

Bacillus Species and Heavy Metals

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Heavy metals are one of the major pollutants that contribute to the escalating problem of environmental pollution, being primarily introduced in sensitive ecological habitats through industrial effluents, wastewater, as well as sewage of various industries. Microbial bioremediation, particularly the use of bacteria, has gained attention due to the feasibility and efficiency of using them in removing heavy metals from contaminated environments. Bacteria have several methods of processing heavy metals through general resistance mechanisms, biosorption, adsorption, and efflux mechanisms. *Bacillus* spp. are model Gram-positive bacteria that have been studied extensively for their biosorption abilities and molecular mechanisms that enable their survival as well as their ability to remove and detoxify heavy metals.

bioremediation

Bacillus

resistance

microorganisms

biosorption

efflux

heavy metals

1. Bioremediation—An Environmentally-Friendly Approach for the Removal of Heavy Metals

Bioremediation is a conventional process that employs the use of plants, animals, and microorganisms for the remediation of pollutants like heavy metals. It is one of most effective, non-invasive, and economically feasible methods for the permanent mitigation of heavy metal pollution and for the complete restoration of the natural environment of many ecosystems, as there is no production of secondary by-products ^[1]. Though methods such as phytoremediation (bioremediation using plants), phycoremediation (bioremediation using algae) and mycoremediation (bioremediation using fungi) have been widely reported in literature for heavy metal removal, our review focuses on bacterial bioremediation with *Bacillus* spp. as potentially active and efficacious agents for the removal of various heavy metal ions present in the environment.

Bacteria are abundantly present in the environment, where their variety in shape, size, morphology, as well as resistance mechanisms makes them suitable for bioremediation of organic and inorganic pollutants. Biosorption mediated by bacteria is a cost-effective, economically feasible method for the removal of heavy metal ions and other pollutants from contaminated sites, as many species have evolved to develop mechanisms which mediate resistance to process heavy metal ions amidst high concentrations ^[2]. Over the past years, many bacterial species have garnered widespread attention for their potential ability to remove heavy metal ions from the environment, whereas bacterial biomass (live and dead) has also been investigated for biosorption of metal ions such as copper, chromium, zinc, nickel, cadmium, and mercury, concomitant on their interactions with the bacterial cell wall and

related peptidoglycans [3][4][5]. Many bacterial species such as *Bacillus*, *Pseudomonas*, *Enterobacter*, *Flavobacterium*, *Geobacter*, and *Micrococcus* spp. have been investigated for potential use in biosorption of various heavy metal ions from contaminated sites, by observing their surface to volume ratio and other feasible characteristics which enhance the binding interactions between bacterial functional groups and heavy metal ions [6][7]. In a recent study, the biosorption ability of many bacterial species such as *B. subtilis*, *B. megaterium*, *A. niger*, and *Penicillium* spp. were investigated for the removal of many heavy metal ions such as lead, chromium, and cadmium, of which *Bacillus* spp. were observed to be the most efficient [8][9].

2. *Bacillus* Species and Heavy Metals

2.1. Arsenic

Arsenic (As) is a naturally occurring toxic metalloid [10] that is reported in soil (5–10 mg/kg), rock (1–2 mg/kg), sea water (1–3 µg/L) [11][12][13], as well as air and volcanic ash (0.02 µg/m³), due to which arsine gas (AsH₃) and methylated arsine species enter into the surroundings [14]. Its anthropogenic sources are herbicides, pesticides [15], fossil fuel combustion, mining, smelting, wood preservation, sludge, manure [16], paint pigments, ceramic, glass industry, and food additives [17][18][19]. It exists as insoluble sulfides and sulfosalts [20]. It has four oxidation states: As³⁻ (arsine), As⁰ (elemental arsenic), As³⁺ (arsenite), and As⁵⁺ arsenate. Among them, As³⁺ and As⁵⁺ are the most abundant forms. As³⁺ is more toxic and mobile in aqueous and oxic environments than As⁵⁺, which is mostly adsorbed to the sediments in an anoxic state [21][22]. The histidine part of cellular proteins is a target site for the interaction of thiols of cysteine residues and/or imidazolium nitrogen with As³⁺, which results in the inactivation of enzymes [23]. As⁵⁺ interferes with protein synthesis by replacing the phosphate group during phosphorylation of the energy transfer process. The existence of either state depends on the redox state of the environmental conditions [24], as well as the geomicrobial population [25]. The US EPA and WHO has allowed 10 µg/L as the permissible concentration of As in drinking water [16]. Above 0.5 ppm, it is toxic for living systems resulting in symptoms of skin cancer [26], loss of appetite, weakness, weight loss, lethargy, chronic respiratory disorders, gastrointestinal disorders, enlargement of liver, spleen disorders, anemia [27], and cardiovascular disease [28]. Introduction of arsenic into the food chain and ground water may lead to serious concerns of arsenicosis [22].

Bioregulation of Arsenic by *Bacillus* spp.

The soluble nature of As makes its removal from the environment difficult [29]. Physical and chemical remediation of arsenic involves an oxidation step for converting As³⁺ into As⁵⁺. It may occur under atmospheric oxygen, which is usually very slow, or by using chemical oxidants like hydrogen peroxide, chlorine, or ozone. This method is very expensive and produces harmful byproducts [30]. Microorganisms use As as an energy source in their metabolic processes and thus transform the toxic As³⁺ into its less toxic form, As⁵⁺ [31][32] by arsenic oxidase, which is present in the protoplasm of arsenic-oxidizing bacteria [10]. Liao et al. [33] reported *Bacillus* as one the important arsenic-reducing bacteria. Arsenic removal by *Bacillus* spp. like *B. megaterium* [34][35], *B. aryabhattai* [36], and *B. cereus* strain W2 was studied by Miyatake and Hayashi [37]. Anaerobic respiration of As⁵⁺ by *B. cereus* was

reported by Ghosh et al. [22]. Various other studies conducted over the years have reported the ability of *Bacillus* spp. to uptake As [38][39][40][41][42] (Table 1). As speciation, solubility, and mobilization are dependent on its methylation [43][44], oxidation [45], reduction, and respiration. The significance of oxidative phosphorylation in living organisms cannot be ignored [19]. Structurally, As^{5+} has similarity with phosphate [16]; thus, it is a potential oxidative phosphorylation inhibitor [19]. As^{5+} enters the organism's living system by employing two pathways; Pit and Pst [45], which are usually used for phosphate uptake. It interferes with phosphorylation metabolic reactions and inhibits synthesis of adenosine triphosphate [10]. The portal of entry for As^{3+} is aquaglyceroporin proteins [16][46][47]. After internalization, it immediately binds to the respiratory enzymes via their sulfur residue [17][48]. Bioremediation of As in *Bacillus* spp. is done by *ars* operon [49] (Table 2) by employing three genes *arsA*, *arsB*, *arsC*, *arsD*, and *arsR*. *arsA* and *arsB* have ATPase activity, *arsC* transforms As^{3+} to As^{5+} , *arsD* works as metallochaperone, while *arsR* acts as a repressor [50][51][52][53]. Normally, As^{5+} (less toxic form) that enters the cell is reduced to As^{3+} (more toxic form) by *ArsC* and then transported out of the cell by *ArsB* [54][55] (Figure 1).

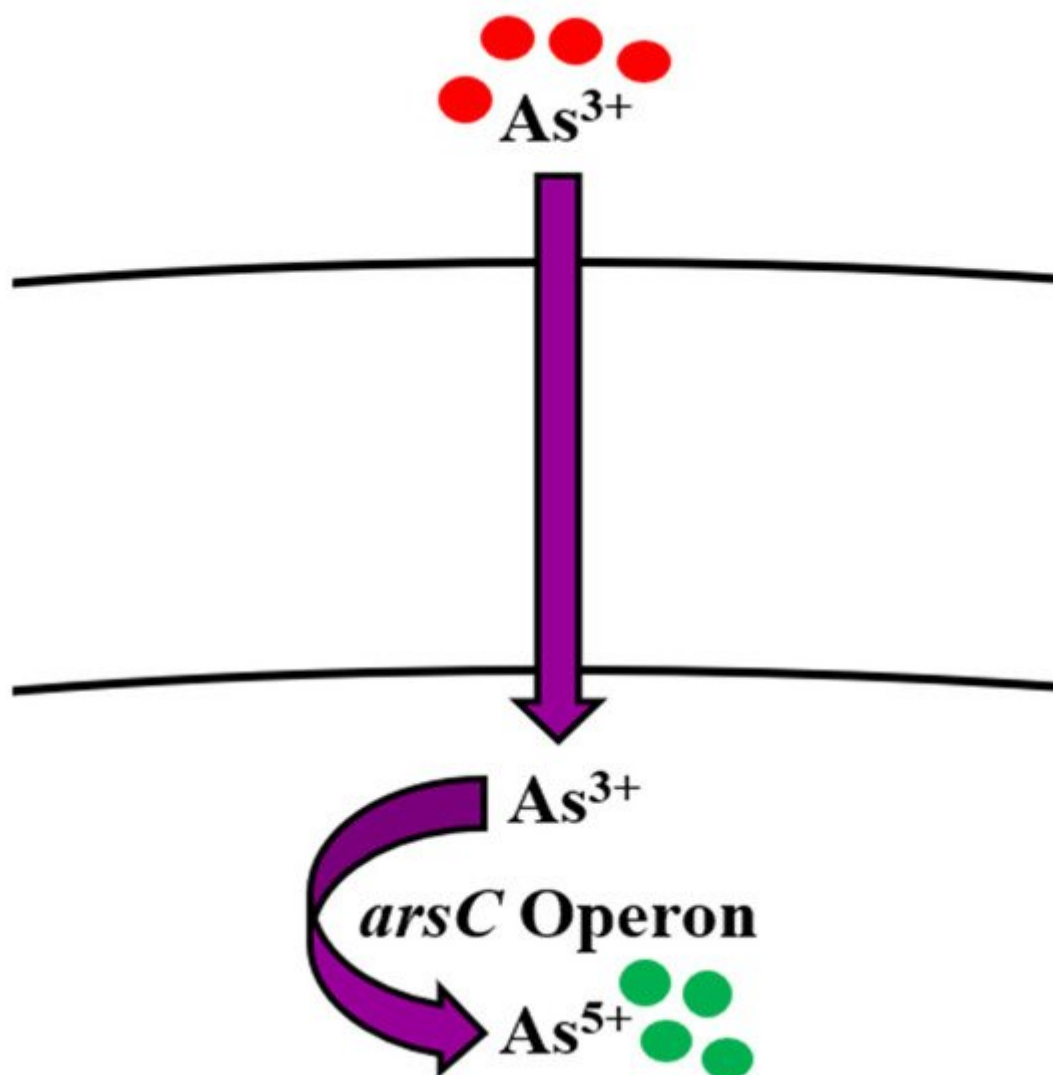


Figure 1. Bioregulation mechanism of arsenic in *Bacillus* spp.

Table 1. Uptake ability of *Bacillus* spp. for various heavy metals.

Metal	Bacterial Strains	Initial Metal Concentration (%/mg/g/mM/ppm/mg/L)	Metal Uptake Ability (%/mg/g/mM/ppm/mg/L/mol/g)	Reference
Arsenic	<i>Bacillus</i> sp. KM02	100 ppm	51.45% (As ³⁺)	[10]
	<i>B. licheniformis</i> <i>B. polymyxa</i>	0–100 mM 0–20 mM	100 ppm (As ⁰) 100 ppm (As ⁰)	[39]
	<i>Bacillus</i> sp. IIIJ3–1	350 mM (As ⁵⁺) 10 mM (As ³⁺)	350 mM (As ⁵⁺) 10 mM (As ³⁺)	[22]
	<i>B. barbaricus</i>	-	20 mM (As ⁵⁺) 0.3 mM (As ³⁺)	[42]
	<i>B. indicus</i> Sd/3T	0 mM 0 mM	20 mM (As ⁵⁺) 30 mM (As ³⁺)	[40]
	<i>B. selenatireducens</i>	10 mM	0 mM (As ⁵⁺) 0.3 mM (As ³⁺)	[38]
	<i>B. arsenicus</i> con a/3	20 mM 0.5 mM	20 mM (As ⁵⁺) 0.3 mM (As ³⁺)	[41]
	<i>B. cereus</i> W2	50 mg/L	1.870 mg/L (As ³⁺)	[37]
	<i>B. cereus</i> EA5 <i>B. fusiformis</i> EA2	15 mg/L	94.9% 99.7%	[35]
	<i>B. arsenicus</i> MTCC 4380	2000 mg/L 1800 mg/L	89.462% (As ⁵⁺) 83.043% (As ³⁺)	[43]
	<i>B. subtilis</i>	178 mg/L	49.7 mg/L	[56]
	<i>Bacillus</i> sp. (KF710041) <i>B. subtilis</i> (KF710042)	-	73.29% 78.15%	[57]
	<i>B. licheniformis</i>	-	53%	[58]
Zinc	<i>B. cereus</i>	0–200 mg/L	66.6 mg/g	[59]
	<i>B. jeotgali</i>	75 mg/l	30%	[60]
	<i>B. subtilis</i> D ₂₁₅	100 mg/L	63.73%	[61]
	<i>B. firmus</i>	100 mg/L	61.8%	[62]
	<i>B. altitudinis</i>	100 mg/L	87 mg/L	[63]

Metal	Bacterial Strains	Initial Metal Concentration (%/mg/g/mM/ppm/mg/L)	Metal Uptake Ability (%/mg/g/mM/ppm/mg/L/mol/g)	Reference
Nickel	<i>B. subtilis</i>	2.14 ppm	85.61%	[64]
	<i>B. subtilis</i> BM1	2–32 mg/L	98.54%	[65]
	<i>B. subtilis</i> BM2		99.2%	
	<i>B. subtilis</i> BM3		96.3%	
	<i>B. subtilis</i>	178 mg/L	57.8 mg/g	[56]
	<i>Bacillus</i> sp. KL1	100 ppm	55.06%	[66]
	<i>B. thuringiensis</i> KUNi1	0–7.5 mM	82%	[67]
Cadmium	<i>B. thuringiensis</i> OSM29	25–150 mg/L	94%	[68]
	<i>B. thuringiensis</i>	250 mg/L	15.7%	[69]
	<i>B. safensis</i>	40 ppm 60 ppm	83.5% 98.10%	[70]
	<i>B. licheniformis</i>	-	98.34%	[71]
	<i>B. catenulatus</i> JB-022	150 mg/L	66%	[72]
	<i>B. thuringiensis</i> DM55	0.25 mM	79%	[73]
	<i>B. pumilus</i> MF472596	100–1000 ppm	96%	[74]
Lead	<i>B. subtilis</i> X3	200–1400 mg/L	590.49 mg/g	[75]
	<i>B. cereus</i>	5–100 mg/L	36.71 mg/g	[76]
	<i>Bacillus</i> S1 <i>Bacillus</i> SS19	75 and 100 mg/L 50 mg/mL	53%, 51% 57%	[77]
	<i>Bacillus</i> sp. AS2	500 ppm	74.5 mg/g (99.5 %)	[78]
Copper	<i>B. cereus</i>	100 ppm	54%	[79]
	<i>B. cereus</i>	400 ppm	48%	[80]
	<i>B. thuringiensis</i> OSM29	25 mg/L	91.8%	[68]
	<i>B. licheniformis</i>	5 gm/L	32%	[81]
	<i>B. thioparans</i>	40 mg/L	27.3 mg/g	[82]

Metal	Bacterial Strains	Initial Metal Concentration (%/mg/g/mM/ppm/mg/L)	Metal Uptake Ability (%/mg/g/mM/ppm/mg/L/mol/g)	Reference
Chromium	<i>B. subtilis</i> D ₂₁₅	100 mg/L	67.18%	[61]
	<i>B. sphaericus</i>	17.6 mg/L	5.6 mol/g	[83]
	<i>B. cereus</i>	44.0 mg/L	5.9 mol/g	
	<i>Bacillus</i> sp.	88.0 mg/L	6.4 mol/g	
	<i>Bacillus</i> sp. SG-1	-	60%	[84]
	<i>B. cereus</i> NWUAB01	100 mg/L	43%	[85]
	<i>B. cereus</i>	100 mg/L	81%	[86]
	<i>B. salmalaya</i> 139SI	50 ppm	20.35 mg/g	[87]
	<i>B. cereus</i> FA-3	1000 µg/ml	72%	[88]
	<i>B. licheniformis</i>	15 mg/L	95%	[89]
	<i>Bacillus</i> sp. B	500–4500 mg/L	47%	[90]
	<i>B. marisflavi</i>	200 mg/L	5.783%	[91]
	<i>B. licheniformis</i>	300 mg/g	69.4%	[92]
	<i>B. thuringiensis</i>	250 mg/L	83.3%	[93]
	<i>B. licheniformis</i> <i>B. laterosporus</i>	-	62 mg/g 72.6 mg/g	[94]
Mercury	<i>B. circulans</i> <i>B. megaterium</i>	0.96 mg/L	34.5% 32%	[95]
	<i>B. thuringiensis</i> CASKS3	200 mg/L 400 mg/L 600 mg/L	62.4% 54% 40%	[96]
	<i>B. licheniformis</i>	50 mg/L	70%	
	<i>B. cereus</i> BW-03(pPW-05)	5–50 ppm	96.4%	[98]
	<i>B. licheniformis</i>	100 µg/mL	70%	[99]
	<i>B. cereus</i>	5 mg/L	104.1 mg/g	[100]
Manganese	<i>Bacillus</i> sp.	1–10 mg/L	7.9 mg/g	[101]
	<i>B. thuringiensis</i> HM7	400 mg/L	95.04%	[102]
Arsenic	<i>ars</i> operon (<i>arsR</i> , <i>arsD</i> , <i>arsA</i> , <i>arsB</i> , <i>arsC</i>)	Reduction (Detoxification) Efflux Cell membrane binding, Adsorption on cell surface Complexation by exopolysaccharides		[10][32][38][50][51][52] [53]

Metal	Bacterial Strains	Initial Metal Concentration (%/mg/g/mM/ppm/mg/L)	Metal Uptake Ability (%/mg/g/mM/ppm/mg/L/mol/g)	Reference	ance
	<i>B. cereus</i> HM-5	600 mg/L	67%	[103] [59] [108] [109]	
	<i>Bacillus</i> sp.	13.3 mg/g	55.56 mg/g	[104]	
	<i>Bacillus</i> sp. Zeid 14	-	200 mg/L	[105]	
	<i>Bacillus</i> sp. strain A.rzi	0.1 mM	Not reported	[106] [110] [111]	
Silver	<i>B. licheniformis</i> R08	100 mg/L	73.6 mg/g	[107] [73] [85] [112] [113] [114]	
Cadmium	<i>yvgW</i> KinA		Efflux	[115] [116]	
Lead	<i>pbr</i> operon		Efflux	[117] [118] [119]	
Copper	<i>copZA</i> operon CueR (CopA, CopZ, CopB) YcnJ		Efflux by chaperone Uptake	[120] [121] [122] [123]	
Chromium	ChrR		Efflux, Uptake Enzymatic reduction (Detoxification)	[124] [125] [126]	
Mercury	<i>mer</i> operon (<i>merR</i> , <i>merA</i> , <i>merB</i>) MerR MerA MerB		Efflux Enzymatic reduction (Detoxification)	[127] [128] [129] [130] [131]	
Manganese	<i>mntABCD</i> operon MntR MntH MneP MneS		Efflux Uptake	[132] [133] [134] [135]	
Molybdenum	<i>modABC</i> operon		Uptake	[99] [136] [137] [138] [139] [140] [141]	
Gold	Not reported		Bioaccumulation	[142] [143]	
Silver	SilP <i>sil</i> genes		Efflux	[144] [145] [146] [147] [148] [149]	

2.2. Zinc

Zinc (Zn) is one of the most profusely abundant transition elements in the Earth’s crust, and is also widely found in biological systems, coming second only to iron. Zn (atomic number 30) is a member of group XII (previously known as II-B) of the periodic table of elements, and as analogous to all members of the group, it is also characterized as

a divalent metal [150]. At room temperature, it occurs as a brittle, lustrous metal with a blue-white hue [151]. In reactions concerning hydrolysis, Zn tends to act as a Lewis acid or electrophile, which catalyzes these reactions and is thereby integrated into assorted metallo-enzymes, transcription factors, and regulatory proteins [152]. In cells, it exhibits antioxidative properties against the formation and mitigation of free radicals and reactive oxygen species, which contributes to the perpetuation of protein stability. The significance of Zn resonates with its function as an essential nutrient in living systems, augmenting its presence in both human beings and bacteria, where more than 5% of bacterial proteins evince their dependency on Zn [153]. These manifold functions preponderate over its toxicity at higher concentrations in cells, which can often be promoted by the blockage of protein thiols via mis-metallation with other metals, resulting in the disruption of various biological functions [154].

In the environment, anthropogenic actions have shaped the presence of Zn and its compounds in industrial and agricultural wastewaters, underscoring the production (more than 12 million tons annually) and then consumption of Zn in a multitude of processes such as galvanization, metallurgy, and the pharmaceutical industry, alloy metal casting, pesticides, and production of several other consumer goods [155]. Moreover, mining activities and contamination of sludge in soils poses a considerable threat of Zn toxicity to the sustainability and quality of crops [156], which further raises concern for the purification of contaminated sites by effective methods. It has been reported that the removal of Zn in low concentrations is mediated by physical and chemical methods, but its removal by biological agents (plants, algae, microorganisms) is a method which has been gaining attention due to its many advantages that eclipse its drawbacks. The treatment of Zn-contaminated wastewaters through plants, biomass, sawdust, mollusk shells, fruit and vegetable peels, agricultural wastes, and polysaccharides such as chitosan and pectin as potentially effective biosorbents has been widely reported [157][158].

Bioregulation of Zinc by *Bacillus* spp.

The action of *Bacillus* spp. in removing Zn from contaminated environments has been highlighted in many bioremediation studies. This ability of *Bacillus* spp. is regulated either by acquiring resistance through plasmids or by evolving mechanisms of resistance [159][160]. In *B. subtilis*, Zn uptake is regulated by the Zur family, which enables the transport of Zn ions via two transporter proteins. Gaballa et al. [108] also reported a third uptake system in *B. subtilis* for Zn ions called ZosA (P-type ATPase), which was expressed in conditions of oxidative stress. Efflux of Zn in high concentrations is facilitated by a CPx-type ATPase efflux pump in *B. subtilis*, known as CadA [108][109] (Table 2, Figure 2). Moreover, the removal of Zn by *Bacillus* sp. such as *B. subtilis*, *B. licheniformis*, *B. cereus*, *B. jeotgali*, and *B. firmus* was reported in recent studies [56][57][58][59][60][61][62] (Table 1). Khan et al. [63] also reported the removal of Zn (87 mg/L) by *B. altitudinis* isolated from industrial wastewater.

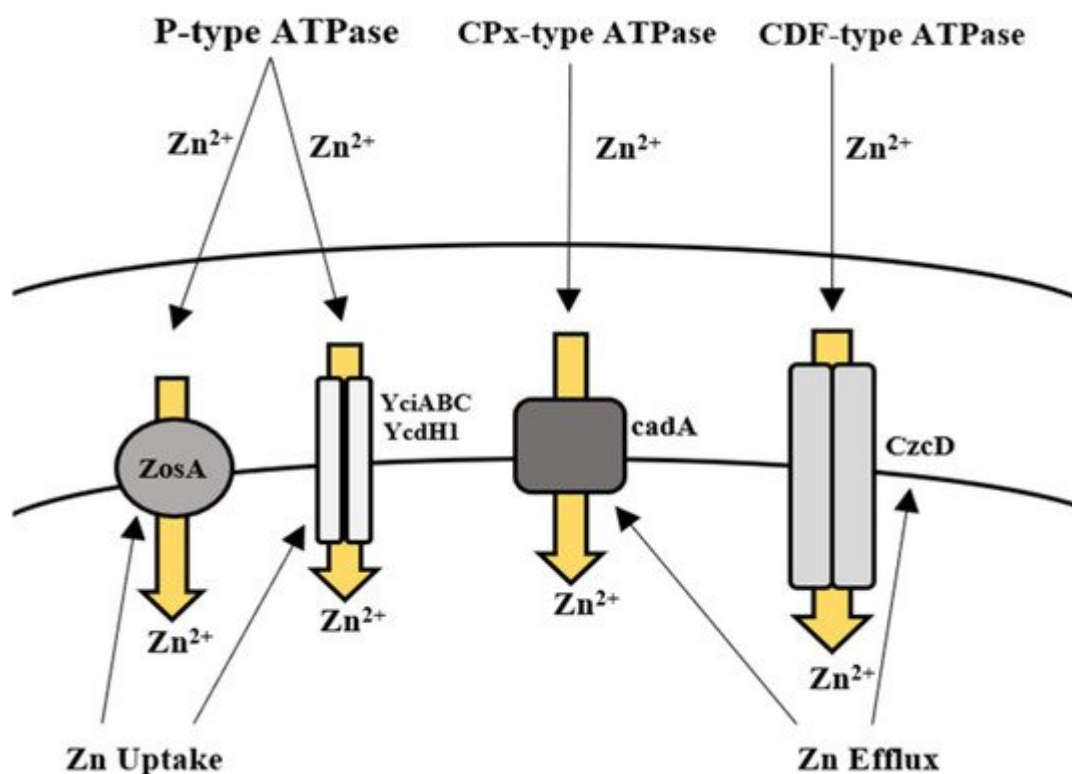


Figure 2. Uptake and efflux mechanism of *Bacillus* spp. for the regulation of zinc.

2.3. Nickel

Nickel (Ni) belongs to group 10 and is the 28th element in the periodic table, discovered by Swedish chemist Axel Cronstedt in its purified form for the first time in 1951. It is a hard, silvery-white transition metal which belongs to the ferromagnetic group of metals with high electrical and thermal conductivity [161]. It is the 24th most copious element found in the Earth's crust, and the 5th most abundantly found in terms of weight. It is naturally found in its oxidation state (2+) which is analogous to most environmental and biological settings, though it may exhibit other valences as well (−1 to +4) [162]. It persists in nature in its hydroxide form at pH > 6.7, while its complexes appear to be readily soluble at pH < 6.5. It is found to exist in various forms of air- and water-resistant minerals (oxides and sulfides) [163], which give rise to Ni salts of strong (readily soluble in water) and weak acids (poorly soluble in water), respectively [164]. Natural sources of Ni in the environment are attributable to soil and rock erosion, volcanic eruptions, meteorite emissions, air-blown dust, as well as foods [165]. Combustion of fossil fuels and leaching from rocks and soil contribute to its presence in air and water, respectively. Moreover, anthropogenic emissions in the form of metal smelting and mining, metal refineries, Ni plating and alloy production, and effluent and sludge disposal into soil and water catalyze its presence in high concentrations in the environment [166]. The commercial use of Ni and its extensive applications such as production of Ni-Cd batteries, use in jewelry, orthodontic equipment, machinery, coins, food processing, clothing, and electronics promote its ubiquity in the environment, where it exists as sulfides, oxides, and less frequently, in its metallic form [167]. Ni toxicity has been the subject of widespread research in humans, where it is highlighted that the metal poses no considerable nutritional value in humans and poses industrial and occupational hazardous risk [168]. Nevertheless, it has been characterized as

essential for the growth of plants, microorganisms and animals [169], where Ni-based enzymes and cofactors are reported to serve a key role in their function [170].

Bioregulation of Nickel by *Bacillus* spp.

There have been many methods of Ni removal from solid matrices, but the most effective are those which are capable of removing/treating Ni before it emanates into the environment [171]. Several physico-chemical methods have been employed over the years for the removal of Ni from aqueous solutions [172]. Regardless of which of these methods have been used in the past, newer, cheaper, and more efficient methods of adsorption have been used for Ni removal, such as the use of biomass, where sugarcane, corn cobs, citrus peels, and bark have been used [173]. In a study, corn hydrochar was treated with KOH and altered by treating polyethyleneimine (PEI) to increase adsorption of Ni ions onto the surface [174]. Bioremediation by Gram-positive bacteria, such as *Bacillus* spp., has been the better method for the removal of Ni ions from Ni-contaminated media. There have been many studies that demonstrate the uptake and/or removal of Ni ions from contaminated environments such as soils, wastewater, and rivers [56][64][65][66] (**Table 1**). *B. thuringiensis* has also been frequently reported to uptake and remove Ni from contaminated environments [67][68][69]. In a recent study, *B. megaterium* was isolated from Ni-contaminated soils and was able to uptake more than 500 mg Ni, where more than 3000 mg/L Ni salt was previously found [175]. The removal of Ni by bacteria is contingent on their inherent mechanisms of resistance, which ultimately facilitate uptake, transportation, and efflux of the metal ions in and out of the cell. According to Moore et al. [110], mechanisms of Ni homeostasis and regulation have not been well characterized in *B. subtilis* when compared to Gram-negative bacteria such as *Escherichia coli* and *Helicobacter pylori*, though some evidence suggests their presence [176]. Members of the cation diffusion facilitator (CDF) family have long been characterized to mediate efflux of multiple metal ions, including Ni [111]. In *B. subtilis*, the cation diffusion transporter CzcD is reported to provide protection to the cell amid high concentrations of Ni^{2+} , Cu^{+} , Zn^{2+} , and Co^{2+} [110] (**Figure 3**). When these ions happen to be bound with citrate, these complexes, during favorable conditions, are taken up by the metal-dicitrate uptake system known as CitM in *B. subtilis*, consequently leading to an increase in toxicity to them [110] (**Table 2**).

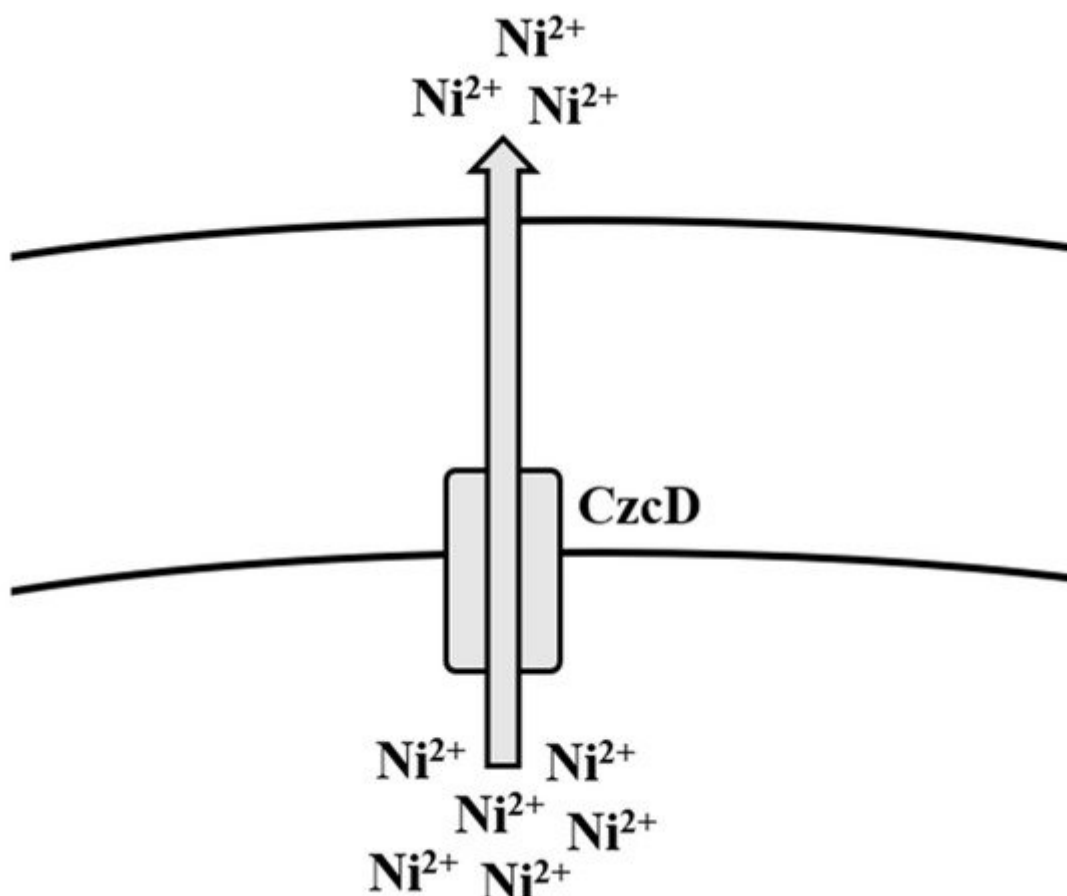


Figure 3. Efflux mechanism of nickel in *Bacillus* spp.

2.4. Cadmium

Cadmium (Cd) is a member of group XII of the periodic table and is a silvery white metal in appearance, with physical and chemical properties similar to both zinc and mercury. It exists in general oxidation state (+2) and is malleable and ductile. Cd is a corrosion-resistant metal, which is not flammable and water-soluble in nature, and is generally regarded as a toxic heavy metal with wide application in the industries of batteries, plating, plastics, and pigments, contributing greatly to its toxicity [170]. Anthropogenic activities have led to its presence being observed in many food sources and drinks [177]. Cadmium oxide is often used in metal plating, catalysis, and ceramic glaze. Alongside cadmium telluride, it has been also used in the form of a thin film for use in diodes, transistors, solar cells, electrodes, and anti-reflective coatings [178]. Cd is also used extensively in industrial strength paints, which can pose an environmental hazard during spraying. Other sources of contamination such as Cd-containing fertilizers can pollute soils which can inadvertently enhance its absorption by humans and other living beings. Cd has no known biological function and is a great threat to all life forms [179], due to which its environmental exposure can be dangerous, and in some cases, fatal [180].

Bioregulation of Cadmium by *Bacillus* spp.

Nature has gifted microorganisms with *cadA* operon to combat Cd toxicity. It is a 3.5 kb operon located on plasmid pI258. It has two genes; *cadA* and *cadC* [181][182]. *cadA* is transcribed into the 727-amino acid protein, which performs the function of energy-dependent Cd efflux ATPase [85], whereas *cadC* encodes relatively a small protein of 122 amino acids, and is a positive transcription regulator of Cd²⁺ operon [182][183]. It is well reported that *cadA* gene is induced in the presence of Cd²⁺ ions. Solovieva and Entian [112] documented their findings on *cadA* as a chromosomal determinant as well as a new gene *yvgW* of *B. subtilis* involved in Cd²⁺ resistance. Moreover, they reported that it has similarity to *cadA* of *S. aureus* plasmid pI258 [184]. Deletion of *yvgW* increased the Cd²⁺ sensitivity in the bacterium. *cadB* is also plasmid-mediated and confers Cd²⁺ resistance through a change in the binding site [113]. In addition to efflux mechanism, KinA and histidine kinase provide phosphate for phosphorylation which leads directly to transcription in *B. subtilis* [114]. Its overexpression results in phosphate flux of the cell, thereby directly affecting the energy state of the cell wall [185]. It also plays a significant role in biosorption of Cd²⁺ ions by phosphorylating the *Bacillus* cell surface magnitude, hence it acting as a major phosphate provider [73]. Cd²⁺ enters the bacterial cell membrane via the zinc and manganese transport systems, which are chromosomally mediated. Cd²⁺ concentration greatly affects the whole process. If the Cd²⁺ ions are present in high quantity in the medium, much extracellular adsorption is observed. Otherwise, intracellular Cd²⁺ concentration is high [186]. The *cad* operon of *Bacillus megaterium* TWSL_4 contains *cadC*, which has Cd²⁺ and Zn²⁺ metal binding motifs [187]. On exposure to metal ions, the first interaction is always with cell wall [188]. Its structure and composition play a significant role in deciding the next step of the process. Cd²⁺ adsorption on the bacterial cell wall deals with exchanging ions like Ca²⁺, Mg²⁺, and H⁺ ions [189]. Chelation is another process in which Cd²⁺ ions are exchanged with cell surface protons like –SO₃H, –COOH, and –NH [190]. It involves sequestration via intracellular metallothionein (MT) [191]. Inorganic deposition of Cd²⁺ in the cell wall or inside cells can take place through interaction with hydroxide, carbonate, sulfate, and phosphorus [192]. In addition to metal concentration, biosorption is dependent on cell wall composition and cell physiology [193]. In Gram-positive bacterial species, resistance to Cd²⁺ is achieved by *cadA* system that is plasmid-borne. Cd²⁺ enters the bacterial cell by the MIT (metal ion transporter) system [115][116] (Table 2). The genes for Cd²⁺ resistance are mostly plasmid-mediated. According to Chen et al. [194] they are found on R plasmid along with antibiotic resistance genes, e.g., in pathogens including *K. pneumoniae*, *P. aeruginosa*, and *S. aureus*. These genes are reported to be directly involved in the uptake of Cd²⁺ ions from the environment (Figure 4). Basha and Rajaganesh [71] reported *B. licheniformis* to be a good biosorbent for Cd²⁺, as it removed more than 98% of Cd²⁺. Other species such as *B. catenulatus* and *B. safensis* are also reported to be effective in removing Cd²⁺ [70][72] (Table 1).

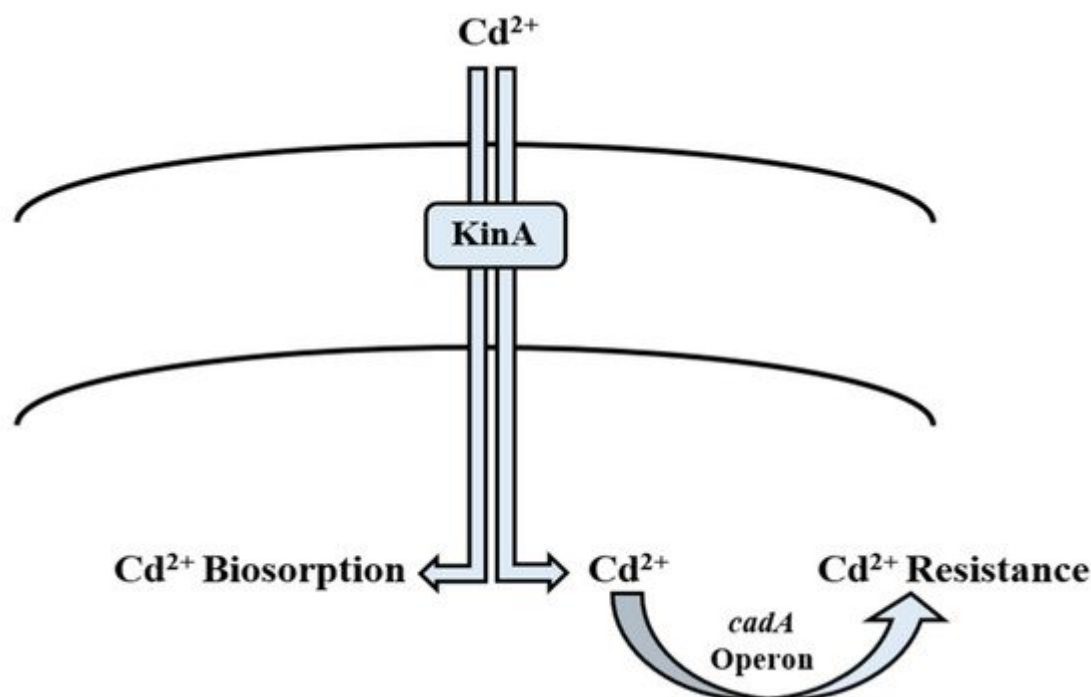


Figure 4. Mechanism of cadmium bioregulation by *Bacillus* spp.

2.5. Lead

Lead (Pb) is a toxic heavy metal that is introduced into the environment via the weathering of rocks. Anthropogenic sources include fossil fuels, extraction and melting of metals, battery-manufacturing industries, insecticides, pigments, and fertilizers [195]. Tetraethyl lead (TEL) has a common application as a gasoline additive, due to which it is a source of heat and electricity [196]. It exists in two states: Pb^{2+} and Pb^{4+} [197]. Its toxicity determines its bioavailability as well as mobility in the soil. Its common forms are oxides, hydroxides, ionic form, metal oxyanion complexes [151], phosphates, and carbonates (at pH above 6). The stable and insoluble forms include oxides, sulfides, and pyromorphites [198]. Its exposure occurs by food, water, and inhalation, which affects the circulatory, gastrointestinal, reproductive, neurological, muscular, kidney, and genetic systems [74]. Dose and exposure time are prime factors [199]. The permissible level of Pb in drinking water is $<10 \mu\text{L/L}$ [182].

Bioregulation of Lead by *Bacillus* spp.

Pb-resistant *Bacillus* spp. have been reported previously [197]. *Bacillus* uses *pbr* operon [117][118][119] and active transport [200] as potential strategies to combat the toxic effects of Pb (Table 2, Figure 5). Microorganisms immobilize it by adsorption, chelation, inorganic precipitation, complexation, and biosorption. These processes involve bacterial cell wall functional groups including phosphate, carboxyl, carbonyl, sulfhydryl, and hydroxyl groups, which confer a negative charge to the cell wall. Binding of Pb to any of them results in insoluble substance. On the outside environment, Pb^{2+} is exchanged by Na or K cations [75]. Another method is adsorption through the cell wall, as it is comprised of organic macromolecules including polypeptides, polysaccharides, and proteins, which have the ability to adsorb Pb via electrostatic forces including Van der Waal's forces, covalent or ionic bonds

[75]. Pb interferes with microbial growth, morphology, and biochemical activities by damaging the DNA, protein, and lipids and even replacing the essential ions within the enzymes [74][201]. Microbes resist Pb toxicity by extracellular precipitation, exclusion, volatilization, biomethylation, cell surface binding, intracellular sequestration, and enhanced siderophore production [74]. Much like other Gram-positive bacteria, *Bacillus* spp. also employ one or several of these methods to remove Pb from the contaminated environments [76][77][78] (Table 1).

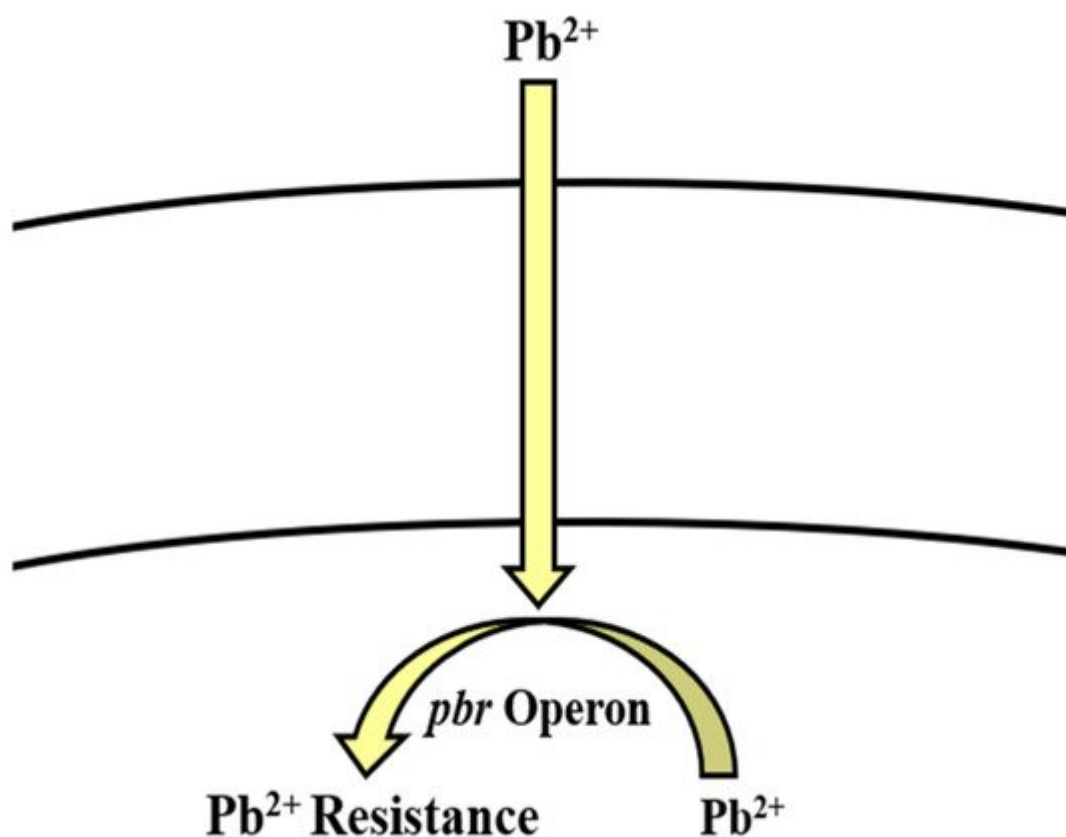


Figure 5. *pbr* operon involved in the regulation of lead resistance in *Bacillus* spp.

2.6. Copper

Copper (Cu) is categorized into the group I-B, and period 4 of the periodic table [151]. It is a soft, diamagnetic, malleable, and ductile metal with remarkable electrical and thermal conductivity. It acts as a soft and intermediate Lewis acid and tends to bind to soft bases (hydride, alkyl, thiol, phosphine) and auxiliary ligands to Cu^{2+} , such as sulfate and nitrate [202]. Apart from being widespread in the environment thanks to anthropogenic actions, it also exists naturally in the form of minerals such as sulfides, carbonates, and oxides. The discovery and use of Cu dates back to ancient times, with its use spanning more than five thousand years. It exists in either of its two oxidation states, which can be the oxidized, divalent cupric form (Cu^{2+}) or the reduced, monovalent cuprous form (Cu^+) [203]. The significance of Cu in biological systems is pivotal; it serves an important role as a micronutrient in several biological processes in both prokaryotic and eukaryotic organisms. However, this stands only for lower concentrations of the metal; higher concentrations tend to induce cell toxicity, resulting in intracellular damage including changes in DNA, respiration, and overall growth [204]. Moreover, Cu is essentially required as a co-factor

in more than thirty known enzymes, due to its ability to reversibly interconvert from its less to more required forms very easily [205]. Elevated levels of Cu exposure are a deep-rooted cause of environmental pollution by Cu, the fundamental reason being anthropogenic processes. Industries using Cu or its compounds, Cu mining, burning of fossil fuels, inadequate treatment of wastewater, accumulation in dumps, production of phosphate-containing fertilizer, and natural processes such as erosion, volcanic eruptions, forest wildfires, and decay are all processes which greatly contribute to its presence in the environment. Furthermore, its production is also a source of direct Cu pollution, capable of harming the fragile ecosystems of soil, water, and air, respectively [206].

Bioregulation of Copper by *Bacillus* spp.

Like many other heavy metal ions, Cu is considered to be essential for *Bacillus subtilis*, while concentrations exceeding normal amounts can be toxic for the cells. Species like *B. thuringiensis*, *B. cereus*, *B. licheniformis*, and *B. sphaericus* are also involved in the removal of Cu, when their concentrations exceed the required limit [68][79][80][81][82][83][84][207][208] (Table 1). In correlation with other bacterial species, Cu in the cytosol is regulated by CueR [209]. *B. subtilis* CueR is responsible for regulating the *copZA* operon which encodes both Cu chaperone and a P-type ATPase for Cu efflux, the latter of which is a member of the integral family which exports metal out of the cell [120]. In the former, CopZ plays a key role as Cu chaperone in transferring Cu over to CopA [121], which contributes to uptake of Cu, while CopB is accountable for Cu efflux and detoxification [122] (Table 2, Figure 1). Chillappagari et al. [123] reported that YcnJ was associated with Cu uptake function of *copZA* operon in *B. subtilis*, where their model proposed that the protein works in conjunction with other Cop proteins to facilitate Cu transport in and out of the cell (Figure 6).

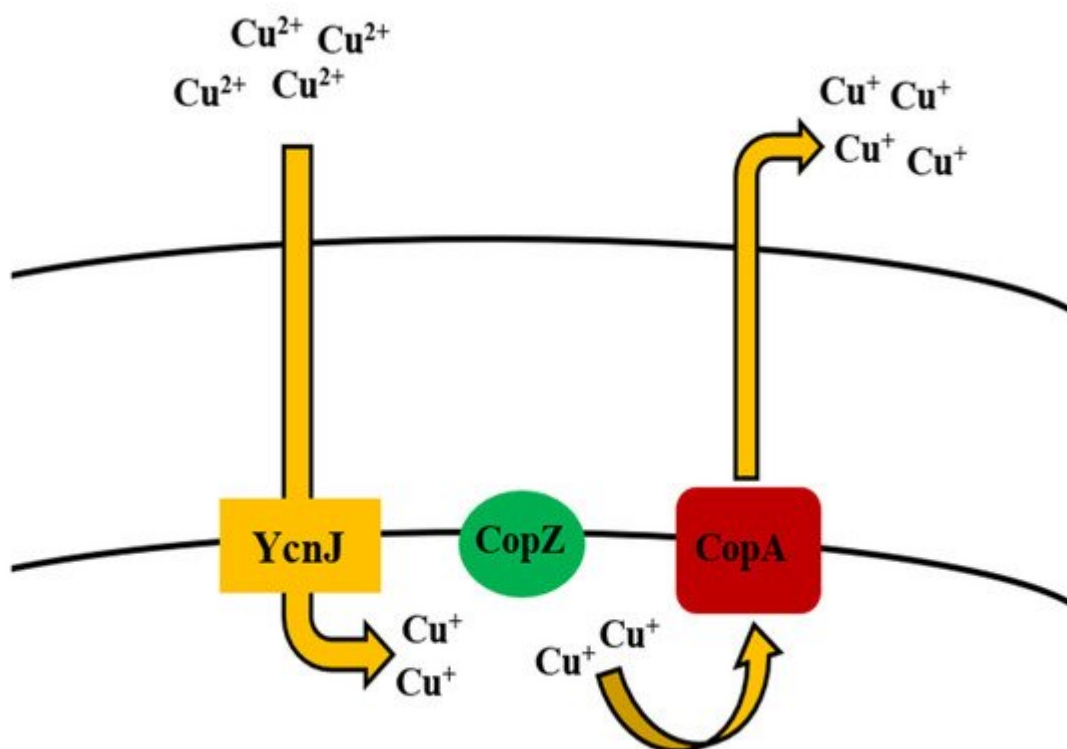


Figure 6. Uptake and efflux mechanism of copper by *Bacillus* spp.

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