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The role of plant growth promoting bacteria on arsenic removal: A review of existing perspectives

Sadiya Alka [a], Shafinaz Shahir [a,*], Norahim Ibrahim [a], Tsun-Thai Chai [b,c], Zaratulnur Mohd Bahari [d], Fazilah Abd Manan [a,*]

[a] Department of Biosciences, Faculty of Science, Universiti Teknologi Malaysia, 81310, Johor, Malaysia
[b] Department of Chemical Science, Faculty of Science, Universiti Tunku Abdul Rahman, 31900, Kampar, Malaysia
[c] Centre for Biodiversity Research, Universiti Tunku Abdul Rahman, 31900, Kampar, Malaysia
[d] IPVolusi Sdn Bhd, A-3-3A, Centrio Pantai Hillpark, No. 1, Jln Pantai Murni, 59200, Kuala Lumpur, Malaysia

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ABSTRACT

Phytobial remediation is an innovative tool that uses plants and microbes to mitigate Arsenic (As) contamination of the environment. Recently, plant growth-promoting bacteria (PGPB) that assists phytoremediation has been highly touted for both improving plant metal tolerance and promoting plant growth while achieving the goal of large-scale removal of As. This review focuses on the PGPB characteristics influencing plants and the mechanisms in which they function to overcome/lessen As-induced adversities. Several recent examples of mechanisms responsible for increasing the availability of As to plants and coping with As stresses facilitated by PGPB will be reviewed. Although drawbacks to phytoremediation have been reported, encouraging results have been developed with regular monitoring. Introducing PGPB-assisted phytoremediation of As in a field requires an assessment of the environmental effects of PGPB, especially with respect to the impacts on indigenous bacteria.

Contents

* Corresponding authors.
E-mail addresses: shafinazshahir@utm.my (S. Shahir), m-fazilah@utm.my, fazilah@fbb.utm.my (F. Abd Manan).

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Abbreviations

As	Arsenic
As(V)	Arsenate
As(III)	Arsenite
Fe	Iron
Zn	Zinc
Cu	Copper
Cd	Cadmium
Cr	Chromium
Pb	Lead
Hg	Mercury
N2	Nitrogen
Pst	Phosphate specific transport
Pit	Inorganic phosphate transport USEPA
ROS	Reactive oxygen species
ATP	Adenosine triphosphate
GLpF	Aquaglyceroporin
SAM	S-adenosyl methionine
GSH	Glutathione
TMA	Trimethylarsine
TMAO	Trimethylarsine oxide
DNA	Deoxyribonucleic acid
ACC	aminocyclopropane-1-carboxylic acid
PGPE	Plant growth promoting endophytic bacteria
PGPR	Plant growth promoting rhizospheric bacteria
ISR	Induced disease resistance
IAA	Indoleacetic acid
VOC	Volatile organic compounds
EPS	Exopolysaccharide
WHO	World Health Organisation
EPA	Environmental Protection Agency
ATSDR	Agency for Toxic Substances and Disease Registry
DMA (V)	Dimethyl arsenic acid
DMA (III)	Dimethyl arseneous acid
MMA	Monomethyl arseneous acid
ACC	1-aminocyclopropane-1-carboxylate
IAA	Indole-3-acetic acid
PGPB	Plant growth-promoting bacteria
ACCD	Acetyl-coenzyme A carboxylase carboxyl transferase subunit beta
MT	Metallothionein
PTEs	Potentially toxic elements
SH	Sufyhydryl
SPE	Solid-phase extraction
EIL	Ecological Investigation Level
MDA	Malondialdehyde
USEPA	United States Environmental Protection Agency

1. Introduction

Arsenic (As) is categorised as the No.1 carcinogenic substance and it is ranked No.5 among the potentially toxic elements (PTEs) according to the Comprehensive Environmental Response, Compensation, and Liability Act (Huang et al., 2007). As (atomic number 33) is the twentieth highest naturally, ubiquitously occurring metalloid in the earth's crust (Shakya and Ghosh, 2019) and it is widely known for its detrimental effects on human health and aquatic creatures (Kim and Baek, 2019; Yin et al., 2017). As pollution presents a high ecological risk and threatens the health of living organisms (Yang et al., 2019). Recent reports of As pollution in drinking water led to the appearance of "cancer villages" in some regions of India, China, Bangladesh, and Pakistan (Cheng et al., 2019).

Millions of people worldwide are affected by As toxicity, and a considerable proportion of cultivated land and drinking water are affected by As contamination through both human activities (anthropogenic activities) and natural weathering (Abbas et al., 2018; Katsoyiannis et al., 2015). Contamination is especially prevalent throughout Europe, Bangladesh, Hungary, Taiwan, India, Malaysia, Vietnam, China, Mexico, Romania and Pakistan (Abbas et al., 2018; Hering et al., 2017). International agencies such as the International Agency of Research on Cancer (IARC), and the World Health Organisation (WHO), as well as the United States based agencies which include the Environmental Protection Agency (EPA), and Agency for Toxic Substances and Disease Registry (ATSDR) (Atsdr, 2007), classify As as a carcinogenic substance when being exposed for extended periods, particularly when the concentrations are above the threshold level of 10 μg/L of As in drinking water (Marinho et al., 2018). As is a lethal metalloid commonly found in aquatic environments and has damaging effects on plant development and efficiency in which it can significantly decrease food production. Of particular concern for major crops, animal by-products and veggies, there exists a significant health risk for humans (Leão et al., 2017; Yañez et al., 2019). Humans are exposed to As in several ways, whereby the ingestion of As-contaminated water and food is the most significant (da Silva et al., 2018; Suriyagoda et al., 2018). High intake of water contaminated with As increases the risk of exposure leading to serious disease (Mohan and Pittman, 2007; Ng et al., 2003).

Different mitigation techniques which include both physicochemical and conventional approaches, have been developed toward overcoming the toxicity of As in groundwater. Though traditional approaches such as the application of fertilisers can reduce the toxicity of As in soils, plants, and animals (Huq et al., 2011), the aforementioned has its disadvantages: adversely affecting plant growth, high cost, complicated operating procedures and require excessive use of resources (Mishra and Mishra, 2018; Singh et al., 2018). Nevertheless, these drawbacks can be addressed through the use of biological approaches that have few difficulties and generate less secondary contamination. Bioremediation is a process in which it utilises either existing or indigenous microorganisms or, alternatively, plants to break down heavy metals in contaminated environments (Martin et al., 2014). Although it has its limitations, such as the potential production of toxic metabolites and microbial competition, a synergy between microbes and plants can address these limitations and enhance remediation efforts (Hrynkiewicz et al., 2018). This technique is a promising strategy for reducing As and other metal contamination and has an advantage as compared to other methods as it is a low cost, proficient, less contaminant, and it can be carried out on a large field scale, and it requires a brief timeframe. There are recent ongoing studies that try to modify the plant growth promoting bacteria (PGPB) in order to increase the adaptation and treatment effectiveness of bacteria in the metal-contaminated environment.

Nevertheless, there is still a lack of a comprehensive review focusing on genetically engineered organisms and materials for As. However, the general mechanism based on genetically modified bacteria on various effects on the level of pollution remains largely unaddressed and unrecognised, especially related to the plant-microbe interactions for As remediation. Thus, the researchers have given a concise review of using genetically-modified PGPB, mechanisms employed, and the living biota remediation methods to treat As polluted soils. In addition, the researchers have also revised past reviews conducted to clarify pathways of PGPB on As. The objective is, therefore, to highlight the current status of PGPB that improves plant As tolerance and growth.

This paper discusses the control factors of As contamination, their advantages, and disadvantages, as well as current knowledge of the toxicological effects of As, phytoremediation, and bioremediation As pollution and hyperaccumulator of As. In addition, the paper also focuses on the recent study of PGPB involvement in enhancing the growth and development of As hyperaccumulator plants, as well as analyses the tools used in their remediation. Finally, the expression on new research guidelines on As contamination, some perceptions, and ways to address the limitations of recent techniques in the future are also discussed.

2. As toxicity

As usually exists in the stable (As(III)) and (As(V)) valence states in which it exists naturally in the forms of oxyanions of arsenite (As (III)) and arsenate (As (V)). There are different concentration ranges in the aquatic environment (Shakya and Ghosh, 2018). The water pH and redox potential (Eh) increase As distribution in water systems (Zakhar et al., 2018). However, in natural water, As(V) predominates and is stable in oxygen-rich aerobic environments, whereas As(III) is predominant in moderately reducing anaerobic environment such as groundwater (Uppal et al., 2019). Organic As forms include dimethyl arsenic acid (DMA (V)), dimethyl arseneous acid (DMA (III)), monomethyl arseneous acid (MMA (III)), and monomethyl As acid (MMA (V)) (Meharg and Hartley-Whitaker, 2002). Recently, As contamination has been the subject of increasing concern for both the media and the researchers alike and is commonly referred to as a life-threating metalloid.

As is a nonessential metalloid that is toxic and harmful with respect to agricultural production since it reduces biomass and yield in plants, in which it has also become a global burden and a source of great environmental concern (Liu et al., 2018a,b). Thus, as a result, As has earned a place as one of the hazardous substances in the United States Environmental Protection Agency (USEPA) priority list (Atsdr, 2007). Anthropogenic activities (Guimarães et al., 2019) have caused As to accumulate in the soil to levels capable of causing the destruction of soil physiochemical properties, and thus, leading to soil infertility. Previous research (Chauhan et al., 2018) mentioned the negative impact of As on its influence on soil fertility and associated microbial community since it affects the agro-ecosystem on microbial community composition, growth-limiting factors (soil nitrogen(N) and phosphorus(P)), and associated soil enzymatic activity and subsequently will lead in reducing in impair ecosystem functioning, microbial metabolic quotient, and diversity. A soil with low microbial activity and solubilisation of C(carbon)-, N- and P-associated insoluble compounds will inevitably impact soil, getting degraded, and its ineptness to the growing crop (Deng et al., 2015; Tang et al., 2019). Contamination interferes with plant metabolic processes causing physiological, morphological, and biochemical disorders (Finnegan and Chen, 2012), which can lead to death (Smith et al., 2010). In plant cells, As(V) interferes with a metabolic pathway involving phosphate replacement during ATP(Adenosine triphosphate) synthesis, causing the loss of energy (Abbas et al., 2018; Geng et al., 2006), and subsequently As(V) is reduced to As(III) in the cytoplasm, resulting in the stimulation of free radical formation and accumulation of reactive oxygen species (ROS). Hence, this leads to the inability of the system to readily detoxify reactive intermediates (Shri et al., 2009).

Phytotoxicity of As varies between and within plant species, As oxidation state, and edaphic conditions (Kashyap and Garg, 2018). As(III) combines with SH (sulfhydryl) groups, inactivating proteins, enzymes, and lipid peroxidation with consequent cellular damage can causing fatality (Ullrich-Eberius et al., 1989; Zanella et al., 2016). During the detoxification of As in the plant, an oxidation–reduction reaction occurs due to valence variations leading to ROS production (Meharg and Hartley-Whitaker, 2002).

Multiple studies have shown that As toxicity contributes to a significant increase in membrane damage coupled with a reduction in stomatal conductance, nutrient deficiency, along with a disruption of phosphate-dependent metabolism during ATP synthesis, chlorosis (Finnegan and Chen, 2012; Garg and Singla, 2011; Kashyap and Garg, 2018), and reduction in plant reproductive capacity. In addition, studies have also indicated that As toxicity also plays a role in a decrease in plant growth and biomass build-up and decrease in crop yield (Dwivedi et al., 2010; Garg and Kashyap, 2017; Shaibur and Kawai, 2009), decline primary leaves area and biomass (Kashyap and Garg, 2018; Zhang et al., 2009), decrease in tillering and root growth (Abedin et al., 2002; Akhtar and Shoaib, 2014; Zhang et al., 2009) and a decrease in photosynthetic and respiratory systems rate (Garg and Singla, 2011). However, visible injuries and significant changes in growth inhibition and poor yield become apparent only after being exposed to relatively high levels of As (100 mg kg^1) or after being exposed for a prolonged growth period (Anjum et al., 2017). It should be noted that the United States Environmental Protection Agency (USEPA) arsenic permissible limit in soils is 24 mg/kg soil (Abbas et al., 2018).

3. Bioremediation

Bioremediation is a technique that involves the removal of toxic heavy metals from contaminated soil (Das and Sarkar, 2018; Hlihor et al., 2017). In principle, it involves the utilisation of bacteria to degrade or remediate environmental contaminants through the actions of their metabolic pathways (Ghosal et al., 2016). Various bacteria have been found to degrade heavy metals such as As, zinc (Zn), lead (Pb), selenium (Se). Their survival strategies in the presence of heavy metals such as As have been reported by many reviewers (Mukhopadhyay and Rosen, 2002a), and their strategies to detoxify As involve redox, intracellular bioaccumulation and methylation reactions (Gadd, 2010; Roy et al., 2015; Satyapal et al., 2016). Degradation pathways, both aerobic and non-aerobic, have been implicated for their association with As. Bioremediation techniques can employ several chemoautotrophic bacteria (either aerobic or anaerobic), which are used in degrading contaminants such as As.

Some As-resistant microorganisms gain energy during detoxification, oxidation or reduction of As (Roy et al., 2015; Satyapal et al., 2016), methylation of As(V) and As(III) (Yin et al., 2011) or demethylation of organic Asals (Guo et al., 2016; Yan et al., 2015; Zhu et al., 2017), which use phosphate transporters to facilitate the uptake of As(V) (Rosen and Liu, 2009) while As(III) passes through aquaglyceroporin (GLpF) across the cell membrane (Páez-Espino et al., 2009, 2015). Microbial isolates are also capable of solubilising As through adsorption (Ahsan et al., 2011), organic ligands production (Drewniak et al., 2010; Nair et al., 2007), practice compartmentalisation (Joshi et al., 2009), biosorption (Prasad et al., 2013) and mineral weathering caused by microbes (Mailloux et al., 2009).

Previous studies have revealed the major means of regulating As contamination (Han et al., 2017; Hettick et al., 2015; Roy et al., 2015), in which, this includes processes utilising both methylation and redox reactions (Roy et al., 2015). As volatilisation is a process that includes the reduction of As(V) to As(III) which is followed by a conversion to dimethyl As(V) DMA(V), TMA(III) (Trimethylarsine) and TMA(III) oxide (TMAO) in the presence of SAM (S-adenosyl methionine) and glutathione (GSH) (Francesconi and Kuehnelt, 2004). It was first found in fungi in the 1980s and later observed in bacteria, archaea, algae, plants, marine animals, and humans. As biomethylation and volatilisation have also been observed in *Aspergillus fumigatus*, *Pseudomonas* spp. (Shariatpanahi et al., 1981), *methanogens* (Michalke et al., 2000), *Rhodopseudomonas palustris* (Ke et al., 2018), *Tetrahymena pyriformis* (Chatterjee et al., 2017; Zhang et al., 2012). Of all the approaches described above, bioremediation is best known for its advantages: efficiency, very low energy consumption, no secondary pollution, no complexity in the technical process, long-term viability and no additional construction required (Shishir and Mahbub, 2019). Therefore, it has been widely and effectively implemented in many countries for several purposes. Shishir and Mahbub (2019) state that there are some limitations to bioremediation, in which it is limited to biodegradable compounds only; therefore, all contaminants cannot be treated using this technique. However, biodegradation is still considered to be safe, as bio-degradation residues can sometimes be more complex and risky than the parent compound. In addition, these techniques are often very specific and depend on many parameters such as the concentration of pollutants, microbial population, site factors, environmental conditions and nutrient levels that make the process difficult. Bioremediation is less efficient and unsuccessful in natural condition but serves as an environment conducive to microbial growth and activity (Shishir and Mahbub, 2019).

Furthermore, microbes are genetically engineered to increase their potential to attain the remediation of various types of contaminants under various environmental conditions. Bioremediation has been used in many river locations around the world in various stages of success, and its advantages have been acknowledged from proportion to its increasing popularity over time. It is worthwhile to note that different species are available from various locations that are effective in the pollution control system, and hence, there is no doubt that with proper research in this area, the bioremediation process will pave the way for safe and decontaminated rivers.

4. Environmental clean-up using plants

Recent studies define phytoremediation as a technique that uses soil microorganisms and green plants to provide a sustainable clean-up method for large areas of contaminated soil (Burges et al., 2018; Khalid et al., 2017; Lourenço et al., 2019; Reeves et al., 2018; Sharma, 2018). Phytoremediation has an advantage over conventional remediation techniques such as physical, chemical, and biological systems, which are costly, economically unsustainable, and do not ensure restoration without residual effects (Willscher et al., 2017; Zhang et al., 2018). Most heavy metals like As adversely affect plants, thereby causing various diseases and, potentially, the death of the plant. There are many studies focussing on finding the different types of plants that can tolerate As/heavy metal contamination. These plants are of three types: those that can tolerate and accumulate As without showing any toxic symptoms in their above-ground parts termed as hyperaccumulator, those that can tolerate As at a certain level that is below or at the threshold level, termed as tolerant and As accumulators are plants that can accumulate As at low to moderate concentration in their root (Roy et al., 2015).

4.1. Different types of as phytoremediation

As can be phytoremediated by using five mechanisms that include: phytoextraction, phytostimulation, phytofiltration, phytostabilization, and phytovolatilisation (Fig. 1). Phytoextraction involves the direct absorption and movement of pollutants from the soil into parts of the plants through the root. Plants have been found that are capable of absorbing metal in large amounts, some of which, accumulating without showing toxicity symptoms (Rascio and Navari-Izzo, 2011). Other plants that absorb limited quantities of toxic metals accumulate certain components of air and water pollution with and without showing toxic symptoms (Kumar et al., 1995; Sharma and Dubey, 2005).

Phytostimulation is the process by which the activity of the microbial biomass is enhanced to reduce the presence of organic contaminants via exudate from a plant's roots. Under metal stress, plants produce ethylene which inhibits root elongation by preventing the cell division and DNA(deoxyribonucleic acid) synthesis (Ojuederie and Babalola, 2017). Phytostimulation prevents the overproduction of ethylene in plants through the enzyme 1-aminocyclopropane-1-carboxylase deaminase (du Jardin, 2015; Saleem et al., 2018a,b). Enzyme activity increases as exudate are released. It maximises plants to be used as carbon and energy sources as well as their ability to degrade metals, and biomass becomes less bioavailable (Shelake et al., 2018; Vacheron et al., 2013). Phytostimulation of As mostly includes immobilisation techniques through adsorption to solid phases and adding or amputation of important As adsorbents on the soil would improve the phytoavailability of As.

Phytofiltration is a phytoremediation process that can be used to absorb or precipitate contaminants in surface or wastewater using either plant roots, seedlings or removed plant shoots (Kaur et al., 2018). Apart from eliminating metal from water, rhizofiltration with plants can also be used in removing heavy metals in soil, but the efficiency of this process is low compared with water filtration. Usually, pH increases the uptake of As a result of the release of root exudates, and in this scenario, the precipitate is accessible to root surfaces which can be collected and discarded after they become saturated.

Phytostabilization is a process whereby plants uptake heavy metals using their extensive root systems. The process allows for the absorption and accumulation of contaminants within the rhizosphere. With the help of the microbes, the process can stabilise As or heavy metals at the site of contamination or, alternatively, translocate As from root to shoot to reduce the risk of its exposure. Many studies have also been conducted on the plants that have the ability to develop dense root systems and at the same time achieve a high level of biomass production in the presence of As (Kaur et al., 2018; Pardo et al., 2017). The studies have shown that plants ameliorate vertical and lateral distribution of As, preventing it from entering the groundwater using vegetation ground cover to overcome the physicochemical limitations. These plants are able to increase the production of root biomass under conditions containing a high level of contaminants and have the ability to minimise immobilisation of metals from roots to shoots, thereby preventing the contaminant from reaching the food chain (Fernández et al., 2016; Santibáñez et al., 2008).

Phytovolatilisation involves the use of plants to volatilise As or metals into the atmosphere with or without the aid of rhizospheric microbes. It is a natural process by which plants uptake As from the environment and released it through transpiration into the atmosphere (Jakob et al., 2010). This process remains an important bioremediation tool (Zhang et al., 2015). The sequential transformation of As into volatile form occurs through microbial actions in which the inorganic form of As is converted to volatile mono-, di-, and tri-methylated species after a sequence of methylation reactions (Cullen and Reimer, 1989; Mukhopadhyay and Rosen, 2002b). Asal derivatives are lost as a result of the microbial process in the soil.

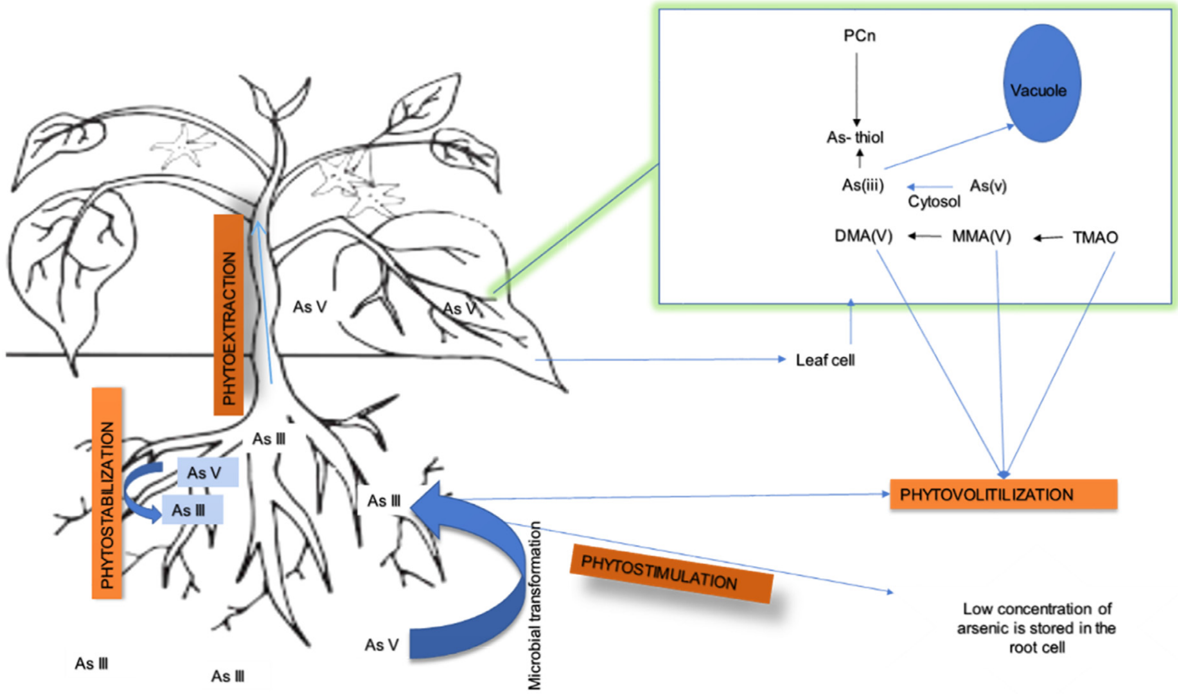

Fig. 1. Overview of Phytoremediation processes that occur in plants.
Source: Modified from Kushwaha et al. (2015).

4.2. As hyperaccumulating plants

Hyperaccumulators are plants that are naturally able to hyper-accumulate, metabolise or otherwise detoxify at molecular, physiological, and biochemical levels (Kumar et al., 2015). Plants that can store metal up to 1% of their dry weight are known as hyperaccumulators, and those whose uptake and translocate metal concentration with and without showing toxicity are termed as indicator and accumulator; excluders restrict the absorption of toxic metal (Roy et al., 2015). Hyperaccumulator plants uptake arsenic in the form of As(V) or As(III) from the soil and are transported to aboveground parts and stored as free As (III) as vital approaches meant for remediating arsenic-contaminated soils and decreasing arsenic in food system, while in non-hyperaccumulator plants, they are transported and sequestered As (III) into vacuoles of root cells with less time owing to their high biomass (Gadd, 2019).

Kumar et al. (2015) mention about 450 plant species from 45 different families that can tolerate as well as hyper-accumulate As. An example of these plants is the Pteridaceae family, which can tolerate and accumulate a large amount of As in their above-ground biomass (Chen et al., 2018; Liu et al., 2018a,b; Ma et al., 2001; Zhao et al., 2002). Fern species including *Pteris criteca*, *Pteris vittata*, *Pteris umbrosa*, *Pitrogramma calomelanos*, and *Pteris longifolia* are also known to be successful As hyper-accumulators and can survive high As soil concentrations (Ali et al., 2013; Meharg, 2003; Verbruggen et al., 2009; Wang et al., 2002). Researchers have reported that plants including *Melastoma malabathricum* (Selamat et al., 2014), *Solanum lycopersicum* L. (Eke et al., 2019), *Silene vulgaris* (Kumar et al., 2015), *Arabidopsis thaliana* (Wang et al., 2018), Rice (Shri et al., 2019; Verma et al., 2018), *Holcus* (Souri et al., 2017), are capable of withstanding maximum As concentrations of 0.04 mg kg^{-1} in soil. Indian mustard (Pickering et al., 2000) are also known to accumulate and show As tolerance (Table 1).

Aquatic macrophytes including *Eichhornia crassipes*, *Egeriadensa*, *Ceratophyllum demersum*, *Hydrilla verticillata*, *water-cress Lepidium sativum*, and *Potamogeton pectinatus* were found to uptake a significant amount of As and show the ability to resist its toxicity. The plants are promising candidates for As phytoremediation in water (Mishra et al., 2016, 2013; Song et al., 2018). Increasing our understanding of the genetic and biochemical mechanisms employed by hyper-accumulators in response to As exposure and accumulation may serve as a useful tool when designing approaches for remediation purposes.

Ma et al. (2001) were the first scientists to discover the hyperaccumulator *Pteris vittata*, known as Edenfern. The fern, along with hyperaccumulating As, has a high As tolerance. It was also found to have an astonishing capacity to either uptake or translocate organic and inorganic As in its both root structures and above-ground biomass (Chen et al., 2018; Ma et al., 2001; Tu and Ma, 2002; Tu et al., 2002). The fern absorbs As at concentrations from 200–1000 times higher than the immediate soil without suffering any apparent phytotoxic effects, an effective defensive strategy for survival in

Table 1
A summary of previous studies investigating the effect of as on hyperaccumulator plants.

Plant species	Effects	Reference
Pteris vittata	Fern species that significantly reduces As concentration in rice grain by 18%–83% by reducing its transfer to the food chain	Ye et al. (2011)
Glycine max L.	Soybean grown in soils augmented with phosphate shows a reduction in the toxicity effects caused by As (28.6%)	Chandrakar and Keshavkant (2018)
Brassica species	Roots accumulate high levels of As and very low levels of As are detected in the stem and leaves. Uptake of As in the root (67%–10%, 61% for As(III)) and leaves (65%–10%)	Mendoza-Hernández et al. (2019)
Helianthus annuus L.	Important antioxidants, ascorbate, and glutathione present in sunflower leaves exposed to As were significantly decreased by Salicylic Acid treatment	Govarthanan et al. (2018)
Arabidopsis thaliana	*Arabidopsis* reduced As(V) to As(III) in the nutrient solution using a solid-phase extraction (SPE) cartridge	Park et al. (2016)
Maize	Toxicity tests examined the concentrations of As(III) or As(V) reduced	Ding et al. (2011) and Requejo and Tena (2005)
P. calomelanos var. austroamericana	It accumulates As but takes a longer period of time to be achieved usually required limit for EIL (Ecological Investigation Level)	Niazi et al. (2012)
Native plants	It takes a longer time to accumulate As owing to their relatively high biomass concentration	Antosiewicz et al. (2008) and Castillo-Michel et al. (2011)
Nicotiana tabacum L	Both As and cadmium (Cd) accumulation in leaves increases to higher levels than in the roots of *Nicotiana tabacum* plants	Degola et al. (2015)
Lettuce Sativa L	The increase in As concentration detected in the leaves was followed by a significant increase in H_2O_2 and malondialdehyde (MDA) concentrations	Silveira et al. (2015)
Pisum sativum L.	Exogenous Pro application alleviated AsV toxicity in eggplant seedlings by reducing the accumulation of As	Rodríguez-Ruiz et al. (2018)
Melastoma malabathrum	*Melastoma malabathricum L.* species.uptake of different metals from contaminated soil	Selamat et al. (2014)
Solanum melongena L.	Sodium hydrosulfide enriched AsV toxicity in pea seedlings	Singh et al. (2015)

metal-polluted areas (Ojuederie and Babalola, 2017; Roy et al., 2015). Recently there have been analytical reports showing that hyperaccumulator species can accumulate major, minor, and trace elements (Liu et al., 2018a,b; Reeves et al., 2018). These plants have a unique ability to remediate soil under metal stress, improve translocation of metal ions, detoxify and sequester heavy metals into above-ground plant structures.

5. Phytobial remediation

Phytobial remediation is a technique that aims to combine the use of microbes and plants to reduce the level of certain types of contamination. Microbes play an important role in the ecosystem; they create stable microbial communities that are the foundation of major biogeochemical processes, assist the growth of plants and assist in taking up toxic material (Van Der Heijden et al., 2008). Apart from these functions, microorganisms form a mutualistic association with indigenous mangrove vegetation, particularly by occupying the rhizosphere as free-living, root symbionts, and root endophytes. While the plants provide the rhizo microbe nutrients and protection, they later produce important metabolites that both improve plant progression (Goswami et al., 2014; Sharma and Raju, 2013; Sharma et al., 2013) and encourage heavy metal removal from encompassing media (Brown and Lester, 1979; Martins et al., 2008). Consequently, these rhizo microbes could be utilised as components for the bioremediation of metal-contaminated waterfront territories.

6. Plant growth-promoting bacteria

PGPB is naturally able to endure high heavy metal contamination and provide benefits to both soil and plants. PGPB, among other microbes, is involved in the bioremediation of contaminants through their mutual interactions with plants, thereby increasing the plant productivity (de Andrade et al., 2019). They much remain to be studied concerning the metabolic and physiological changes that occur within these bacteria (soil pH alteration, the release of chelators and oxidation/reduction reactions) to improve the phytoremediation process by increasing the metal bioavailability (Rajkumar et al., 2012; Tara et al., 2019). PGPB plays a vital role in facilitating the growth of plants in the presence of high levels of metals in soils by altering metal mobility and bioavailability (Rehman et al., 2019; Tara et al., 2019; Yahaghi et al., 2019). PGPB can be either free-living bacteria, in symbiotic associations with the plants, or endophytic bacteria that colonise within the plants (Soldan et al., 2019; Ullah et al., 2015). Moreover, PGPB improves plant growth under metal stress by producing substances such as siderophores, phytohormones, and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase (Ma et al., 2010; Santoyo et al., 2016).

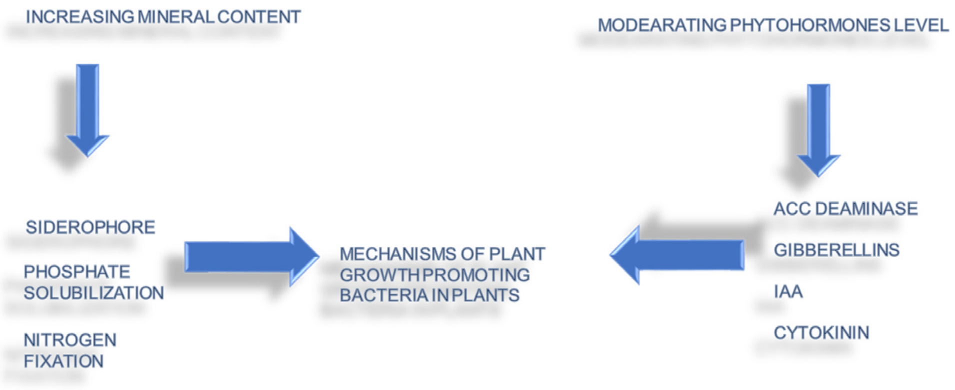

Fig. 2. PGPB traits that enhance plant growth under as stress.
Source: Modified from Kong and Glick (2017).

They supply nutrients and inhabit the rhizosphere of plants, leading to enhanced development of the plant through different mechanisms (Fig. 2) (Arslan et al., 2017; Bhattacharyya et al., 2017; Tara et al., 2019). PGPB increases the growth of hyperaccumulator plants with natural low biomass and stunted growth. Syndication of these metal-specific hyperaccumulators and appropriate PGPB species under field conditions has resulted in reliable demonstrations under a controlled environment, demonstrating the combined practice to restore As polluted areas with a justifiable source (Asad et al., 2019). Since this technology is not expensive, it can be used for applications on a commercial scale where appropriate. PGPB does not only increase plant growth and development but also neutralises the ROS system by decreasing the toxicity of As and increasing the supply of iron to plants (Liu et al., 2015). The siderophore production by PGPB has been reported to increase under nutrient deficiency and with As toxicity (Khanna et al., 2019). Earlier reports stated that PGPB increases metal solubility and iron supply by producing siderophores under As contamination and depleted nutrient environment (Asad et al., 2019; Khanna et al., 2019). Moreover, it has been reported that there is an increase in bio-metal toxicity due to its strong affinity with bivalent metal ions (Neilands, 1981).

Microbes are known to reduce As(V) to As(III) in the plant to adsorb As (III) in their aboveground parts. As(V) are present in the soil more than As(III) because plant uptake of As(III) relies on the competition with phosphate present in the soil, making it difficult for the plant to remediate it. This results in an increased abundance of As(III) in soil. With the help of PGPB, phytoremediation efficiency is increased by improving plant tolerance, plant growth, or by eliminating metal accumulation by plants. The mechanism of action comprises phytohormone production that facilitates the ability of the plant to endure contaminants through reduction of ethylene levels leading to the formation of longer roots (Glick, 2010; Kong and Glick, 2017). ACC deaminase hydrolyses ACC into ammonia and α-ketobutyrate and thereby decreasing the amount of ethylene produced by the plant (Ullah et al., 2015). Rhizosphere bacteria act as biocontrol agents detoxifying contaminants, whereby they can ameliorate metal toxicity, metal accumulation and prevent metal bioavailability (Choudhary and Varma, 2016; Kong and Glick, 2017). PGPB consists of different species including *Klebsiella*, *Enterobacter*, *Flavobacterium*, *Gluconacetobater*, *Burkholderia*, *Erwinia, Serratia*, *Beijerinckia*, *Bacillus*, and *Pseudomonas* (Mrkovački et al., 2012; Ullah et al., 2015).

6.1. The strategy of using PGPB in plants

PGPB facilitating metal uptake can either bind to the plant's phyllosphere or rhizosphere or established an endophytic association within internal plant tissues (Kong and Glick, 2017). There are two categories of bacteria that possess PGPB traits, and these include plant growth promoting endophytic bacteria (PGPE) and plant growth promoting rhizospheric bacteria (PGPR) (Afzal et al., 2019; Vurukonda et al., 2016).

PGPR is found in the rhizosphere around the seed surface, or plant root and PGPE colonise internal plant tissues (Afzal et al., 2019). Both types help plants utilise nutrients from the environment, enhance plant growth via modulation of plant hormones and biocontrol of pathogens. In addition, they also improve plant tolerance to metal stress, enhancing a plant's ability to bioaccumulate and bioabsorb metals. Finally, they affect concentrations of metals and heavy metal mobility (Bilal et al., 2018; Santoyo et al., 2016).

These bacteria use similar mechanisms (directly or indirectly) to help in the development of plants via siderophore production, in which, they prevent plants from infection of pathogens, promote phosphorous solubilisation, enhance plant growth regulation by hormones and increase biomass (Ashraf et al., 2017). As mentioned above, the mechanism employed by PGPB in improving plant survival under As stress works by increasing As uptake in the plant, improving As phytotoxicity, decreasing the bioavailability of As and decreasing uptake in some plants through resistance, detoxification, accumulation, transformation and sequestration (Kong and Glick, 2017).

Table 2
A summary of findings describing the phytoremediation of metals assisted by Plant Growth Promoting Bacteria (PGPB).

Plant	Plant growth promoting trait	PGPB	As	Other metals	Effect of PGPB	Reference
Brassica juncea and *Lupinus albus*	Metal, Indoleacetic acid (IAA) production, mineral solubilising ability, siderophore, proteases, ammonia, exopolysaccharides, in vitro biofilm formation, en-dopolygalacturonase and endopolyglucanase, and VOCs, phosphate solubilisation and nitrogen fixation.	*Actinomycetales* (*Gordonia alkanivorans*, *Microbacterium paraoxydans*, and *Rhodococcus equi*), *Betaproteobacteria* (*Cupriavidus necator* and *Achromobacter denitrificans*) *Bacilli* (*Bacillus megaterium*, *Lysinibacillus macroides*, and *Sporosarcina luteola* isolated from contaminated soil.	(41.1 mg kg^{-1}) exceeded recommendation limits	Mercury (Hg) (67 mg kg^{-1})	Indigenous PGPB had a positive effect on plant biomass and assisted phytoextraction strategies	Franchi et al. (2017)
Cicer arietinum L.	IAA and siderophore production, the capability to solubilised phosphate and activity of ACC deaminase	*Acinetobacter* sp.was isolated from contaminated soil.	(10 mg kg^{-1}) exceed recommendation limits		Plant growth and production of the plant was increased. Decrease the toxic effect of As	Srivastava and Singh (2014)
Vigna Radiata	The solubilisation of phosphate, production of indole-3-acetic acid (IAA) and exopolysaccharide (EPS)	*Exiguobacterium* isolated from contaminated soil	(100 mg kg^{-1}) exceed recommendation limits		Plant growth and As uptake increased. Increased the shoot and root biomass	Pandey and Bhatt (2016) and Pandya et al. (2015)
Rice seedlings	IAA production, siderophore production, and exopolysaccharide (EPS)	*Kocuria flava* and *Bacillus vietnamensis* isolated from mangrove rhizosphere	(>300 µg/l) As		It promotes growth parameters and decreases As uptake	Mallick et al. (2018)
Spirulina Platensis	Increases in IAA, mineral content, siderophores, phosphate solubilisation, and ACC deaminase production	*Burkholderia* sp. D54		Lead (Pb) (1223 mg k^{-1}, Cd (20 mg kg^{-1}), Zn (534 mg kg^{-1}), and Cu (589 mg kg^{-1})	Increased in the growth of plant and uptake of metals	Guo et al. (2011)
Grapevine	Produce siderophores solubilised phosphates and fixed N2	As (III) tolerant bacterial strains which were As(III) tolerant bacterial strains	150 µM (+As)		Decreased As (III) toxic effects, activated antioxidant enzymes	Pinter et al. (2017)

(*continued on next page*)

Direct plant growth promotion occurs both in PGPE and PGBR that have the capability of enhancing plant growth promoting traits. These include improving nutrient attainment and hormonal stimulation (Berg, 2009). Indirect plant growth promotion occurs in PGPE and PGBR by reducing damage caused by the phytopathogens via induced disease resistance (ISR) of plants against necrotising pathogens (Harish et al., 2009; Ma et al., 2016; Vinodkumar et al., 2018). Alteration of the host plant physiology and changes in the microbial balance of the rhizosphere are the main pathways for the complex growth promotion mechanism by PGPR (Ryu et al., 2003; Verma et al., 2010). Below are some successful studies focused on phytobial remediation of As and other metals (Table 2).

PGPR naturally can produce plant growth hormones that can be beneficial or toxic to plants (Goudjal et al., 2013). Hormones are used to support/control plant growth under As stress, allowing plants to withstand stress, promote resilient roots and surface area of the root (Asad et al., 2019). The inoculation of PGPB on hyperaccumulator plant can help overcome the extent of some limitations. PGPR promoting plant growth by synthesising several enzymes, either directly or indirectly. ACC-deaminase, a precursor of ethylene, breaks down the amino-cyclopropan carboxyl (ACC) (Çakmakçı et al.,

Table 2 (*continued*).

Plant	Plant growth promoting trait	PGPB	As	Other metals	Effect of PGPB	Reference
Helianthus annusvar	Phytohormones, siderophore production, and phosphate solubilisation	*Pseudomonas fluorescens* strain isolated in soil		Pb (300, 600 and 900 mg kg^{-1})	Enhanced antioxidant activities, proline, plant yield, physiology, growth, and reduced the malanodialde-hyde content	Saleem et al. (2018a,b)
Plants	Solubilise soil phosphorus, produce siderophore and indole-3-acetic acid (IAA), ACC deaminase	*Pseudomonas jessenii* strain			Increase plant growth and increases metal uptake	Lozecznik (2018)
Zea mays	Flagella biosynthesis, biofilm formation, exopolysaccharides, IAA and siderophores production, acetoin, butanediol, and phosphate solubilisation	*Bacillus aryabhattai* AB211 isolated from *Camellia sinensis*		Heavy metal	Enhance plant growth by synthesising IAA, stress tolerance, and produces extracellular polysaccharides (EPS) necessary for optimal colonisation.	Bhattacharyya et al. (2017)
Cirsium Arvense	ACC deaminase, IAA and siderophores	*Alphaproteobacteria*, *Betaproteobacteria*, and *Gammaproteobacteria*	(100 mM) As(V) and (10 mM) As(III)		Improve the phytoremedia-tion process	Cavalca et al. (2010)
Rice	Solubilise phosphate, produce siderophores, IAA-like molecules, and ACC deaminase	*Pseudomonas* sp., *Geobacillus* sp., *Bacillus* sp., *Paenibacillus* sp., *Enterobacter* sp. and *Comamonas* sp**.** were isolated from the agricultural soil	75 μM As(III) or 250 μM As(V)		Improve bioremediation	Das et al. (2016, 2014)
Pteris vittata	Siderophores	*Pseudomonas* sp., *Comamonas* sp. and *Stenotrophomonas* sp	5.04–7.37 mg L^{-1}		Enhance phy-toremediation	Ghosh et al. (2011)
Zea mays	Siderophores, solubilisation of phosphorus, atmospheric nitrogen fixation, and minerals in the soil, production of plant growth regulators	*Microbacterium* sp.		Cr (Vi) (35 mg kg^{-1})	Improved growth and yields of plants	Soni et al. (2014)
Salix Caprea	ACCD (Acetyl-coenzyme A carboxyl TMA ase carboxyl transferase subunit beta) activity, IAA production, and siderophore release	*Proteobacteria*, *Actinobacteria* and *Bacteroidetes/Chlorobi*		Zn and Cd (200 mg kg^{-1})	Increase metal uptake	Kuffner et al. (2010)

(*continued on next page*)

2017), which contributes to plant growth and enabling plants to recover the shock under contaminated heavy metals (Ma et al., 2016).

Table 2 (*continued*).

Plant	Plant growth promoting trait	PGPB	As	Other metals	Effect of PGPB	Reference
Triticum aestivum L.	Fixing and producing the highest amounts of N and auxin, respectively, with P solubilising and ACC-deaminase activities, producing siderophore	*Azospirillum sp*		Fe, Zn, Cu (<3 mg/kg)	Enhance plant growth and alleviate drought stress	Abbas et al. (2018) and Arzanesh et al. (2011)
Zea mays	Production of siderophore indole acetic acid, hydrogen cyanide, and ammonia, ACC-deaminase activity	*Chryseobacterium palustre* and *Chryseobacterium humi*, *Sphingobacterium*, *Bacillus*, *Achromobacter*, and *Ralstonia* were isolated from a metal contaminated site	As (5 mg kg^{-1})	Heavy metal	Increase plant growth, biomass production, and nutrient status	Marques et al. (2010)
Atriplex lentiformis	Plant growth hormones	*Azospirillum brasilense* strain and *Bacillus pumilus* strains	91 mg kg^{-1}	Heavy metals	Increase uptake and plant biomass and nutrition	De-Bashan et al. (2010)
Populus deltoids	Produced siderophores and IAA	*Agrobacterium radiobacter*	300 mg kg^{-1}		Increase As phytoremediation	Wang et al. (2011)
Brassica juncea (L.)	IAA, 1- (ACC) deaminase and siderophores	*Staphylococcus arlettae* isolated from As contaminated soil	15 mg kg^{-1}		Increase As accumulation in the root and increased biomass, carotenoid, chlorophyll and protein content	Srivastava et al. (2013)
Zea mays	IAA, nitrogen fixation and phosphate solubilisation.	*Enterobacter cloacae* (CR1), *Pseudomonas putida* (CR7) and *Stenotrophomonas maltophilia* (CR3) isolated from corn		Nitrogen	Improve plant growth and yield	Mehnaz et al. (2010)
Panicum virgatum L.	Indole acetic acid production, 1-aminocyclopropane-1-carboxylic acid deaminase (ACCD) activity, and phosphate solubilisation	*Pseudomonas grimontii, Pantoea vagans, Pseudomonas veronii*, and *Pseudomonas fluorescens were* isolated from upper parts of plants from CD contaminated soil		Cd concentration (20 μM)	Increase biomass and Increases Cd uptake	Begum et al. (2018)

In the presence of salinity and heavy metals, PGPB *Halobacillus* sp. and *Halomonas* sp. enhance the root growth of *Sesuvium portulacastrum* as well as augment the accumulation efficiency of *Sesuvium portulacastrum* grown in saline soils. The effect is attributed to the plant growth promoting the ability of PGPBs, in which the bacteria enhances the production of IAA and solubilisation of phosphate (Desale et al., 2014). In addition, PGPB has also been reported to affect metal bioavailability and its translocation in plants, allowing for metal toxicity reductions and metal accumulation enhancement in plants (Kong and Glick, 2017). As-resistant endophytic bacteria have shown plant growth promoting characteristics, such as promoting the production of IAA and siderophores, solubilisation of phosphate, enhancing plant growth in *Pteris Vittata* and effective phytoremediation (Xu et al., 2016).

Previous work by Mohd Bahari (2017) found that the As-resistant *Microbacterium* sp. strain SZ1 isolated from As-bearing gold ores can potentially be used for phytobial remediation as its genome was found to possess the genes responsible for siderophore production. A recent study reported that As-resistant *Bacillus aryabhattai* alleviates As-induced toxicity, resulting in decreases in As accumulation in rice under As-spiked agricultural soil (Ghosh et al., 2018). Li et al. (2017) proposed an increase in root weight and root morphology, photosynthetic properties, and growth promotion in field trials could be due to PGPR mixtures (Liu et al., 2018a,b). PGP bacterial research has gained a lot of attention in recent years due to its unique nature of metal ions extraction, promoting plant growth and development for sustainable development in agriculture (Gouda et al., 2018). A study conducted on Italian oregano, wild marigold, sweet marjoram, and sweet red showed significant increases in secondary plants and metabolic growth after major PGPR improvements seen in oil yields (EO) varying at various levels (del Rosario Cappellari et al., 2019). Pb-solubilising bacteria have been isolated and characterised by the production of acetic acid and siderophores and inoculation of these bacteria into *Brassica juncea* plants enhances the growth and absorption of Pb in metal-contaminated soils in order to develop new microbial assisted phytoremediation strategies for contaminated soil (Yahaghi et al., 2018).

6.2. Genetically modified PGPB

Genetically-engineered, PGPB-assisted phytoremediation is a technique used for the remediation of heavy metals. Bacterial engineering allows researchers to use non-endogenous genes, which can be injected to create bacteria with improved remediation capabilities (Ullah et al., 2015). The use of current techniques to improve PGPB can play a vital role in plant yield and tolerance and sustaining soil fertility and a composed nutrient cycling. The relationship between the modified PGPB and hyperaccumulators and the resulting metal bioremediation accomplished has been previously studied (Barac et al., 2004; Doty, 2008; Ullah et al., 2015). Bacteria genetically modified are exposed to complex environments with various microbial interactions and a variety of substrates, and only a few of them are involved in the removal of contaminants. However, there are few reports on symbiotic relationships that function to enhance As remediation (Ike et al., 2008; Koechler et al., 2010; Martínez et al., 2017; Mobar, 2018; Nie et al., 2002; Shukla et al., 2013; Singh et al., 2010, 2008; Tsai et al., 2012; Villadangos et al., 2014).

PGPB and hyperaccumulator plants have resulted in reliable showings under controlled conditions, signifying the usage of combined biotic agents to restore As contaminated soils. However, there are some limitations to the synergistic combination of plants and microbes. Shulse et al. (2019) report that plants and soil microorganisms have developed various mechanisms for phosphate extraction from existing sources in soil but are unable to produce high yields without the presence of additional phosphate fertilisers. However, Belgaroui et al. (2016) reported engineering plants for the metabolism of alternative forms of phosphate. Though each plant species must be individually formed and must be labelled as a genetically modified organism, and the alternative is to develop phosphate-containing soil microorganisms that grow around plant roots and release phosphate-containing plants (Richardson, 2001). Bacteria are better suited for engineering at scale and can be used for many types of plants and the environment. In addition, different bacteria are expected to be successful in colonising different crops and different soil environments. Therefore, it may be useful to develop several designed bacterial strains, which can be used separately depending on the plant and the environment (Shulse et al., 2019).

Gouda et al. (2018) suggest that genetic manipulation is developed to enhance the novel PGPB strains by improving their characteristics. *Pseudomonas putida* was genetically modified to increase its resistance to and binding affinity for Cd. Introducing metallothionein (MT) genes in *Ralstonia eutropha* increases plant growth and development and enhances the abilities of plants to withstand stressful environmental conditions (Singh et al., 2011). Research on engineered plants and microbe have been carried out by inserting As-resistance genes (Rahman et al., 2014). This is accomplished by the introduction of plasmids and protoplast during metallothionein (MT) strain modification, and it was reported to be successful and to have a better effect on the degradation of pollutants. Despite the successful application of bacterial genetic engineering, there are still some problems encountered during the treatment process (Liu et al., 2019). One of the problems encountered is that there are many plasmids in a single strain that can cause a load on bacterial cells, which will lead to a slow growth rate and strain replication and subsequently, is difficult for bacterial protection with good properties (see Fig. 3). In addition, protoplast fusion causes the ability to decrease bacterial degradation as a result of poor gene recognition for degradation. Thus, research investigating the effects of multiple gene combinations is still incomplete.

7. Conclusion and further research

As contamination is currently a grave concern throughout the world since it affects both plants and animals, including humans. Bioremediation of such a widespread contaminant appears to be a feasible solution to environmental contamination by As. The benefits of remediation include low cost, minimal environmental damage, and eco-friendliness. However, the process also has some limitations. To overcome these, the combined use of plants and microbes can be used to generate more effective, affordable and fast-acting approaches. Recently, researchers have developed a method utilising PGPB-enhanced phytoremediation to overcome the challenges of plant stress in As-contaminated soils. This work showed an improvement in the efficiency of phytoremediation, thus altering metal bioavailability in the soil while increasing metal translocation within the plant and alleviating metal phytotoxicity.

Further investigation is needed to evaluate the effect of environmental conditions on plant-microbe interactions in contaminated soils, but various reports confirm the key role of PGPB in supporting and enhancing plant activities. While the effectiveness of phytoremediation has been well studied, more work will be needed to fully understand the stability, composition, and the bioactivity of the indigenous microbes. Little is known about the role of enzymes in bioremediation.

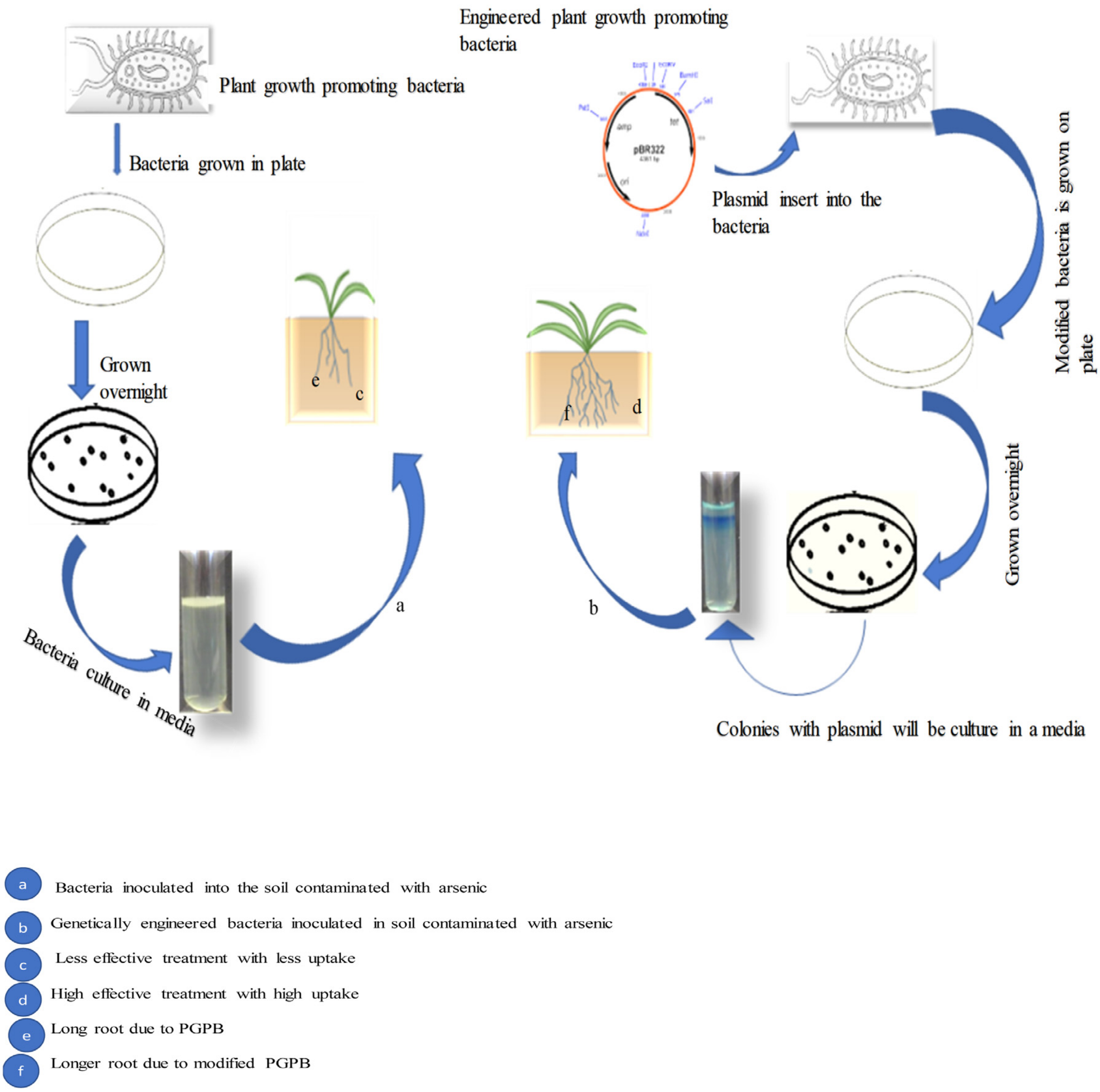

Fig. 3. Inoculation of genetically modified PGPB.

Thus, more research is required to fully understand the pathways in which enzymes function. In addition, it is not known on how many of them enhance the defensive capacity induced by PGPB in the bioremediation of contaminants and the existence of any possible side effects.

An effort has been made to reduce As contaminants utilising transgenic plants and microbes, yet little is known about the type of effects this can have on the environment. The specific gene required for metal tolerance in PGPB needs to be broadly studied to understand the selection of metal- and plant-specific strains of PGPB. Consideration should be given to the effects of engineering strain on human survival and ecological balance. Understanding phytobial remediation at the molecular level could enhance the ability of researchers to design conditions and combinations of hyperaccumulator plants and PGPB strains for removing As and thus enhancing remediation efforts.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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