosadati 2003; Raungsomboon et al. 2006, 2007; Amoozegar et al. 2012; Kalita and Joshi 2017). The structural and compositional make up of EPS varied according to phase of bacterial growth

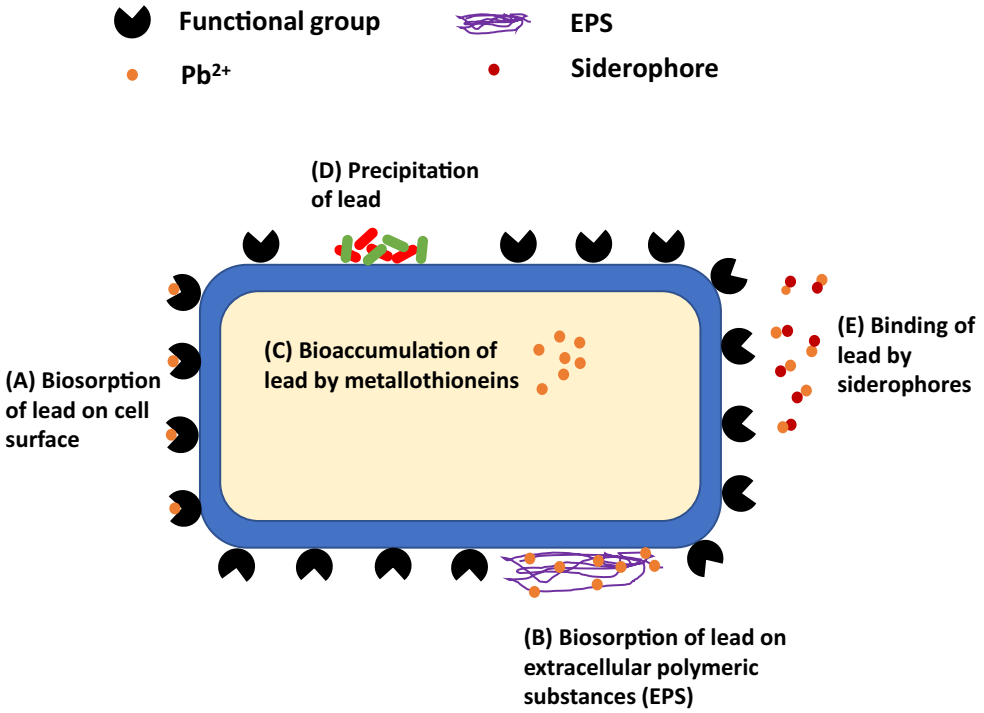

Fig. 1 Lead absorption mechanisms in bacteria. **a** Biosorption of lead on cell surface. **b** Biosorption of lead on extracellular polymeric substances (EPS). **c** Bioaccumulation of lead by metallothioneins. **d** Precipitation of lead. **e** Binding of lead by siderophores

and thus higher lead removal is seen during stationary phase due to high net acidic sugar incorporation in the EPS (Raungsomboon et al. 2006). In case of *Gloeocapsa gelatinosa*, abundance of acidic sugar in EPS resulted in much higher lead ion sequestration around 82–86 mg Pb g^{-1} of EPS (Raungsomboon et al. 2006). Likewise, *Calothrix marchi*ca display similar pattern of Pb^{2+} adsorption where higher acidic sugar content of EPS was responsible for the enhanced Pb^{2+} complexation of almost 65 mg Pb^{2+} g^{-1} of EPS (Raungsomboon et al. 2007). Enzymatic activities in EPS also assist in detoxification of metals by transformation and subsequent precipitation in the polymeric mass making them ideal lead biosorbent agent for bioremediation.

The cation binding ability of EPS from biofilms, activated sludges, and biogranules has been studied to establish the role EPS as the key component in heavy metal bioremediation (Gupta and Diwan 2017). Metal binding to biofilm EPS is influenced by surrounding pH, metal concentration, presence of organic matter, biomass and protein (C/P ratio) to remove heavy metals in the wastewater. In *Burkholderia cepacia* biofilms, 90% of the total lead uptake occurred at pH < 4.5, which subsequently led to the accumulation nanoscale crystals of pyromorphite ($Pb_5[PO_4]_3[OH]$) in the biofilm (Templeton et al. 2003). Activated sludges have always been a rich source of several metal-resistant bacterial species. EPS from sludges exhibit greater metal complexation than that of pure cultures of bacteria (Xie et al. 2006). In activated sludge bioreactor, the biosorption yield of Pb^{2+} is higher (0.793 mM min^{-1}) than Cu^{2+} (0.242 mM min^{-1}) (Sag et al. 2003). Anaerobic biogranules prepared from sludge of wastewater treatment plant have also proved to be effective biosorbing agents for removal of Pb^{2+} from metal-contaminated wastewater (Hawari and Mulligan, 2006). The lead removal can be as high as 1.23 mM g^{-1}.

Various factors influence metal sorption by the EPS including the initial metal concentrations, pH, and sodium chloride concentrations on binding of lead (Pb^{2+}). In *Enterobacter cloacae* P2B, a significant increase in EPS production (108 mg l^{-1} dry weight) was observed when the cells are exposed to 1.6 mM lead nitrate in Tris buffered minimal medium (pH 7.2) (Naik et al. 2012a). Perez et al. (2008) noted that the immobilization of Pb^{2+} in the EPS is strictly pH dependent. In their study, they found that *Paenibacillus jamilae* achieve maximum binding capacity (303 mg g^{-1} EPS) for lead at pH 6 (Perez et al. 2008). For *Marinobacter* sp., both Cu^{2+} and Pb^{2+} ions are sorbed more at near neutral pH than acidic pH (Bhaskar and Bhosle 2006). The estimated maximum binding ability of the EPS is 182 nmol copper and 13 nmol lead mg^{-1} EPS. However, the sorption of these metals decreased with increased sodium chloride concentrations (Bhaskar and Bhosle 2006).

Bioaccumulation of lead by metallothioneins

Bioaccumulation is an active metabolic process that requires energy (Velásquez and Dussan 2009). Unlike the biosorption process described above, bioaccumulation binds metals intracellularly (Joutey et al. 2015). Possibly the best-known mechanism involves metal-binding with metallothioneins.

Metallothioneins are low molecular weight, cysteine-rich proteins that facilitate the sequestration or bioaccumulation of toxic metals inside the cell (Hamer 1986). This resistance mechanism is often plasmid-borne, which facilitates its dispersion from one cell to another (Das et al. 2016). Bacteria synthesize metallothioneins in response to increased metal exposure (Blindauer et al. 2002; Gadd 1990; Liu et al. 2003; Turner et al. 1996). The production of metallothioneins in the presence of Pb^{2+} has been detected in *Bacillus cereus*, *Bacillus megaterium*, *Proteus penneri* GM-10, *Providencia vermicola* strain SJ2A, *Pseudomonas aeruginosa* strainWI-1, *Salmonella choleraesuis*, and *Streptomyces* sp., 4A (Huckle et al. 1993; Murthy et al. 2011; Naik et al. 2012b; Roanne 1999; Rifaat et al. 2009; Sharma et al. 2017).

The presence of plasmid-borne bacterial metallothionein genes, *bmt*A and *smt*AB in lead-resistant strains may be attributed to the intracellular sequestration of lead. Sharma et al. (2017) investigated the intracellular sequestration of 155.12 mg g^{-1} of lead by metallothionein (BmtA)-producing *P. vermicola*. *P. aeruginosa strain* WI-1 also possesses metallothionein (BmtA), which bioaccumulated 26.5 mg g^{-1} of lead intracellularly to reduce lead toxicity (Naik et al. 2012a). *P. penneri* expressed metallothionein (SmtAB), bioaccumulating 22 mg g^{-1} of lead (Naik et al. 2012b, 2012c). Several bacterial strains have been reported to encode metallothioneins including *Synechococcus* PCC 7942 (SmtA), *Anabaena* PCC7120 (SmtA), *Oscillatoriabrevis* (BmtA), and *Pseudomonas putida* (BmtA) (Blindauer et al. 2002; Turner et al. 1996; Liu et al. 2003). Hence, these metallothionein-producing bacteria can be used for bioremedaition of lead in contaminated environmental sites.

Precipitation of lead

Precipitation is another mechanism used by several bacteria to lower the concentration of free metals to insoluble complexes and therefore reducing their bioavailability and toxicity. Pb^{2+} has been known to react with several anions such as chlorides, phosphates, sulfides, carbonates, and hydroxyl ions to form insoluble precipitates. The precipitation process occur outside (extracellularly) or inside (intracellularly) the cell (Levinson et al. 1996). Bacteria reported to precipitate lead into lead phosphate include *Providencia alcalifaciens* 2EA (Naik et al. 2013), *Pseudomonas fluorescens* ATCC13525 (Al-Aoukaty et al. 1991), *Staphylococcus aureus* (Levinson et al. 1996), *Vibrio harveyi* (Mire et al. 2004), and *Bacillus thuringiensis* 016 (Chen et al. 2015). A phosphate-solubilizing bacterium, *E. cloacae*, is found to resist lead by immobilizing lead as insoluble lead phosphate, pyromorphite (Park et al. 2011). The lead-resistant *Bacillus iodinium* GP13 and *Bacillus pumilus* S3 and *Klebsiella aerogenes* NCTC418 precipitate lead into lead sulfide (Aiking et al. 1985; De et al. 2008).

Recently, Mwandira et al. (2017) used the microbially induced calcium carbonate precipitation (MICP) technique in conjunction with the bacterium *Pararhodobacter* sp. to bioremediate lead-contaminated mine wastes. Laboratory-scale experiments showed complete removal of 1036 mg L^{-1} of lead and the coprecipitation of calcium carbonate and lead. *Pararhodobacter* sp. is effective at complete removal of Pb^{2+} in soils. This result is comparable to other ureolytic bacteria such as *Rhodobacter spharoides*, which achieved 90.31% (Li et al. 2016); *Sporosarcina pasteurii* (Mugwar and Harbottle 2016); and *Terrabacter tumescens* achieved 100% (Li et al. 2015), which achieved 90 to 100% lead removal. Varenyam et al. (2012) used the calcite-precipitating bacterium *Kocuria flava* and saw reduction in Pb bioavailability in Pb-contaminated soils. These findings proved that precipitation of lead by MICP has the potential for remediation of lead-contaminated soils. The capability of ureolytic bacteria to completely remove lead lies in its ability to efficiently hydrolyze urea to generate carbonate ions and elevate the pH to alkaline conditions (8.0–9.1), which promotes the precipitation of lead and calcium carbonate.

The effect of pH on the precipitation metals is well documented. For example, at pH levels of 6.6 and higher, various Pb phosphates (in noncalcareous soils) and $PbCO_3$ may be precipitated (Santillan-Medrano and Jurinak 1975). Complexation of metals also appears to decrease in increasingly acidic conditions (Elliott et al. 1986). Thus, these reports argue for the importance of accounting for pH changes when using the precipitation strategy in bioremediation of metals.

Binding of lead by siderophores

Siderophores are a major class of chelators secreted by microorganisms in various habitats. They function mainly as mediators of iron transport to the cell. Although these metal chaperones are specific for iron, they also bind effectively with other metals outside the cell (Saha et al. 2016). *P. aeruginosa* 4EA has been found to produce siderophores (pyochelin and pyoverdine), which are involved in the complexation of Pb^{2+} (Naik and Dubey 2011). The siderophore production of this lead-resistant bacterial strain is enhanced by the presence of up to 0.5 mM lead nitrate. The production of pyoverdines by the plant growth promoting strain *Pseudomonas putida* KNP9 has been found to reduce the concentration of Pb^{2+} in mung bean roots by 93% and in shoots by 56% (Tripathi et al. 2005). Braud et al. (2010) found that the siderophore pyochelin contributes to Pb^{2+} binding in *P. aeruginosa* PAO1, seemingly with higher affinity to Pb^{2+} than pyoverdine. In field studies, the siderophore-overproducing mutant of *Kluyvera ascorbate* SUD165

(another plant growth promoting bacterial strain) has been implicated in the reduction Ni, Pb, and Zn toxicity (Burd et al. 2000). The ability of siderophores to reduce the mobility of lead in the environment by forming stable metal–ligand complexes makes them an ideal strategy for lead remediation.

Genetic engineering for enhanced Pb bioremediation

The introduction of genetic engineering has opened up avenues for designing microorganisms that possess high affinity and selectivity to metals. Wei et al. (2014) developed a selective lead-sensing system and a remediation system respectively using the gene elements of the lead-specific operon *pbr*, including the lead-specific binding protein PbrR from *Cupriavidus metallidurans* CH34 (Fig. 2a). For highly sensitive and selective whole-cell detection of lead ions, the lead-specific binding protein (PbrR) and the lead-specific promoter (*pbr*) from *C. metallidurans* CH34 is inserted into *E. coli* in along with an engineered downstream red fluorescence protein (rfp) (Fig. 2b). The subsequent engineering of the *E. coli* cell surface to display the unique lead binding protein, PbrR, permits the selective adsorption and immobilization of lead from solution containing various heavy metal ions. This method of lead removal has several advantages over traditional biosorption methods. It eases the burden of intracellular accumulation of toxic metal ions, which often results not only in decreased absorption efficiency, but also poor growth of the cells (Kuroda and Ueda 2010). It allows for faster interaction between the cell surface-displayed binding proteins and metal ions in the environment. It increases the cell's tolerance for metals (Wei et al. 2012). The latter is particularly important when treating metals using engineered live cells.

Some metal-binding proteins found in nature along with novel metal-chelating peptides obtained in the laboratory have been introduced into bacteria. For instance, engineering of *E. coli* BL21 (DE3) by the transfer of C.gMT metallothionein from *Corynebacterium glutamicum* results in significantly greater Pb^{+2} and Zn^{+2} than did the non-engineered *E. coli* BL21 (DE3) (Jafarian and Ghaffari 2017). The expression of mice metallothionein in *E. coli* (pMt-Thio) enhances metal biosorption efficiency of bacterial biosorbents for Pb^{2+} and Cd^{2+} ions. The results show that pMt-Thio significantly increases the overall biosorption capacity, especially for biosorption of lead (Almaguer-Cantú et al. 2011).

One effective approach to the surface display of metal coordinating moieties is cytoplasmic expression in conjunction with the introduction of specific heavy metal membrane transporters (Chen and Wilson 1997). This approach overcomes metal uptake limitations across the cell membrane, but is restricted to those metals for which there are active import systems (e.g., mercury, copper, lead, and nickel). The cytoplasmic expression in conjunction with the introduction of specific metal membrane transporters can increase both specificity to a particular metal (e.g., lead) and bioaccumulation yield.

Another powerful technique for obtaining novel and unpredicted metal chelators is the artificial selection of peptide variants from libraries that include millions of random sequences. Phage display technology has been used as a powerful tool in the discovery of peptides capable of exhibiting specific affinity to various metals or metal ions. A polypeptide selected by this method is able to confer increased survival to toxic concentrations of the metal when expressed in *E. coli* as a fusion to the OmpA outer membrane protein (Mejare et al. 1998). Phage display technology in conjunction with chromatography procedure have been used by Nian et al. (2010) to select for peptides with high affinities for lead. In their study, a peptide sequence ThrAsnThrLeuSerAsnAsn (TNTLSNN) found and its high relative binding affinity and specificity to lead was confirmed.

Conclusions and future perspectives

The examples outlined above indicate that lead remediation technologies using bacteria are feasible alternatives to conventional technologies (e.g., physical cleansing of soils or the concentration of metals in polluted waters by physical or chemical means). Microbe-based approaches have several advantages over traditional physical and chemical methods including (1) higher specificity, (2) their suitability to in situ techniques, and (3) their potential for improvement by genetic engineering. Possible developments in the lead bioremediation include further genetic improvement of strains. Molecular techniques may permit the design of strains with

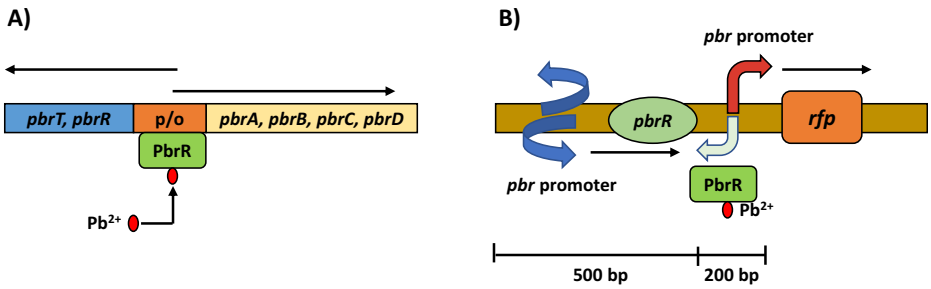

Fig. 2 **a** Genetic organization of the *pbr* operon locus in *Cupriavidus metallidurans* CH34 genome. In the presence of Pb2+, PbrR binds to the pbr promoter (p/o) and initiates its transcription in two opposite directions. **b** Genetic organization of the lead inductive RFP expression plasmid in *Escherichia coli*

specific metal-binding properties through the expression of metal-chelating proteins and peptides; to further improve lead biosorption and precipitation processes and the introduction of metal transformation activities in robust strains. Other techniques include engineering with a single gene or operon, alteration of existing gene sequences, and pathway switching (Das et al. 2016). The prospect of creating artificial combination of genes not present in nature offers an opportunity for these genetically modified bacteria to be used for in situ removal of lead pollutants.

The adaptation of existing methodologies to in situ and large-scale decontamination processes also needs to be developed. Large-scale biological applications are still rare due to the inherent difficulty of reproducing these processes at large scale. Likewise, field experiments go through much more adverse environmental conditions where strict regulation and control of temperature, pH, ionic strength, and other physicochemical parameters are often difficult, compared with lab-scale settings in which laboratory conditions can be controlled. The exploration and study of newly isolated heavy lead-resistant bacteria may contribute to progress in situ bioremediation. For instance, to date, little is known about the metal transformation properties of archaea, which often colonize extreme environments and may have advantageous activities in more adverse environmental conditions.

Acknowledgements Work in author's laboratory is funded by the Office of Research and Sponsored Programs at the University of Michigan-Dearborn.

Compliance with ethical standards

Conflict of interest The author declares that she has no conflict of interest.

References

Aiking H, Govers H, van't Riet J (1985) Detoxification of mercury, cadmium, and lead in *Klebsiella aerogenes* NCTC 418 growing in continuous culture. Appl Environ Microbiol 50:1262–1267

Akmal M, Jianming X (2009) Microbial biomass and bacterial community changes by Pb contamination in acidic soil. J Agric Biol Sci 1:30–37

Al-Aoukaty A, Appanna VD, Huang J (1991) Exocellular and intracellular accumulation of lead in *Pseudomonas fluorescens* ATCC13525 is mediated by the phosphate content of the growth medium. FEMS Microbiol Lett 83:283–290

Almaguer-Cantú V, Morales-Ramos LH, Balderas-Rentería I (2011) Biosorption of lead (II) and cadmium (II) using *Escherichia coli* genetically engineered with mice metallothionein I. Water Sci Technol 63:1607–1613

Amoozegar MA, Ghazanfari N, Didari M (2012) Lead and cadmium bioremoval by *Halomonas* sp., an exopolysaccharide producing halophilic bacterium. Prog Biol Sci 2:1–11

Bhaskar PV, Bhosle NB (2006) Bacterial extracellular polymeric substances (EPS) a carrier of heavy metals in the marine food-chain. Environ Int 32:192–198

Blindauer CA, Harrison MD, Robinson AK, Parkinson JA, Bowness PW, Sadler PJ, Robinson NJ (2002) Multiple bacteria encode metallothione in sand SmtA-like fingers. Mol Microbiol 45:1421–1432

Boeckx RL (1986) Lead poisoning in children. Anal Chem 58:274A–288A

Bowman N, Patel D, Sanchez A, Xu W, Alsaffar A, Tiquia-Arashiro SM (2018) Lead-resistant bacteria from Saint Clair River sediments and Pb removal in aqueous solutions. Appl Microbiol Biotechnol 102: 2391–2398

Braud A, Geoffroy V, Hoegy F, Mislin GLA, Schalk IJ (2010) Presence of the siderophores pyoverdine and pyochelin in the extracellular medium reduces toxic metal accumulation in *Pseudomonas aeruginosa* and increases bacterial metal tolerance. Environ Microbiol Rep 2: 419–425

Burd GI, Dixon DG, Glick BR (2000) Plant growth-promoting bacteria that decrease heavy metal toxicity in plants. Can J Microbiol 46: 237–245

Chen S, Wilson DB (1997) Construction and characterization of *Escherichia coli* genetically engineered for bioremediation of Hg^{2+}-contaminated environments. Appl Environ Microbiol 63: 2442–2445

Chen Z, Pan X, Chen H, Lin Z, Guan X (2015) Investigation of lead(II) uptake by *Bacillus thuringiensis* 016. World J Microbiol Biotechnol 31:1729–1736

Cleveland LM, Minter ML, Cobb KA, Scott AA, German VF (2008) Lead hazards for pregnant women and children. Am J Nurs 108: 40–49.

Das S, Dash HR, Chakraborty J (2016) Genetic basis and importance of metal resistant genes in bacteria for bioremediation of contaminated environments with toxic metal pollutants. Appl Microbiol Biotechnol 100:2967–2984

De J, Ramaiah N, Vardanyan L (2008) Detoxification of toxic heavy metals by marine bacteria highly resistant to mercury. Mar Biotechnol 10:471–477

Elliott HA, Liberati MR, Huang CP (1986) Competitive adsorption of heavy metals by soils. J Environ Qual 15:214–219

Enger ED, Smith BF (1992) Hazardous and toxic wastes. In: Enger ED, Smith BF (eds) Environmental science: a study of interrelationships, 4th ed. WC C Brown publishers, pp 444–464

Fomina M, Gadd GM (2014) Biosorption: current perspectives on concept, definition and application. Bioresour Technol 160:3–14

Gabr RM, Hassan SHA, Shoreit AAM (2008) Biosorption of lead and nickel by living and non-living cells of *Pseudomonas aeruginosa* ASU 6a. Int Biodeterior Biodegrad 62:195–203

Gadd GM (1990) Heavy metal accumulation by bacteria and other microorganisms. Experientia 46:834–840

Gadd GM (2009) Biosorption: critical review of scientific rationale, environmental importance and significance for pollution treatment. J Chem Technol Biotechnol 84:13–28

Grant LD (2009) Lead and compounds. In: Lippmann M (ed) Environmental toxicants: human exposures and their health effects. 3rd edition. Wiley-Interscience, pp 758–809

Gupta P, Diwan B (2017) Bacterial exopolysaccharide mediated heavy metal removal: a review on biosynthesis, mechanism and remediation strategies. Biotechnol Rep 13:58–71

Hamer DH (1986) Metallothioneins. Annu Rev Biochem 55:913–951

Hawari AH, Mulligan CN (2006) Biosorption of lead(II), cadmium(II), copper(II) and nickel(II) by anaerobic granular biomass. Bioresour Technol 97:692–700

Higham DP, Sadler PJ, Scawen MO (1984) Cadmium resistant *Pseudomas putida* synthesizes novel cadmium binding proteins. Science 225:1043–1046

Huckle JW, Morby AP, Turner JS, Robinson NJ (1993) Isolation of a prokaryotic metallothionein locus and analysis of transcriptional control by trace metal ions. Mol Microbiol 7:177–187

Jafarian V, Ghaffari F (2017) A unique metallothionein-engineered in *Escherichia coli* for biosorption of lead, zinc, and cadmium; absorption or adsorption? Microbiology 86:73–81

Jaishankar M, Tseten T, Anbalagan N, Mathew BB, Beeregowda KN (2014) Toxicity, mechanism and health effects of some heavy metals. Interdiscip Toxicol 7:60–72

Jarosławiecka A, Piotrowska-Seget Z (2014) Lead resistance in microorganisms. Microbiology 160:12–25

Joutey NT, Sayel H, Bahafid W, El Ghachtouli N (2015) Mechanisms of hexavalent chromium resistance and removal by microorganisms. Rev Environ Contam Toxicol 233:45–69.

Kalita D, Joshi SR (2017) Study on bioremediation of lead by exopolysaccharide producing metallophilic bacterium isolated from extreme habitat. Biotechnol Rep 16:48–57

Kumar M, Upreti RK (2000) Impact of lead stress and adaptation in Escherichia coli. Ecotoxicol Environ Saf 47:246–252

Kundu D, Mondal S, Dutta D, Haque S, Ghosh AR (2016) Accumulation and contamination of lead in different trophic levels of food chain in sewage-fed East Kolkata Wetland, West Bengal, India. Int J Environ Tech Sci 2:61–68

Kuroda K, Ueda M (2010) Engineering of microorganisms towards recovery of rare metal ions. Appl Microbiol Biotechnol 87:53−60

Leung WC, Wong MF, Chua H, Lo W, Yu PHF, Leung CK (2000) Removal and recovery of heavy metals by bacteria isolated from activated sludge treating industrial effluents and municipal wastewater. Water Sci Technol 41:233–240

Levinson HS, Mahler I, Blackwelder P, Hood T (1996) Lead resistance and sensitivity in *Staphylococcus aureus*. FEMS Microbiol Lett 145:421–425

Li M, Cheng X, Guo H, Yang Z (2015) Biomineralization of carbonate by *Terrabacter tumescens* for heavy metal removal and biogrouting applications. J Environ Eng https://doi.org/10.1061/(ASCE)EE.1943-7870.0000970. C4015005-C4015005

Li X, Peng W, Jia Y, Lu L, Fan W (2016) Bioremediation of lead contaminated soil with *Rhodobacter sphaeroides*. Chemosphere 156:228–235

Liu T, Nakashima S, Hirose K, Uemura Y, Shibasaka M, Katsuhara M, Kasamo K (2003) A metallothionein and CPx-ATPase handle heavy-metal tolerance in the filamentous cyanobacteria *Oscillatoriabrevis*. FEBS Lett 542:159–163

Lombardi PE, Peri SI, Verrengia NR (2010) ALA-D and ALA-Dreactivated as biomarkers of lead contamination in the fish *Prochilodus lineatus*. Ecotoxicol Environ Saf 73:1704–1711

Mejare M, Ljung S, Bulow L (1998) Selection of cadmium specificc hexapeptides and their expression as OmpA fusion proteins in *Escherichia coli*. Protein Eng 11:489–494

Mire CE, Tourjee JA, O'Brien WF, Ramanujachary KV, Hecht GB (2004) Lead precipitation by Vibrio harveyi: evidence for novel quorum-sensing interactions. Appl Environ Microbiol 70:855–864

Moncrieff AA, Koumides OP, Clayton BE, Patrick AD, Renwick AGC, Roberts GE (1964) Lead poisoning in children. Arch Dis Child 39:1–13.

Mugwar AJ, Harbottle MJ (2016) Toxicity effects on metal sequestration by microbially- induced carbonate precipitation. J Hazard Mater 314:237–248

Murthy S, Geetha B, Sarangi SK (2011) Effect of lead on metallothionein concentration in lead-resistant bacteria *Bacillus cereus* isolated from industrial effluent. Afr J Biotechnol 10:15966–15972

Mwandira W, Nakashima K, Kawasaki S (2017) Bioremediation of lead-contaminated mine waste by *Pararhodobacter* sp. based on the microbially induced calcium carbonate precipitation technique and its effects on strength of coarse and fine-grained sand. Ecol Eng 109:57–64

Naik MM, Dubey SK (2011) Lead-enhanced siderophore production and alteration in cell morphology in a Pb-resistant *Pseudomonas aeruginosa* strain 4EA. Curr Microbiol 62:409–414

Naik MM, Pandey A, Dubey SK (2012a) Biological characterization of lead-enhanced exopolysaccharide produced by a lead resistant *Enterobacter cloacae* strain P2B. Biodegradation 23:775–783

Naik MM, Pandey A, Dubey SK (2012b) *Pseudomonas aeruginosa* strain WI-1 from Mandovi estuary possesses metallothionein to alleviate lead toxicity and promotes plant growth. Ecotoxicol Environ Saf 79:129–133

Naik MM, Shamim K, Dubey SK (2012c) Biological characterization of lead resistant bacteria to explore role of bacterial metallothionein in lead resistance. Curr Sci 103:1–3

Naik MM, Khanolkar DS, Dubey SK (2013) Lead resistant *Providentia alcalifaciens* strain 2EA bioprecipitates Pb^{2+} as lead phosphate. Lett Appl Microbiol 56:99–104

Nian R, Kim DS, Nguyen T, Tan L, Kim CW, Yoo IK, Choe WS (2010) Chromatographic biopanning for the selection of peptides with high specificity to Pb^{2+} from phage displayed peptide library. J Chromatogr A 1217:5940–5949

Nies DH (1999) Microbial heavy-metal resistance. Appl Microbiol Biotechnol 51:730–750

Pagnanelli F, Papini MP, Toro L, Trifoni M, Veglio` F (2000) Biosorption of metal ions on *Arthrobacter* sp.: biomass characterization and biosorption modeling. Environ Sci Technol 34:2773–2778

Pal A, Paul AK (2008) Microbial extracellular polymeric substances: central elements in heavy metal bioremediation. Indian J Microbiol 48:49–64

Park JH, Bolan N, Meghraj M, Naidu N (2011) Concomitant rock phosphate dissolution and lead immobilization by phosphate solubilizing bacteria (*Enterobacter* sp.). J Environ Manag 92:1115–1120

Perez MPJA, Garcıa-Ribera R, Quesada T, Aguilera M, Ramos-Cormenzana A, Monteoliva-Sanchez M (2008) Biosorption of heavy metals by the exopolysaccharide produced by *Paenibacillus jamilae*. World J Microbiol Biotechnol 24:2699–2704

Raungsomboon S, Chidthaisong A, Bunnag B, Inthorn D, Harvey NW (2006) Production: composition and Pb2+ adsorption characteristics of capsular polysaccharides extracted from a cyanobacterium *Gloeocapsa gelatinosa*. Water Res 40:3759–3766

Raungsomboon S, Chidthaisong A, Bunnag B, Inthorn D, Harvey NW (2007) Lead (Pb^{2+}) adsorption characteristics and sugar composition of capsular polysaccharides of cyanobacterium *Calothrix marchica*. Songklanakarin, Songklanakarin. J Sci Technol 29:529–541

Rifaat HM, Mahrous KF, Khalil WKB (2009) Effect of heavy metals upon metallothioneins in some *Streptomyces* species isolated from Egyptian soil. J Appl Sci Environ Sanit 4:197–206

Roanne TM (1999) Lead resistance in two bacterial isolates from heavy metal-contaminated soils. Microb Ecol 37:218–224

Sag Y, Tarar B, Kutsal T (2003) Biosorption of Pb(II) and Cu(II) by activated sludge in batch and continuous flow stirred reactors. Bioresour Technol 87:27–33

Saha M, Sarkar S, Sarkar B, Kumar B, Bhattacharjee S, Tribedi P (2016) Microbial siderophores and their potential applications: a review. Environ Sci Pollut Res 23:3984–3999

Salehizadeh H, Shojaosadati SA (2003) Removal of metal ions from aqueous solution by polysaccharide produced from *Bacillus firmus*. Water Res 37:4231–4235

Santillan-Medrano J, Jurinak JJ (1975) The chemistry of lead and cadmium in soil: solid phase formation. Soil Sci Soc Am Proc 39:851–856

Sharma J, Shamim K, Dubeya SK, Meena RM (2017) Metallothionein assisted periplasmic lead sequestration as lead sulfite by *Providencia vermicola* strain SJ2A. Sci Tot Environ 579:359–365

Schwab AP, He YH, Banks MK (2005) The influence of organic ligands on the retention of lead in soil. Chemosphere 61:856–866

Shen L, Xia JL, He H, Nie ZY (2008) Comparative study on biosorption of Pb(II) and Cr(VI) by *Synechococcus* sp. Trans Nonferrous Metals Soc 18:1336–1342

Taghavi S, Lesaulnier C, Monchy S, Wattiez R, Mergeay M, vander Lelie D (2009) Lead(II) resistance in *Cupriavidus metallidurans* CH34:

interplay between plasmid and chromosomally-located functions. Antonievan Leeuwenhoek 96:171–182

Templeton AS, Trainor TP, Spormann AM, Newville M, Sutton SR, Dohnalkova A, Gorby Y, Brown GE (2003) Sorption versus biomineralization of Pb(II) within *Burkholderia cepacia* biofilms. Environ Sci Technol 37:300–307

Tong S, von Schirnding YE, Prapamontol T (2000) Environmental lead exposure: a public health problem of global dimensions. Bull World Health Org 78:1068–1077

Tripathi M, Munot HP, Shouche Y, Meyer JM, Goel R (2005) Isolation and functional characterization of siderophore-producing lead- and cadmium-resistant *Pseudomonas putida* KNP9. Curr Microbiol 50: 233–237

Turner JS, Glands PD, Samson ACR, Robinson NJ (1996) Zn^{2+}-sensing by the cyanobacterial metallothione in repressor SmtB: different motifs mediate metal-induced protein-DNA dissociation. Nucl Acid Res 24:3714–3721

Varenyam A, Pan X, Zhang D, Fu Q (2012) Bioremediation of Pb-contaminated soil based on microbially induced calcite precipitation. J Microbiol Biotechnol 22:244–247

Veglio F, Beolchini F, Gasbarro A (1997) Biosorption of toxic metals: an equilibrium study using free cells of *Arthrobacter* sp. Process Biochem 32:99–105

Velásquez L, Dussan J (2009) Biosorption and bioaccumulation of heavy metals on dead and living biomass of *Bacillus sphaericus*. J Hazard Mater 167:713−716

Wei W, Zhu T, Wang Y, Yang H, Hao Z, Chen PR, Zhao J (2012) Engineering a gold-specific regulon for cell-based visual detection and recovery of gold. Chem Sci 3:1780–1784

Wei W, Liu X, Sun P, Wang X, Zhu H, Hong M, Mao ZW, Zhao J (2014) Simple whole-cell biodetection and bioremediation of heavy metals based on an engineered lead-specific operon. Environ Sci Technol 48:3363−3371

Xie B, Gu JD, Li XY (2006) Protein profiles of extracellular polymeric substances and activated sludge in a membrane biological reactor by 2-dimensional gel electrophoresis. Water Sci Technol 6:27–33