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Exploration of As(III)-oxidizing Bacteria as Sustainable Arsenic Bioremediation Strategy

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ABSTRACT: Currently arsenic(As) contamination is of the leading public health concern and environmental distress. To deal with such a hazardous impact, living system has developed various mitigating strategies. Prokaryotic organisms in particular have evolved mechanisms that allow them to withstand and metabolize As at a higher concentration. Arsenic metabolizing bacteria play an indispensable role in maintaining the biogeochemical cycle of As through changing the redox state by oxidation, methylation or reduction of As species. Among these, As(III) oxidizing bacteria are more important because they operate a detoxifying mechanism by converting arsenite [As(III)] into the comparatively less toxic, insoluble arsenate [As(V)]. Since, the product of As(III) oxidation, the As(V), always gets readily adsorbed onto potent adsorbents, As(III) oxidation is thus being more investigated for bioremediation. Isolation of aerobic As(III) oxidizers from As-contaminated environments is being the subject of interest in recent years. This article evaluates the challenges faced due to As toxicity in As-contaminated areas. It also encompasses the present status and progress in As-decontamination to provide a brief comparison between standard As removal procedures and the newly emerging bioremediation technology. Additionally, it covers the current knowledge of the complex molecular biology and biochemistry of natural As metabolisms. Finally, the study focuses on As methylation, reduction and oxidation processes in microorganisms that involve a wide range of genes and operons that lead to the emergence of constructive methods for the application of potential bioremediation programs.

Keywords: Arsenic, As(III)-oxidizing bacteria, arsenic oxidation, bioremediation.

INTRODUCTION

Metals and metalloids are abundant in nature and all life forms through their metabolic processes play an indispensable role in maintaining biogeochemical cycle of such elements. Nevertheless, at higher concentrations most elements are toxic to all branches of life due to the formation of toxic unspecific complex compounds that prevent normal functioning of essential enzymes in cell. Metals and metalloids, with relatively high density, are known as heavy metals (Fergusson, 1990; Tchounwou *et al.,* 2012). Arsenic, a toxic metalloid substitutes essential metals due to its structural similarity and binds to specific ligands although it does not have substantial biological roles and is lethal for nearly all organisms (Sherene, 2010; Balali-Mood *et al.,* 2021). Geogenic and anthropogenic activities, often release high concentration of As into the environment which create a selection pressure on the microorganisms resulting in evolution of metal-resistant determinants (Kaur *et al.,* 2011). Redox reactions, influx and consequent efflux of As by As-resistant microorganisms and other bio-transformations of As contribute to the biogeochemical cycle (Zhu *et al.,* 2017). Arsenic biogeochemical cycling is again dependent and coupled to the biogeochemical cycle of other elements and ions such as iron, phosphate, and nitrogen (Senn and Hemond, 2002; Oremland and Stolz 2003; Borch *et al.,* 2010).

The As biogeochemical cycle can be better understood by the genetic analysis of As resisting microorganisms (Schlesinger *et al.,* 2022). One can predict the effect of microbial metabolism on As biogeochemical cycle only when there is a proper understanding of the genes involved in the redox reactions and the environmental conditions that impact on the expression of these genes (Biswas and Sarkar 2022). In this review, we have emphasized on the roles of various known genes so far related to As biotransformation, especially As(III) oxidation and its role on As biogeochemistry.

Speciation of Arsenic. The prevalence and behavior of As in the environment are significantly influenced by the chemical speciation caused by As-resistant microorganisms, which in turn directly influence both its concentration and toxicity (Sharma and Sohn 2009; Jomova *et al.,* 2011). Around 20 different forms of As are typically found in the environment depending on its availability, mobility, and magnitude of toxicity. Among which arsenite [As(III)] and arsenate [As(V)] are the two oxidation states of As that are most common in nature (Abbas *et al.,* 2018). Inorganic species of As are generally more toxic than its organic counterparts, of which As(III) is more hazardous than

As(V), because it has a propensity for interacting with functional groups like thiol and imidazolium groups of many biomolecules (Tchounwou *et al.,* 2012). Methylated species like monomethylarsenite (MMAIII) and dimethylarsenite (DMAIII) are, however, more toxic than inorganic As(V) and As(III) (Petrick *et al.,* 2000).

Arsenic Toxicity and Remediation. One of the most persistent environmental pollutant found in the environment is As (Mandal and Suzuki 2002). Arsenic contaminants in groundwater can also have an impact on the state of the aquifers (Polya *et al*., 2019). After coming in touch with such arsenic-rich rocks, groundwater seeps in and picks up large concentrations of As deposits. The chemical composition of groundwater varies greatly depending on the kind of aquifer, the period of rock-water contact, and inputs from different natural sources. Reports of As contamination of groundwater have come in over the past few decades from all throughout the world (Shaji *et al.,* 2021). Groundwater with critically high levels of As is frequently used for domestic and irrigation purposes in As-contaminated regions (Brammer, 2008; Banerjee *et al.,* 2013). The use of such groundwater for irrigation raises the As concentration in the crop fields, potentially raising the risk of bio-accumulation and further entry in the food chain (Rahman *et al*., 2007; Bhattacharya *et al.,* 2009). Chronic exposure to an elevated level of As in drinking water and crops could cause the development of arsenicosis, collective term for the diseases (Hong *et al.,* 2014).

Environmentalists consider the remediation of As-contaminated soils to be a challenging factor. Due to the high cost and ineffectiveness of current physiochemical methods for eliminating As from the environment, interest in environmentally benign and economically viable technology is booming up (Reichenauer and Germida 2008). Bioremediation, mainly uses microorganisms or plants, to detoxify contaminants in the environment. Microbial processes are the main variables influencing As mobilization because they change the flow of As between biotic and abiotic compartments (Vahter, 2002; Oremland and Stolz 2005; Lièvremont *et al.,* 2009; Gadd, 2010; Irshad *et al.,* 2021; Anand *et al*., 2022; Kabiraj *et al*., 2022). For the purpose of surviving under As stress, microorganisms adapt biotransformation mechanisms like methylation, oxidation and reduction (Fig. 1).

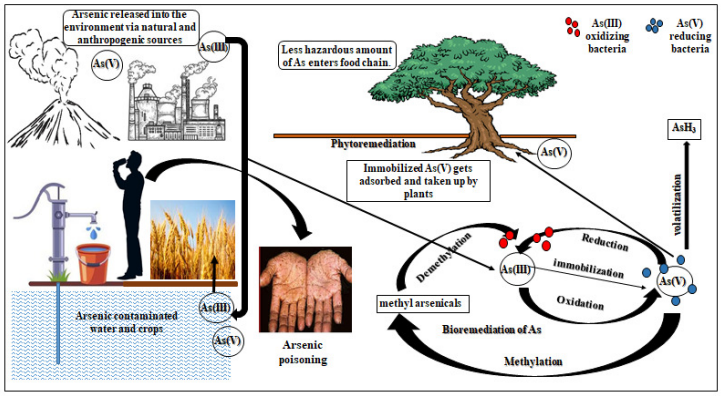

Fig. 1. Schematic diagram of Arsenic biogeochemical cycle and its possible bioremediation strategy.

Arsenic Methylation. It was initially proposed that As(III) is biotransformed into substantially less toxic As(V) methylated species during the process of As methylation, as a means of detoxification. Since it had been already established that phosphate transport systems are the pathways by which As(V) enters cells, As(V) would first be reduced to As(III), and then by oxidative methylation it would be transformed to methylarsenate [MAs(V)] by transferring a methyl group from S-adenosylmethionine (SAM) methyltransferase. Finally, MAs(V) would be reduced to generate the substrate methylarsenite [MAs(III)] which subsequently yields dimethylarsenate [DMAS(V)] by oxidative reaction (Challenger, 1951). Methylated As(V) species, contributing to decontamination were promptly removed, which also supported this hypothesis (Gebel, 2002). The enzymes that catalyzed the reactions weren't known at the time. Later SAM methyltransferase, also known as ArsM in microorganisms, was found to catalyze the biomethylation of As(III) (Qin *et al*., 2006; Chen and Rosen 2020; Thomas, 2021).

The crystal structure of ArsM isolated from *Cyanidioschyzon merolae* was studied to understand the methylation mechanism intricately (Ajees *et al*., 2012). ArsM contains three main domains, SAM binding N-terminal, an As(III) binding site and a C-terminal domain whose function is unknown. The As(III) binding domain consists of 4 conserved cysteine residues which can only bind trivalent arsenicals (Li *et al.,* 2016). In the first methylation step two cysteine residues forms a disulfide bond and a methyl group is transferred from SAM to As(III) to create an enzyme-bound MAs(V) moiety (Marapakala *et al.,* 2015). In the next step, the conserved cysteine residues reduce MAs(V) to MAs(III) and are oxidized which in turn has to be reduced by thioredoxin in subsequent methylation step (Dheeman *et al.,* 2014). As a result, the uptake of methylated As species in plants is regulated by the microbial As-methylation in soil. Therefore, increasing the volatilization of methylated As is a probable mitigation process for As toxicity in the environment.

Reduction of Arsenic. As(V) reduction caused by microbial processes has an impact on the environment

because it changes the oxidation state of As(V), making it more mobile and toxic in aquatic systems. Microorganisms may resist high levels of As in the environment by As(V)reduction or As(V) may be used as an electron acceptor for anaerobic respiration in order to generate energy (Biswas *et al.,* 2019). Numerous different anaerobic bacteria have the ability to utilize As(V) as a terminal electron acceptor for heterotrophic respiration due to the presence of anaerobic respiratory As(V) reductase (ArrAB) (Macy *et al.,* 1996; Oremland and Stolz, 2003; Malasarn *et al*., 2004; Lukasz *et al.,* 2014). ArrAB is a heterodimer protein with a larger molybdopterin subunit (ArrA) having high-potential [4Fe-4S] cluster and ArrB is the smaller subunit which has a[Fe-S] center protein (Lukasz *et al.,* 2014). A typical *arsDABC* operon for As(V) resistance is located upstream of the two genes *arrA* and *arrB*that encodes ArrAB (Saltikov *et al.,* 2003). Arsenate reductase (ArsC), encoded by *arsC* is a part of the *arsDABC* operon, which catalyzes the transformation of As(V) to As(III) (Silver and Phung 2005). ArsC, containing 135 amino acid residues is a monomeric protein, involved in a number of enzyme reactions. There are two distinct families of ArsC; in the first class, glutathione and glutaredoxinin *Escherichia coli* plasmid R773, is employed as electron donors for the reduction of As(V), while, the second family, discovered in *Staphylococcus aureus*, uses thioredoxin (Kruger *et al.,* 2013). ArsA and ArsB together forms the efflux channel for As(III) extrusion. As(III) specific efflux pump expels As(III) out of the cell and is encoded by *arsB*, by employing proton motive force, while *arsA* encodes an anion translocating ATPase protein, that helps this efflux pump occasionally, by allowing it to function independently or by supplying energy through ATP hydrolysis (Yang *et al.,* 2012). ArsR binds to the operator DNA in the absence of As, and regulates the gene expression of the operon. Whereas, ArsD is a chaperone protein that facilitates the transfer of As(III) to ArsA, which in turn activates the operon and promote the activity of the efflux pump (Lin *et al*., 2007).

Arsenite oxidation. Glycerol transporters, such as GlpF, allow As(III) to enter cells in bacteria, yeasts, and humans (Mukhopadhyay *et al.,* 2014). Numerous α, β, δ- proteobacteria from various habitats have been found which can enzymatically oxidize As(III) to less toxic As(V). The first most intensively studied As(III)-oxidizing bacteria is *Alcaligenes faecalis* (Anderson *et al*., 1992). As(III)-oxidizing microbes are further divided into two categories based on their favored growth substrates. Heterotrophic group in presence of oxygen uses organic carbon as a source of energy and convert As(III) to As(V) (Vanden-Hoven and Santini 2004). They do not get their energy from oxidizing As(III); instead, they typically use the process as a way to detoxify the microbe (Shi *et al.,* 2020). *A. faecalis*, *Agrobacterium* sp, and *β-Proteobacteria* are a few heterotrophic As(III) oxidizers (Anderson *et al*., 1992; Kashyap *et al*., 2006; Bachate *et al*., 2012). Aerobes or anaerobes can be chemolithoautotrophic bacteria, which only use carbon dioxide as a source of carbon. As(III) reduces oxygen or nitrate by acting as an electron donor during cellular respiration. Two well-studied species in this class are the aerobic bacteria NT-26, a member of the *Agrobacterium* or *Rhizobium*, and the facultative anaerobe MLHE-1, a member of the δ-Proteobacteria, which was later identified as *Alkalilimnicola ehrlichii* sp. nov (Santini and vanden Hoven 2004; Hoeft *et al.,* 2007)

Arsenite oxidase genes. The structural genes *aioAB* of *aio* operon encode the larger and smaller subunits of the heterodimeric enzyme As(III) oxidase (Kashyap *et al.,* 2006; Corsini *et al.,* 2018). In *A. tumefaciens* 5A, advanced genetic research has revealed a signal transduction having a sensor kinase encoded by the gene *aioS*, and a response regulator encoded by *aioR* gene (Kashyap *et al.,* 2006). These two proteins have been demonstrated to play an essential role in the transcriptional control of the *aioAB* genes, and loss or inactivation of these regulatory genes *aioRS* results in As(III) oxidase dysfunction (Muller *et al.,* 2007).

Interruption of the *aio* operon results in loss of oxidation and reduction in As(III) oxidizers (Kashyap et al., 2006; Corsini *et al*., 2018). ArsR-type repressor often controls As(III) oxidation with inorganic phosphate stress, which eventually contribute in As detoxification (Rawle *et al.,* 2021). Total loss of As(III) oxidation due to a transcription mutation of *aioAB* might require RpoN alternative sigma factor σ54 for the *aioAB* expression in *Herminiimonas arsenicoxydans* (Koechler *et al.,* 2010; Sardiwal *et al.,* 2010). AioR and RpoN interact in *H. arsenicoxydans*, initiating transcription and controlling the activity of the *aioAB* operon. *aioC* and *aioD*, two more genes of this operon, contribute cytochrome activity and molybdoprotein production, respectively (Santini and vanden Hoven 2004; Koechler *et al.,* 2010; Kang *et al.,* 2012). Numerous bacteria have been used to characterize an *aioX*-encoded periplasmic arsenite binding protein as well (Kruger *et al.,* 2013).

Arsenite oxidase structure and mechanism of oxidation. Arsenite oxidase is controls microbial oxidation of As(III) (Lebrun *et al.,* 2003). Often in soil, As positively regulate arsenite oxidase activity in bacteria, thus most As(III) oxidizing bacteria have reported to express arsenite oxidase under induced conditions, but only a very small number of strains do show constitutive nature (Lieutaud *et al*., 2010; Bahar *et al*., 2013; Koechler *et al.,* 2013). Two subunits make up arsenite oxidase: a larger 85kDa subunit is designated as AioA and the smaller subunit AioB is 14 kDa encoded by *aioAB* respectively (Lett *et al.,* 2012; Warelow *et al.,* 2013). Arsenite oxidase is one of the molybdenum-containing DMSO reductase enzyme, and it can be distinguished from other enzymes of the DMSO family because an endogenous protein ligand is absent (Ellis *et al*., 2001; Wells *et al*., 2020). Azurin, cytochrome-c oxidase, and cytochrome-c are electron carriers which are associated to this enzyme through the electron transfer chain (Anderson *et al.,* 1992; Watson *et al.,* 2017). HiPIP [4Fe-4S] or [3Fe-4S] centre with 825 residues were found using electronic paramagnetic resonance (EPR) spectroscopy, as well as a Rieske

[2Fe-2S] centre with around 134 residues (Ellis *et al.,* 2001). In the larger subunit pyranopterin cofactors and a [3Fe-4S] cluster is coupled to molybdenum (Warelow *et al.,* 2017). The larger subunit consists of 4 domains. Domain I is bound to the Rieske-subunit and [3Fe-4S] cluster present in the smaller subunit while, domains II and IV are connected by a pseudo-two-fold axis and both include homologous dinucleotide binding motifs that aid in binding molybdenum. While, two parallel β-sheets make up the molybdenum center-binding domain III (Ellis *et al.,* 2001; Warelow *et al.,* 2017).

The smaller subunit serves as an electron shuttle that transports electrons to respiratory chain proteins and features a Rieske-subunit that is specific to these families of enzymes (Kumari and Jagadevan 2016). AioB forms the N-terminal transmembrane helix, which holds the enzyme to the membrane (Warelow *et al.,* 2017). The Rieske subunit is involved in enzyme transportation across the membrane, and is bound to the cytoplasmic membrane by the TAT sequence (Lebrun *et al.,* 2003). The leader sequence of AioB serves in the export whereas the TAT secretory pathway facilitates the transfer of the enzyme to the periplasm (Santini and vanden Hoven 2004; Kumari and Jagadevan 2016).

As(III) oxidase reduces the core molybdopterin by two electrons from As(III), thus Mo(VI) is transformed to Mo(IV) during this catalytic process, which eventually releases As(V) (Ellis *et al*., 2001; Kumari and J agadevan 2016; Warelow *et al.,* 2017). The electrons are transported from the larger component molybdopterin via the small Rieske subunit, inner membrane respiratory chain via carrier proteins like cytochrome-*c* or azurin, to the terminal electron acceptor oxygen (Anderson *et al.,* 1992; Ellis *et al.,* 2001; Warelow *et al.,* 2017). As(III) oxidizer distribution in natural habitats has thus been better understood primarily because of the identification of these genes, and *aioA* is often considered as a possible molecular marker for studying community diversity among As(III) oxidizers in As-contaminated environment (Quemeneur *et al.,* 2008; Kumari and Jagadevan 2016). Fig. 2 represents the known genes responsible for As resistance in these resistant microbes.

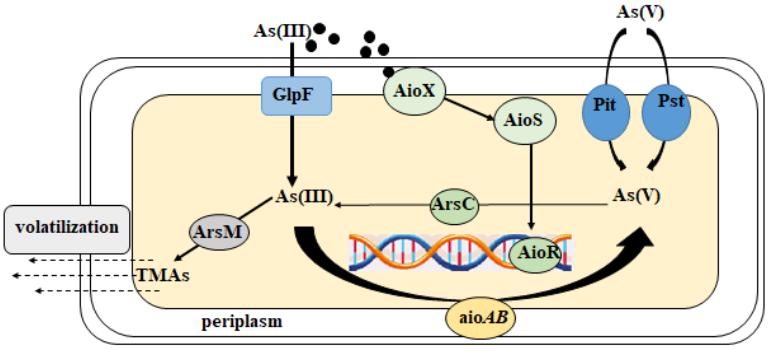

Fig. 2. Bacterial mechanism of As-transformation. a) ArsM catalyzes the transfer of a methyl group from S-adenosyl-L-methionine to As(III) and may play a role in As-metabolism. Volatilization of arsenicals in the form of trimethylarsine (TMAs). b) The pit &pst transporter system and glycerol transporters namely GlpF in bacterial cells transport As(V) and As(III) inside the cell respectively. c) *aio AB* and *ars C* encode the two enzymes namely AioAB and ArsC required for oxidation and reduction of As respectively. d) Regulatory proteins AioX, AioS, AioR encoded by genes *aioX*, *aioS* and *aioR* respectively, controls transcriptional regulation of the *aioAB* operon.

Interconnection between As(III) oxidation and Pi. Phosphorus is often sparse and only sometimes found in soil and water at less than a nanomolar (Vieira *et al.,* 2008). It is an essential component for most biological activities. Numerous studies has showed that As(V) may substitute for its molecular counterpart P_i in bacteria (Wang *et al.,* 2015; Wang *et al.,* 2018). Although the instability of As-ester bonds cannot generate nucleic acid and ATP, it is often found to produce arsenosugars and lipids having a methylated As(V)-C bond (Rosen *et al.,* 2011). Thus several reports documented the accumulation of As in lichens, fungi, marine organisms, and plants by this process (Dembitsky and Levitsky 2004). A systematic regulatory link that coordinates P_i signal transduction and As regulation exists in As(III)-oxidizing bacteria. When As(III) is present in absence of P_i, ArsR1 a negative regulator detaches from the promoters of P_i-specific transporters (PhoB1 and PstS1) and binds to As(III) (Garbinski *et al.,* 2019). Histidine kinases PhoR which is constitutively expressed phosphorylates PhoB1 and consequently activates the expression of both P_i-specific transporters and *aioXSR* regulatory genes (Shi *et al.,* 2018; Rawle *et al.,* 2019). Presence of As(III) in the environment is recognized by AioX, and thus, AioS self-phosphorylates itself and also phosphorylates AioR which eventually activates the expression of *aioAB,* thus As(III) oxidase activity (Wang *et al*., 2018; Rawle *et al.*, 2019). Oxidase enzyme then oxidizes As(III) to As(V), which then binds to PstS1 and finally P_i transporter system to transfer it into bacterial cells.

Effect of iron and nitrate on As(III)-oxidation. In the absence of oxygen, microbial As(III) oxidation can be facilitated by nitrate, an ecologically significant oxidant. It was reported that in absence of nitrate As(III) was present, but As(V) predominated in presence of anoxic nitrate (Zhu *et al.,* 2017; Li *et al.,* 2019). Later, it was discovered that the *Alkalilimnicol aehrlichi* strain MLHE-1, a nitrate-dependent As(III)

oxidizing bacterium, could couple partial denitrification with As(III) oxidation (Oremland *et al.,* 2002; Hoeft *et al.,* 2007). Due to the indirect relationship between nitrate reduction and Fe(II) oxidation, nitrate also has an impact on the bioavailability and mobility of As (Cai *et al.,* 2022). Nitrate supplementation in paddy fields decreases As uptake because of Fe(III) reduction, and decreases As mobilization. Nitrate-dependent Fe(II)-oxidizing bacteria, stimulate Fe(II) oxidation and cause As to co-precipitate with Fe(III) minerals in soil thereby decreasing the accessibility of As uptake (Zhu *et al.,* 2017). Fe(II) oxidation to particulate ferric oxides, which bind As, and catalyzing the transformation of As(III) to As(V), nitrate significantly influences the cycling of As in the nitrate-rich water bodies (Sennand Hemond, 2002).

CONCLUSIONS

It is well established that enzymes from various microorganisms catalyze the biotransformation of As, and these enzymes are connected to the biogeochemical cycles of phosphorus, nitrogen, sulphur and iron. Thus, microorganisms have a significant impact on the metabolic cycle of As because they have the ability to change the solubility and mobility of As in different oxidation states. Therefore, to get rid of this toxic metalloid from the habitable ecological niche and crop fields, As-resistant bacteria might have a potential role in sustainable bioremediation. Modern life forms contain a wide variety of As-resistant modifications that serve as evolutionary tools for long-term environmental As detoxification.

FUTURE SCOPE

For bioremediation to be successful, further research is required to correlate the As-resistant traits of microorganisms with respect to their environmental impacts on decontamination of As. More genes that are directly or indirectly involved in As-metabolism therefore, has to be identified and characterized in various As-resistant microbes. In order to limit As pollution, modelling approaches linking the As biogeochemical cycle with metagenomics data must be developed. Such technologies have to be cost-effective and easily accessible for As remediation so that it can provide safe drinking water in As-contaminated areas.

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Conflict of Interest. None.

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