International Journal of Research in Engineering and Science (IJRES)
ISSN (Online): 2320-9364, ISSN (Print): 2320-9356
www.ijres.org Volume 9 Issue 7 ǁ 2021 ǁ PP. 24-29

Potential of soil-resident bacterial species in counteracting arsenic toxicity

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Abstract
Arsenic, a class-1 carcinogen, is a ubiquitous metalloid found in the atmosphere, soil, natural water and organisms. Agricultural practices in arsenic-contaminated environment pose a severe threat to human health, causing arsenic contamination of food crops and introduction of the metalloid in the food chain. Conventional and physical methods are expensive and not effective in areas with low arsenic toxicity. Soil-resident rhizospheric bacteria improve plant growth under arsenic stress through different mechanisms like increase of nutrients in plants, improving soil quality, siderophore and hormone production, causing changes in biochemical properties of plants, etc. Certain bacteria also cause altered speciation of arsenic in the soil through methylation and subsequent change in the uptake, transport and bioavailability of arsenic to plants. Hence, reclamation of arsenic-contaminated agricultural fields can be performed via inoculation of such bacteria (single or mixed species), as an eco-friendly and cost-effective strategy of arsenic bioremediation. The challenges rely on the application of these novel approaches under field conditions. The present review aims to discuss the role of different soil-inhabiting rhizospheric bacteria in arsenic bioremediation, thereby highlighting the recent advancements in this field of research.

Keywords: *ars operon; arsenic; bacteria; bioremediation; rhizosphere*

Date of Submission: 25-06-2021 Date of acceptance: 08-07-2021

I. INTRODUCTION

Arsenic (As), a ubiquitous toxic metalloid and natural component of the earth's crust is widely distributed throughout the environment, as well as added through anthropogenic activities, e.g., application of insecticides, chemical fertilizers and arsenic-containing agrochemicals, tanning of hides, mining extraction procedures, smelting, industrial processes, coal combustion, etc. The four oxidation states in which As exists include arsenate [As(V)] and arsenite [As(III)] and to a lesser extent arsenic [As(0)] and arsine As(III). The arsenite species is more mobile and is ∼100 times more toxic, as compared to As(V). Arsenite, As(III), is present in slightly reducing conditions, such as rice paddy fields and arsenate, As(V), is present in oxidizing conditions. Arsenic is toxic to all forms of life including plants, animals and human beings. The level of As in drinking water has increased beyond the standard drinking water limits (0.01 mg L^{-1}) as set by World Health Organization. Long-term exposure to As, especially through drinking water, can cause arsenicosis which is manifested in humans as different types of cancers and skin lesions and allergies, pulmonary disease, peripheral vascular disease, arterial hypertension, diabetes mellitus, neuropathy and cardiovascular diseases (Ojuederie and Babalola 2017). The worst-affected areas are in South and Southeast Asia, where millions of people have been exposed to high concentrations of As in drinking water, extracted from shallow tube-wells. As(V) is a phosphate analogue and interferes with essential cellular processes, such as oxidative phosphorylation and ATP synthesis, whereas the toxicity of As(III) is due to its tendency to bind to sulfhydryl groups, affecting general protein functioning. The accumulation of As in crops constitutes a serious threat to public health. Thus, removal of As is of utmost importance for human welfare.

II. TECHNIQUES FOR ARSENIC REMOVAL

Decontamination of As-polluted soil has therefore been a technical challenge to environmentalists. The conventional techniques such as chemical precipitation, chemical oxidation and reduction, ion exchange, filtration, reverse osmosis, etc. are used for removing heavy metals including arsenic from dilute solution. However, these techniques are often inappropriate or expensive, particularly when such contaminants are present in very low concentration or in large solution volume. Considering the cost and inefficiency of existing physiochemical techniques for removing As from the environment, several eco-friendly and cost-effective technologies are gaining attention (Seshadri et al. 2015). Bioremediation of As using micro-organisms or phytoremediation using certain hyperaccumulator plants has gained a lot of popularity in recent times due to

their potential in cleaning up soil and water samples. Microorganisms play a major role in the biochemical cycle of As which can be converted to different oxidation states with different solubility, mobility and toxicity. In As-contaminated soil, rhizospheric microorganisms play a crucial role, since their metabolic abilities (reduction, oxidation and methylation) can affect As speciation and bioavailability, and consequently As phytotoxicity. Although As(V) is less toxic than As(III), resistance to As(V) requires its reduction to As(III), which can then be stored in vacuoles or extruded outside. Furthermore, As(III) oxidation, which constitutes an electron source for some microorganism metabolism, transforms As(III) to As(V).

III. MICRO-ORGANISMS AS AGENTS OF ARSENIC BIOREMEDIATION

Bioremediation of As deals with the use of micro-organisms, especially bacteria and fungi, to detoxify the contaminated environment. The following mechanisms are used for microbial bioremediation: (i) Alteration of biochemical pathways to block metal uptake; (ii) reduction of intracellular concentration of metals using precise efflux systems; (iii) conversion of metals to innocuous forms by enzymes; (iv) sequestration of toxic metals by cell wall components or by intracellular metal-binding proteins and peptides such as metallothioneins (MT) and phytochelatins along with compounds such as bacterial siderophores which are mostly catecholates, compared to fungi that produce hydroxamate siderophores (Ojuederie and Babalola 2017). Rhizobacteria alter plant metabolism by changing their physiology through ion and nutrient uptake, nitrogen fixation or intracellular sequestration. They can decrease the mobility of anions and metal ions extracellularly in the rhizosphere by promoting extracellular sequestration of metals in insoluble phosphate particles, or through detoxification mechanisms of the metal contaminant. The high surface to volume ratio of bacterial cells enables a high uptake of metal, either actively or passively. The existence of As-resistant genes within the microbiota has led to the prevalence of diverse resistant mechanisms, which could be exploited for developing As-bioremediation strategies. Microorganisms have evolved several resistance mechanisms for surviving under As stress conditions. The microbial communities in the rhizosphere soil and rhizoplane in As-contaminated areas are able to withstand high concentrations of the metalloid. Arsenic-resistant bacteria are known to have effects on As oxidation/reduction, methylation and demethylation, together with sorption and desorption capability. Plants can release secondary metabolites that attract and allow the growth of specific endophytic, rhizoplane and rhizospheric bacterial communities that can further metabolize the exudates (Mallick et al. 2015). With regard to As bioremediation in the rhizosphere, one group of microbe restricts As mobilization in plants, while the other group assists As accumulation in plants, favoring phytoremediation. Because of the complexity and severity of As-contaminated sites, the microbe should have a large metabolic diversity, so as to thrive under different environmental situations (Jaiswal 2011). The reported mechanism of As resistance in bacteria is represented in the table below.

Mechanism	**Microorganisms**
Mobilization	Iron(III)-reducing bacteria
Immobilization	Aerobic and anaerobic iron-oxidizing bacteria
Adsorption	*Bacillus megaterium* UM-123, *Acidothiobacillus ferrooxidans*
Volatilization by methylation, using the protein product ArsM and S-adenosyl methyltransferase confers sequential methylation of inorganic As to methylated arsenicals	*Methanobacterium bryantii*, *Pseudomonas* sp.

IV. RHIZOSPHERIC AND ENDOPHYTIC BACTERIA FOR MITIGATING ARSENIC TOXICITY

Rhizobacterial strain, *Ochrobactrum tritici* SCII24T (strain LMG 18957T) was reported to be a highly As-resistant bacterium, having As resistance operons, *ars1* and *ars2* (Branco et al. 2008) that confers resistance up to 50 mM As. The genes, *arsB* and *Acr3_1* encode two different arsenite efflux pumps and double mutation for these two genes exhibited low As(III) resistance, up to 1 mM and increased As accumulation ability. Inoculation of rice plants at the rhizosphere with the hyperaccumulator strain, As5 of *O. tritici* resulted in an even smaller As uptake in the rice plants, compared to SCII24T. The total negative effect on plant length and weight was reduced when As was present in the medium (Moens et al. 2020). In another study by Belogolova et al. (2015), soil inoculation with rhizospheric bacteria affected the inter-phase As transfer in rhizospheric soil and influence As mobilization and immobilization in "soil–plant" system. The soil inoculation with *Azotobacter* and *Bacillus* rhizobacteria resulted in reduction of the intensity of As accumulation in plants. In presence of these bacteria, As in chelate forms and combined with Fe-hydroxides could become a major source of its accumulation and residence in rhizospheric soil. Moreover, As was adsorbed to the cells of soil bacteria, *Azotobacter* and *Bacillus*, thereby creating a barrier for its supply into plants. Soto et al. (2019) isolated two As-resistant bacterial isolates, classified as *Pseudomonas gessardii* and *Brevundimonas intermedia*, from

contaminated soil from the Puchuncaví valley at Chile. *P. gessardi* was able to produce siderophores and solubilize phosphate, while *B. intermedia* could produce indole-3-acetic acid (IAA). Plant biomass and growth in wheat was increased and the relative expression of plant metallothionein, superoxide dismutase, ascorbate peroxidase and phytochelatin synthase genes was enhanced when *P. gessardii* plus *B. intermedia* were inoculated, proving the potential of the microorganisms isolated from polluted soil to contribute to the restoration of contaminated soils. In another study by Wang et al. (2011), inoculation of a strain D14 of *Agrobacterium radiobacter* contributed to the increase in the As tolerance in poplar (*Populus deltoides*), promotion of growth, increase in the As uptake efficiency and enhancement of As translocation. Indole acetic acid released by rhizobacteria could directly promote the growth of roots by stimulating elongation of the plant cells or increasing cell division, which may enhance the root As absorption. The siderophore production by strain D14 might mobilize As (V) in the soil in the process of taking up iron which rendered As more soluble and bioavailable to plants. A total of 116 arsenite-resistant endophytic bacteria were isolated by Gu et al. (2018) from the roots of As hyperaccumulator plant, *Pteris vittata* with different As concentration. The major genera included *Agrobacterium, Stenotrophomonas, Pseudomonas*, *Rhodococcus* and *Bacillus*, which exhibited high levels of IAA production and carried *arsB/ACR3(2)* genes, which were horizontally transferred among the strains. Oller et al. (2013) isolated several bacterial strains including γ-proteobacteria such as *Enterobacter* sp. and *Pseudomonas* sp., and actinobacteria like *Rhodococcus* sp. from the rhizosphere of soybean (*Glycine max*) grown in an Argentinean agricultural field, all of which exhibited high level of As resistance in presence of very high arsenite (over 24 mM) and arsenate (over 400 mM) concentrations. *Rhodococcus erythropolis* AW3 was the most As-resistant strain that removed and accumulated the greatest amounts of the metalloid. Armendariz et al. (2015) showed that inoculation with *Azospirillum brasilense* Az39 could positively contribute to promoting the growth of different plant species under As treatment. The ability of *A. brasilense* Az39 for accumulating As from solutions that initially contained As(III), accounts for phytotoxicity mitigation using this bacteria. Banerjee et al. (2011) isolated bacterial strains from As-affected areas, of which seven isolates belonged to γ - *proteobacterium,* two isolates belonged to *Firmicutes* and one was identified as *Kocuria* genera, as revealed by 16S RNA and phylogenetic analysis. Some of these bacteria could oxidize arsenite to arsenate and all others could reduce arsenate to arsenite. 17 morphologically distinct As-resistant bacteria that belongs to the genera *Exiguobacterium, Aeromonas, Bacillus, Pseudomonas, Escherichia, Acinetobacter* were isolated, and all the bacteria showed high tolerance capacity for arsenic (0–100 mM arsenate or 0–20 mM arsenite). Six bacterial groups including the Proteobacteria, Bacteroidetes and Firmicutes were also isolated, capable of growing at high levels of arsenate (up to 275 mM), although arsenite tolerance was much lower (10 mM). Mohamed and Farag (2015) observed that *Bacillus cereus* strains EA4, EA5 and EA6 were able to resist As up to 15 mg/L. *B. cereus* strain EA5 and a mixed culture of *Lysinibacillus sphaericus* EA1, *Bacillus fusiformis* EA2, and *Lysinibacillus* sp. EA3 were found to be efficient in bioremediation of As oxychloride, up to 94.9% and 99.7%, respectively. Through 16S rRNA gene sequencing, Batool et al. (2017) identified As-resistant purple nonsulfur bacteria, belonging to *Rhodopseudomonas faecalis* SS5 and *Rhodopseudomonas palustris* CS2 which showed As(V) resistance up to 150 and 100 mM, respectively, along with the highest level of auxin production. *R. palustris* CS2 exhibited the ability to reduce As(V) into As(III), whereas *R. faecalis* SS5 had the potential to oxidize As(III) to As(V). Both the bacteria also promoted plant growth in As-contaminated sites. Inoculation of the hyperaccumulator plant species such as *Pteris vittata* with As-resistant, growth-promoting bacteria that can reduce As(V) to As(III), particularly bacteria that are indigenous to contaminated sites earmarked for remediation, improved the efficiency of As phytoextraction (Lampis et al. 2015). Such bacteria included (i) siderophore-producing and arsenate-reducing bacteria *Pseudomonas* sp. P1III2 and *Delftia* sp. P2III5; (ii) siderophore and IAA-producing bacteria *Bacillus* sp. MPV12, *Variovorax* sp. P4III4, and *Pseudoxanthomonas* sp. P4V6. The presence of growth-promoting rhizobacteria increased plant biomass by up to 45% and increased As removal efficiency from 13% without bacteria to 35% in the presence of the mixed inoculum. Lakshmanan et al. (2016) also reported that rice plants primed with rhizospheric isolate, *Pantoea* sp. attenuates As uptake. *Brevundimonas diminuta* NBRI012 is an As-resistant, IAA-producing rhizobacteria, which can alleviate the negative effects of As stress in rice and improve the growth. Arsenic-resistant bacterial strains, *Bacillus altitudinis, B. megaterium,* and *Lysinibacillus* sp. strain SS11 were isolated from paddy fields, of which *Lysinibacillus* strain was found to tolerate up to 3, 256 mg L^{-1} As(V) and 1, 136 mg L^{-1} As(III) (Singh et al. 2016). Das et al. (2014) identified 12 potential As-resistant bacteria isolates from agricultural soil of Taiwan. Out of these, As(III) oxidizing ability was found in bacteria belonging to *Pseudomonas, Acinetobacter, Klebsiella,* and *Comamonas.* Various strains of *Pseudomonas* sp., *Geobacillus* sp., *Bacillus* sp., *Paenibacillus* sp., *Enterobacter* sp. and *Comamonas* sp. also possessed plant growth promoting properties. Shagol et al. (2014) have also identified potential As-tolerant and plant growth promoting bacterial strains from a metal contaminated site in South Korea and found that three strains (*Rhodococcus aetherivorans* JS2210, *Pseudomonas oreensis* JS2214 and *Pseudomonas* sp. JS238) could induce growth of maize roots in response to As(V) stress. Mallick et al. (2018) isolated two As-resistant bacteria from rhizosphere of mangrove plants in

Sunderban area, viz., *Kocuria flava* and *Bacillus vietnamensis*. Both the strains improved growth and decreased As uptake in rice plants. Arsenic-tolerant microbes like *B. licheniformis*, *Micrococcus luteus* and *Pseudomonas fluorescens* were found to possess siderophore producing, phosphate solubilizing as well as nitrogen fixing properties (Ivan et al. 2017). In another study by Mesa et al. (2017), the siderophore and IAA producers of the endophytic bacterial consortium (*Variovorax paradoxus*, *Phyllobacterium myrsinacearum*) enhanced As accumulation in the leaves and roots of *Betula celtiberica*, whereas the rhizosphere isolate, *Ensifer adhaerens* strain 91R mainly promoted plant growth in the contaminated field.

V. MECHANISM OF ACTION OF BACTERIAL POPULATION IN LOWERING ARSENIC STRESS

Arsenic is not usually adsorbed by the microorganisms, but it can be altered by them throughout redox transformations. However, many *Bacillus* species such as *B. megaterium* were reported to remove As through adsorption. Microorganisms are known to play an important role in the biochemical cycling of As through its conversion to species with different solubility, mobility, bioavailability and toxicity. Plant roots secrete secondary metabolites, which attract the microbial population by providing sufficient nutrition. The organic metabolites include amino acids, fatty acids, nucleotides, organic acids, phenolics, putrescene, sterols, sugars and vitamins. Arsenic-bioavailability, especially in rice fields, is related to water management and Fe-As cycling by microbial colonies inhabiting the rhizospheric zone of the rice plants. Further, Fe forms specific iron plaque on rice roots that can bind As strongly on root surface itself and modulate As bioavailability (Upadhyay et al. 2018). The process of As attachment to the surface of bacterial cells may be caused by ion exchange chelate formation, adsorption and light chemosorption. Arsenic migration processes in rhizospheric soil depend not only on their inoculation with bacteria, but also pH. At increased pH values (up to 8), As immobilization in rhizospheric soil decreased; As mobility and increase of As content in plants was observed (Belogolova et al. 2015). The beneficial effect of microbes is also due to stimulated release of IAA and siderophores and phosphate solubilization. Siderophores are organic molecules with a high affinity for Fe(III) and form complexes with other metals, thus participating in nutrient mobilization and metal availability to plants. The major microbial methylating agent is S-adenosylmethionine (SAM), involved in the methylation of As and such biomethylation is effective in forming volatile compounds such as alkylarsines, which could be easily lost to the atmosphere. The efficiency of As detoxification depends on the bioavailability of As to plants (through secretion of protons, organic acids, redox reactions and metabolic reactions) and chemical form of As (generated through reduction, oxidation, methylation and demethylation), effect on As interactions with other elements like Fe, Si, etc., alteration of plant growth (by IAA and 1-aminocyclopropane-1-carboxylate deaminase production, extracellular enzymes, nitrogen fixation and extracellular polysaccharides). Horizontal gene transfer (HGT) also plays an important role in allowing a microbial community to rapidly adapt to As stress. The full genome sequence of strain *Brevibacterium linens* AE038–8 contains three *ars* operons (*arsC*, *ACR3* and *arsR*) and two copies of the *arsO* gene. *Thiomonas* sp. possesses two operons (*aio* and *ars* system), while *Rhodopseudomonas palustris* CGA009 carries three sets of As resistance determinants (ars1, ars2, and ars3). Soil bacteria could acquire multiple resistance determinants, via chromosomal duplication or horizontal gene transfer. In fact, transfer of *arsenite transporter* genes have been reported from *Aeromonas*, *Stenotrophomonas* and *Comamonas* in highly As-contaminated soil (Gu et al. 2018).

VI. ARSENIC REMOVAL VIA BACTERIAL *ARS* OPERON

The *arsR* gene encodes a metalloregulatory protein (ArsR) that acts as the main sensor and a transcriptional repressor of the whole operon in its homodimeric form. ArsR is a member of the SmtB/ArsR family having a helix-turn-helix DNA-binding domain and metal-binding sites. Under non-As conditions, *arsR* represses the expression of the downstream genes. Arsenic even at low concentration interacts with the ArsR homodimer, inducing its dissociation from the DNA. The *arsC* encodes an arsenate reductase involved in the reduction of As(V) to As(III) using glutathione (GSH) and glutaredoxin (GRX) as electron donors. The third gene, *arsB* encodes a membrane protein which functions as a proton antiporter, involved in As(III) extrusion, coupled to electrochemical energy, in an ATP-independent way in certain species. ArsB in *Escherichia coli* appears to be complexed with ArsA that encodes an ATPase and acts as potent ATPase-dependent As pump, named ArsAB. ArsD was initially believed to act as a metalloregulatory protein allowing transcriptional regulation of the *ars* operon, similar to ArsR. ArsD is however now known to act as a metallochaperone and not a regulatory protein. As(III) is able to bind to ArsD, forming the complex ArsD-As(III), which can subsequently strongly interact with ArsAB, allowing As(III) extrusion (Mateo et al. 2019). Microbial driven methylation, and potential subsequent volatilization, mediated by arsM, also plays a crucial role in biogeochemical cycling of As (Afroz et al. 2019).

VII. CONCLUSION

Arsenic stress has turned out to be a global threat, affecting huge crop losses and severe health hazards. Hence, assessing appropriate measures for soil management under field conditions so as to reduce As uptake and accumulation in plants is urgent need of the hour. Soil-resident rhizospheric bacteria have a tremendous potentiality to lower the uptake of As using several mechanisms like biosorption, immobilization, precipitation, enzymatic transformation to less toxic forms and complexation with the metalloid. Therefore, sustainable agricultural practices involve either stimulation of the growth of the rhizospheric bacteria by providing appropriate nutrients and other physical factors, or inoculating the rhizospheric region with such bacterial consortia. However, the field application of rhizobacteria for As bioremediation is still very limited due to the lack of knowledge on the formulation of the bioinoculant and on their economic efficiency. The reality is that formulation of site-specific, cost-effective and commercially successful microbial inoculum for efficient As bioremediation still remains a challenge. Moreover, this procedure needs to be standardized for different plant species as well as for different environmental conditions. The appropriate combinations of bacterial species for a particular plant for best efficiency of As detoxification also need to be clearly assessed. With the development of molecular biology techniques, the rhizobacteria, overexpressing As-resistant or arsenic-degrading genes, can be genetically engineered for undergoing bioremediation. It should be ensured that (i) the strain should be stable after cloning and the target gene should have a high expression, and (ii) the strain should be tolerant or insensitive to the contaminant. Keeping the devastating effect of As pollution in mind, optimization of each of these techniques would play a vital role for rhizoremediation of As. The developed strategies should also be economically lucrative, so that the common mass and farmers really derive the maximum benefit. Future studies are also needed to examine the relationship between As-biovolatilizing bacteria and environmental factors (biotic or abiotic) at different temporal and spatial scales. Overall, despite certain limitations, the prospect for successful stimulation and exploitation of microbial metabolism for As-rhizoremediation appears to be really promising.

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