Chapter 8
Mitigating Arsenic Toxicity in Plants: Role of Microbiota

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Abstract Arsenic (As) pollution, particularly in soil and water, is a very prominent environmental issue which seriously threatens plant growth, development, and productivity. Since As is ubiquitous in the natural environment, microorganisms have developed mechanisms to resist the toxic effects of this metalloid. A large number of microorganisms, viz. *Acinetobacter*, *Aeromonas*, *Bacillus*, *Exiguobacterium*, and *Pseudomonas*, are capable of growing in the presence of high concentrations of As. But relatively less information is available on accumulation, mobilization, distribution, and speciation of As by rhizospheric microbiota and their impact on plant growth and development. The use of As-resistant and plant growth promoting microorganisms (PGPMs) for the restoration of plants growing on contaminated soils is the need of the time. The use of PGPM occupies a small but growing niche in the development of organic agriculture and has attracted attention during the last decade only. There are several reports revealing the multifarious role of soil microbiota in amelioration of As toxicity and improving metal tolerance in plants. Colonization of PGPMs helps the host plant to overcome As-induced phosphate (P) deficiency and consequently maintain favorable P:As ratio. Further, they also improve nutritional status and reduce As uptake and translocation in plants. Inoculation of bacteria/fungi can exert protective effects on vascular plants under As contamination by transforming more toxic inorganic forms into less toxic organic forms or via reducing the concentration of As by enhancing plant biomass. The PGPMs also result in higher activities of the antioxidant enzymes (superoxide dismutase, catalase, ascorbate peroxidase, and guaiacol peroxidase) and accumulation of nonenzymatic antioxidants (carotenoids, ascorbic acid, proline, and α-tocopherol). Increased concentrations of cysteine, glutathione, and non-protein thiols, and activity of glutathione *S*-transferase have also been reported that facilitate sequestration of As into nontoxic complexes. Thus, application of As-resistant PGPMs could pro-

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vide a low cost and eco-friendly mitigation approach to diminish As accumulation in plants, thereby promoting higher growth, development, and yield responses. There is also a need to improve our understanding of the mechanisms involved in extenuating toxic effects of As by rhizospheric microbiota and to improve the stabilization of plants in contaminated sites.

Keywords Phytoremediation · Plant-microbe interactions · Plant growth · Rhizosphere · Toxic metalloids

8.1 Introduction

Arsenic (As) is a toxic metalloid of global concern, as it cannot be degraded to harmless products instead persists indefinitely in the environment. It occurs in trace quantities in rocks, soil, water, and air but can be intensified by anthropogenic activities (Garelick et al. 2008). Consequently, elevated levels of As have been reported in soils and groundwater worldwide. The amount of As in a plant depends on the amount of As it is exposed to. Terrestrial plants may accumulate As by root uptake from the soil (Li et al. 2015) or by adsorption of airborne As deposited on the leaves. Background As concentrations in terrestrial biota are usually less than 1 mg kg^{-1}. The highest As concentration occurs in the roots of plants (Álvarez-Ayuso et al. 2015).

Arsenic is a nonessential element for plant and is expected to negatively affect growth responses. Plants cope with As toxicity by employing various detoxification mechanisms such as accumulation, sequestration, and compartmentalization. Nevertheless, failure of any once of these mechanisms leads to symptoms of phytotoxicity (Moreno-Jiménez et al. 2012). Alteration in plant growth usually occurs at higher levels of As application leading to different physiological and chemical changes in plants, such as necrosis and wilting, inhibition of seed germination, decrease in plant growth, restricted root and shoot length, lower fruit and grain yield, reduced enzymatic activity, and replacement of As with phosphorus in reactions (Zhao et al. 2009; Chandrakar et al. 2016). Bioavailability, uptake, and phytotoxicity of As in plants are influenced by factors like concentration and speciation of As, plant species, soil properties such as pH, redox potential, and soil phosphorus content (Fitz and Wenzel 2002).

Remediation of As-contaminated soils and groundwater is necessary for limiting the entry of this toxic metalloid in the food chain. The use of microorganisms in the bioremediation of contaminated ecosystems showed a great prospective for future developments due to its environmental compatibility and possible cost-effectiveness. Microorganisms have evolved dynamic mechanisms for facing the toxicity of As which enable them to survive in As-rich environments. The strategies developed by microbes to counteract As toxicity include the active exclusion of it from cells by establishing permeability barrier, intra- and extracellular sequestration, active efflux pumps, and microbial bioaccumulation (Tsai et al. 2009; Wang et al. 2013). Microorganisms are also known to survive As exposure by transforming it through oxidation-reduction reactions and methylation-demethylation processes into less toxic forms (Cai et al. 2009; Liao et al. 2011; Kuramata et al. 2015). A variety of microbes are known today which utilize As in their metabolism, using either arsenate [As(V)] as a terminal electron acceptor in anaerobic respiration or generating energy by oxidation of arsenite [As(III)] during chemolithoautotrophic growth (Kruger et al. 2013).

The application of metal-resistant and plant growth promoting soil microbes as bioinoculants for supplying nutrients and/or stimulating plant growth are gaining momentum. These microbes have an extensive range of growth modes and are capable of growing, utilizing a variety of organic substrates. These properties make them ideal for the treatment of contaminated soils, assisting in possible remediation. Several rhizospheric metal-resistant microbes are also known to have plant growth promoting abilities, viz. nitrogen fixation, phosphate solubilization, and production of siderophores and phytohormones, suggesting their substantial role in As-biogeochemistry and bioremediation (Beneduzi et al. 2012; Bhattacharyya and Jha 2012; Gupta et al. 2015; Batool et al. 2017).

8.2 Microbial Diversity in Arsenic-Contaminated Ecosystems

Diverse microbial community exists in As-contaminated sites that can uptake and transform As in the environment (Banerjee et al. 2011; Sarkar et al. 2013; Ao et al. 2014). Although As is toxic to microbes, certain bacteria and fungi survive its exposure by developing As detoxification mechanisms that permit the cell to neutralize its toxic effects (Srivastava et al. 2011; Kruger et al. 2013). Countless native, As-resistant, phylogenetically diverse, and metabolically versatile bacteria and fungi have been isolated from varied habitats, including soil, water, and sediments, contaminated with high levels of As (Tables 8.1 and 8.2). Presence of As-resistant microbial species in the As-rich environment is highly expected since high levels of metallic species are likely to exert a strong selective pressure thereby reducing the overall growth of sensitive microbial population (Sarkar et al. 2013). This favors the survival of indigenous As-resistant microorganisms in the As-rich habitats (Pepi et al. 2007). Long-term association of microorganisms with toxic metal within metal-rich sites often promotes adaptation of the microbes in such environmental conditions (Banerjee et al. 2013; Majumder et al. 2013).

Microbial activities account direct effect on the bioavailability of As in soil, water, and sediments (Sarkar et al. 2013). Studies on the existence and dispersal of innate metal-tolerant microbial flora bear tremendous applicability in microbial bio-network to understand the degree of metal pollution of the ecosystem. Such potential microbes may be channelized not only in detecting environmental alterations but also in treating toxic substances. Development of advanced technologies involving complex microbial reactions is utmost important for the enhanced bioremediation of As-contaminated milieus (Kruger et al. 2013).

Table 8.1 Arsenic-resistant bacteria reported from As-contaminated ecosystems

Bacterial strain	Source	Contaminated site	References
Pseudomonas sp.	Soil	Karamy, Xinjiang, China	Karn et al. (2017)
Pseudomonas sp. HN2	Soil	Hunan, China	Zhang et al. (2016)
Exiguobacterium, Bacillus	Soil	Kaudikasa village, Chhattisgarh, India	Pandey and Bhatt (2015)
Acinetobacter, Pseudomonas, Psychrobacter, Alishewanella	Groundwater	Hetao Basin, Inner Mongolia, China	Li et al. (2015)
Pseudomonas, Flavobacterium, Brevundimonas, Polaromonas, Rhodococcus, Methyloversatilis, Methylotenera	Groundwater	Barasat and Chakdaha of Parganas and Nadia Districts, West Bengal, India	Paul et al. (2015)
Actinobacteria, Rhizobium Microbacterium, Pseudomonas	Groundwater	Barasat and Chakdaha areas of Parganas, West Bengal, India	Paul et al. (2014)
Lysinibacillus	Soil	Chuadanga District, Bangladesh	Rahman et al. (2014)
Brevundimonas, Acidovorax, Acinetobacter, Pseudomonas, Undibacterium, Bosea, Herbaspirillum, Bacillus, Rhodococcus, Ralstonia, Staphylococcus, Caulobacter, Rhizobiales	Groundwater	Assam, India	Ghosh and Sar (2013)
Pseudomonas	Sediment	Taiwan	Kao et al. (2013)
Actinobacteria, Agrobacterium Ochrobactrum, Rhizobium Brevundimonas	Groundwater	Kolsure village, West Bengal, India	Sarkar et al. (2013)
Micrococcus, Pseudomonas, Vibrio Bacillus	Water	Rautahat District, Nepal	Shakya et al. (2012)
Geobacillus kaustophilus strain A1	Soil	Metallifere Hills, Italy	Cuebas et al. (2011)
Bacillus idriensis, Sphingomonas desiccabilis	Soil	Beijing, China	Liu et al. (2011)
Acinetobacter, Agrobacterium, Arthrobacter, Comamonas, Rhodococcus, Stenotrophomonas, Pseudomonas	Soil	Tieshan District, Huangshi City, Hubei Province, Central China	Cai et al. (2009)

8.3 Mechanisms of Arsenic Resistance in Microorganisms

8.3.1 Bacteria

It is well established that a number of microorganisms possess metabolic mechanisms to resist the disruptive effects of As and to survive in its presence (Rosen 2002; Li et al. 2010). The greater part of As resistance and detoxification studies have been performed in bacteria, and their molecular mechanism has been elucidated precisely (Rahman and Hassler 2014). The strategies to manage or neutralize

Table 8.2 Arsenic-resistant fungi reported from arsenic-contaminated ecosystems

Microorganisms	Source	Contaminated site	References
Aspergillus oryzae, Fusarium sp., *A. nidulans, Rhizomucor variabilis, Emericella* sp.	Soil	Middle Indo-Gangetic Plains, India	Singh et al. (2015)
Penicillium coffeae	Soil	India	Bhargavi and Savitha (2014)
Aspergillus, Trichoderma Neocosmospora, Sordaria, Rhizopus, Penicillium	Soil	West Bengal, India	Srivastava et al. (2011)
Trichoderma asperellum SM-12F1, *Penicillium janthinellum* SM-12F4, *Fusarium oxysporum* CZ-8F1	Soil	Beijing, China	Su et al. (2011)
Aspergillus niger, A. clavatus, A. fischeri	Soil	Pezinok, Slovakia	Cernanský et al. (2009)
Neosartorya fischeri, *Talaromyces wortmannii*, *Talaromyces flavus*, *Eupenicillium cinnamopurpureum*	Sediment	Landsberg, Germany	Heinrich (2007)

As toxicity mainly include accumulation (Wang et al. 2013; Rahman et al. 2014), active extrusion of As, extracellular precipitation, complexation into peptides (Kruger et al. 2013; Kuramata et al. 2015), and As transformation including methylation, demethylation (Bentley and Chasteen 2002), oxidation, and reduction (Liao et al. 2011). Some bacteria even use As compounds to fuel their energy metabolism, either as an electron donor or as an electron acceptor (Silver and Phung 2005).

Of all the processes, enzymatic reduction of As(V) to As(III) mediated by the gene products of the widespread *ars* operon followed by efflux of As(III) from the cell is the most common one and is found in both gram positive and gram negative bacteria (Silver and Phung 2005; Vishnoi and Singh 2014). The As resistance gene systems which are responsible for the metabolism and detoxification of As may be found either in plasmids (Drewniak et al. 2013) or chromosomes (Bhat et al. 2011).

8.3.1.1 Arsenic Uptake Systems

Pathways for uptake of As into bacterial cells have only recently been discovered. The most common and abundantly existing forms of As oxyanions, arsenate and arsenite, use uptake systems that transport these compounds into cells (Fig. 8.1). Arsenate is a substrate analogue of phosphate and is taken up via the phosphate transporters by most of the organisms (Rosen 2002). Two phosphate transporters, *Pit* and *Pst*, have been identified in different bacterial groups, both of which catalyze As(V) uptake. Of the two transporters, *Pit* is the major transport system (Tsai et al. 2009).

Arsenite shows very strong similarity with the conformation of glycerol and is adventitiously taken up by a trivalent metalloid transporter identified as *GlpF* (Rosen and Liu 2009; Tsai et al. 2009) (Fig. 8.1). Transporter GlpF is an aquaglyceroporin and a member of the major intrinsic protein (MIP) superfamily that allows the transport of water and small solutes such as glycerol and urea by an energy-independent mechanism (Rosen 2002).

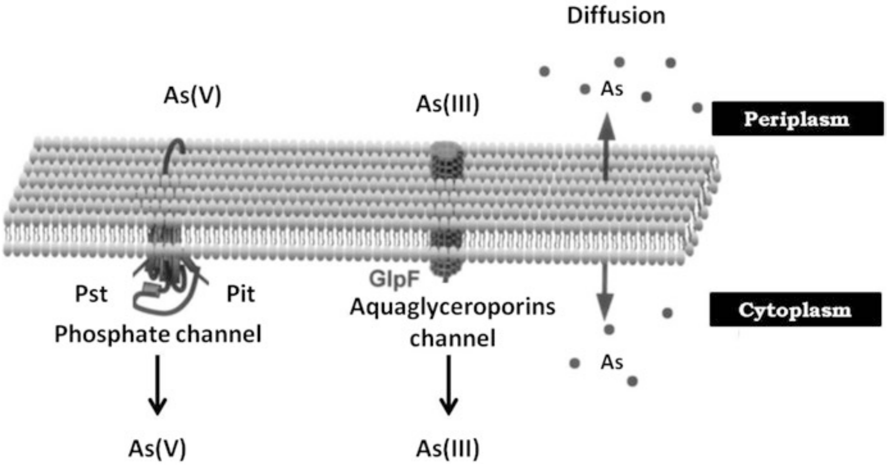

Fig. 8.1 Transporters for arsenic uptake in bacteria

8.3.1.2 Arsenate Reduction: Detoxification

A wide range of microorganisms have evolved As resistance mechanisms to survive in As-contaminated environments (Tsai et al. 2009; Nagvenkar and Ramaiah 2010). One such process involves the reduction of As(V), which has the purpose of detoxification by converting As(V) to As(III) (Páez-Espino et al. 2009). Microorganisms combat the importation of As(V) by a two-step mechanism in which this compound is first reduced to As(III) by a cytoplasmic As(V) reductase (Rosen 2002). Although As(III) is a more potent toxicant than As(V), the former is selectively expelled from the interior of the cell via membrane efflux pump (Mateos et al. 2006).

8.3.1.3 Arsenate Reduction: Energy Generation

In addition to the detoxification of As(V), certain bacteria can reduce As(V) as the terminal electron acceptor during anaerobic respiration for generating energy (Hudson-Edwards and Santini 2013; Kruger et al. 2013). These are defined as dissimilatory As(V)-respiring bacteria (Oremland and Stolz 2005), in which respiration is recognized to be mediated by a specific enzyme or respiratory chains (Silver and Phung 2005). Arsenic respiration can influence both the speciation of As and its mobility. Dissimilatory As(V)-respiring bacteria are able to reduce both sorbed and dissolved As(V) to As(III) coupled to As(III) efflux systems, presumably because the enzymes responsible for As(V) reduction are located in the periplasmic membrane (Silver and Phung 2005).

8.3.1.4 Arsenite Oxidation: Detoxification and Energy Generation

Bacterial oxidation of As(III) to As(V) is very well documented, particularly with isolates from As-impacted environments (Bahar et al. 2012). Many heterotrophic bacteria oxidize As(III) to As(V) to speedily detoxify their surroundings, while others use As(III) as an electron donor. Over 30 strains representing at least 9 genera of As-oxidizing prokaryotes have been reported (Stolz et al. 2002). The transformation reaction involving the energy gain by conversion of more toxic As(III) into less toxic As(V) has increased the ecological significance of these bacteria over other microorganisms. Since As(V) is less soluble and is much more effectively removed by physicochemical methods, oxidation of As(III) can be important for As removal (Tsai et al. 2009).

8.3.1.5 Methylation

Methylation was formerly thought to be a detoxification step; however, recent information suggests that not all methylated As products are less toxic (Páez-Espino et al. 2009). Methylation process produces both volatile and nonvolatile methylated compounds of As (Qin et al. 2006). The major volatile methylated As compounds are mono-, di-, and trimethylarsine, while the major nonvolatile compounds are methylarsonate and dimethylarsinate (Fig. 8.2).

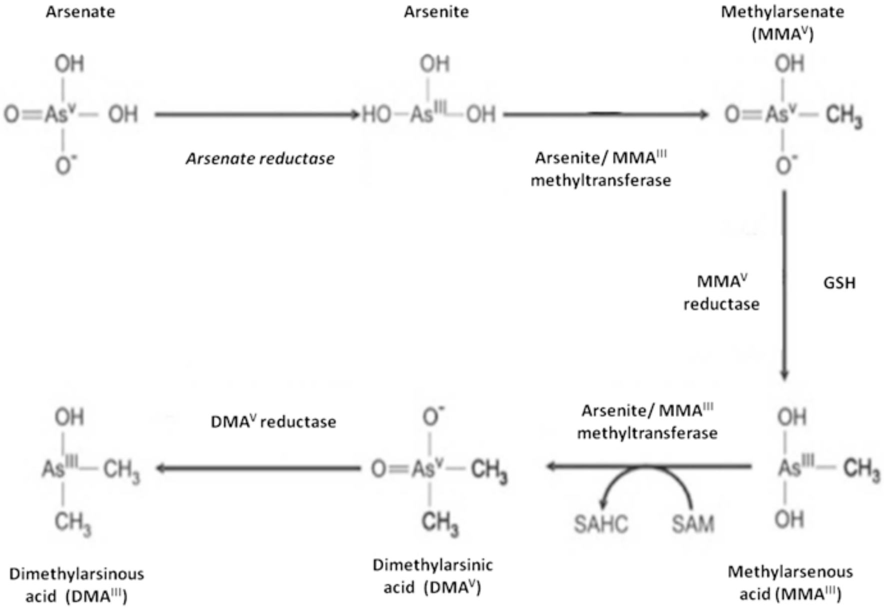

Fig. 8.2 Bacterial methylation of arsenic

The methylation reaction follows the reduction of As(V) and subsequent oxidative addition of methyl groups, thus generating arsines and methyl arsenicals (Páez-Espino et al. 2009; Kruger et al. 2013). The volatile methylated forms of As are readily released into the environment where oxidation might convert them back to the oxidized form, As(V). A variety of microorganisms have been implicated as the major contributors of As methylation (Wang et al. 2015) and are included in the genera: *E. Coli* (Yuan et al. 2008), *Pseudomonas* (Chen et al. 2014), *Streptomyces* (Kuramata et al. 2015), and *Clostridium* (Wang et al. 2015). Understanding of these mechanisms will not only shed light on the As mobilization but may also open up new horizons in metabolic pathway engineering to exploit those for As remediation (Huang et al. 2015).

8.3.2 Yeast and Fungi

Arsenate [As(V)/$H_2AsO_4^-$] is a chemical analogue of phosphate and hence gets transported by high-affinity phosphate uptake system Pho87. Moreover, As(III) (H_3AsO_3) is not a phosphate analog and therefore is transported into the cell either through *GlpF* or passive diffusion (Sharples et al. 2000). Although the mechanisms of As detoxification remain unstudied in fungi, several pathways mediating detoxification of As have been elucidated in the yeast *Saccharomyces cerevisiae*. It is now an established fact that the most common mechanism of resistance in yeast is mediated by the products of three adjacent genes *ACR1*, *ACR2*, and *ACR3*. The putative product of the *ACR1* gene showed similarity with the yeast transcriptional regulatory proteins, encoded by *YAP1* and *YAP2* genes. Gene *ACR2* encodes arsenate reductase enzyme which is known to mediate a rapid internal reduction of As(V) to As(III), which then initiates efflux of As(III) from the hyphae (Mukhopadhyay et al. 2000). Reduction of As(V) to As(III) is also mediated by *P37* in species like *Aspergillus*; however, it does not methylate As to any significant extent (Ca'novas et al. 2004).

Arsenite efflux has As(V) resistance in *S. cerevisiae* and many other fungi and is mediated by an As(III) transporter gene *ACR3*. Likewise, *ACR3* encodes a putative plasma membrane As(III) efflux transporter protein that pumps As(III) out of the cell, whose expression is strongly induced by the presence of both As(III) and As(V) (Wysocki et al. 1997). In addition, conjugation of As(III) with glutathione by *GstA* and its subsequent transport into vacuoles by an *ABC* metal ion transporter is also one of the methods of detoxification. Moreover, biovolatilization via methylation by *Cyt19* for detoxification purposes has been further proposed to increase As resistance in fungi (Ghosh et al. 1999; Choe et al. 2012).

8.4 Influence of Microorganisms on the Speciation and Bioavailability of Arsenic

The accumulation of different As species in various ecosystem compartments is regulated by different microbial processes. Microorganisms play an important role in the speciation and cycling of environmental As with a variety of mechanisms affecting As transformation between soluble and insoluble forms. Although As is highly toxic to most of the life forms, some microorganisms have developed As resistance mechanisms while some even thrive on the metalloid, using it as a source of energy for growth (Wang et al. 2011; Kruger et al. 2013). The actual state of As strongly depends on microbial transformations in soils, including reduction, oxidation, and methylation processes. Microbial enzymatic activities catalyze the conversion of the As species into forms having a different solubility, mobility, bioavailability, and toxicity (Lièvremont et al. 2009). The inorganic As forms, especially As(V) and As(III), are subjected to microbiologically mediated oxidation-reduction reactions. Microbes could even derive metabolic energy by the oxidation of As(III) or could use it as the sole energy source. Arsenate, on the other hand, is reduced by dissimilatory reduction and utilized as a terminal electron acceptor for anaerobic respiration. In addition, microorganisms may possess As(V) reduction mechanisms that are not coupled to respiration but instead are thought to impart As resistance. The detoxifying reductases present in the cytoplasm reduce As(V) to As(III) for its rapid extrusion from the cell. Even microbes capable of both As(III) oxidation and As(V) reduction are recognized (Pandey and Bhatt 2016). Soil microbes are also able to biomethylate inorganic arsenicals to monomethyl arsenic acid (MMAA) and dimethylarsenic acid (DMAA), and to other organic arsenicals (e.g., arsenocholine, arsenobetaine, arsenosugars, arsenolipids). The organo arsenicals are further metabolized to complete the As cycle (Dhuldhaj et al. 2013). In contrast, demethylating microorganisms carry out the conversion of methylated As species back to inorganic forms. Further, microbial activity can also methylate As(III) resulting in volatilization of As to gaseous arsines, viz. trimethylarsine gas, thereby releasing As into the atmosphere (Islam et al. 2007). Arsines are toxins which may travel in air for indefinite time period, or they may be rapidly oxidized subject to environmental conditions. Oxidation again yields inorganic As species, As(V) or As(III), or organic forms, MMAA and DMAA, which are deposited back to the soil by rain or by dry deposition, thereby completing the cycle of As.

8.5 Plant Growth Promoting Microorganisms

The plant health and soil fertility are the determinants of beneficial plant-microbe interactions in the rhizosphere which play a pivotal role in transformation, mobilization, solubilization, and subsequent uptake of essential nutrients by the plants (Dey et al. 2004). Despite the long history of interest in As-resistant plants and microbes, the attention of microbiologists toward plant-associated bacteria from heavy metal enriched habitats is more recent (Sessitsch et al. 2013). It has been well established that the soil hosts a large number of microbes, including bacteria and fungi. The microbial count of different soils is subjective to the soil conditions including temperature, pH, moisture, salinity, and presence of other chemicals, as well as by the type of vegetation of that area. There is a huge diversity of soil microbial communities which is exceptionally rich and has developed diverse As resistance and detoxification mechanisms thereby redistributing As in soil (Sheik et al. 2012). Soil microorganisms affect As mobility and availability to the plant; they produce iron chelators and siderophores, solubilize metal phosphates, and produce growth hormones (Cavalca et al. 2010). Numerous metal-resistant microbes could transform As compounds by oxidation, reduction, methylation, and demethylation (Stolz et al. 2002) and are known to promote plant growth by direct and/or indirect mechanisms (Rajkumar et al. 2012). They act as a barrier and limit the transfer of As into plant tissues, thereby improving growth of the host plant (Fitz and Wenzel 2002). These microbes may prove beneficial for the revegetation and phytostabilization of As polluted sites. Thus, the need of the hour is to enhance the efficiency of the beneficial microbes for sustainable agricultural production (Khan 2005).

8.5.1 Rhizobacteria

The beneficial, free-living bacteria that colonize roots and establish a symbiotic relationship with plants to promote growth are referred to as plant growth-promoting rhizobacteria (PGPR). The abundance of bacteria in the rhizosphere is because of the presence of nutrients including sugars, amino acids, organic acids, and other small molecules released from plant root exudates (Gupta et al. 2015). While only 1–2% of bacteria promote plant growth in the rhizosphere, even lesser is known about the heavy metal–resistant PGPR. Additionally, it is also recognized that PGPR unwilling As are widespread in nature and are phylogenetically diverse (Table 8.3). They can have the advantages of oxidizing/reducing As and promoting plant growth in As stressed soil (Das et al. 2016). Moreover, it is now an accepted fact that the bacterial inoculation significantly reduces As uptake and its accumulation in shoot and grains of many plant species. Owing to its wide action spectrum, the As-resistant PGPR could serve as a potential bioinoculant for mitigation of As in different plants, thereby contributing to sustainable crop production in As-contaminated areas (Bhattacharyya and Jha 2012).

Plant growth promoting rhizobacteria are broadly categorized into extracellular plant growth promoting rhizobacteria (ePGPR) and intracellular plant growth promoting rhizobacteria (iPGPR) (Viveros et al. 2010). These rhizobacteria effect plant growth either directly or indirectly, even in As stressed soils. The direct effect on plant growth is facilitated by the production of phytohormones (e.g., IAA), antibiotics, inorganic phosphate solubilization, increased production of iron-chelating siderophores, ammonia, and exopolysaccharides, thereby stimulating many important pathways (Fig. 8.3). However, their indirect effects can occur by antibiosis, synthesis of hydrolytic enzymes, struggle for the availability of nutrients with pathogenic bacteria

Table 8.3 Arsenic-resistant and plant growth promoting rhizobacteria

Bacterial class	Beneficiary plant	Mechanism	References
Rhodopseudomonas palustris CS2, *Rhodopseudomonas faecalis* SS5	*Vigna mungo*	As transformation and plant growth promotion	Batool et al. (2017)
Klebsiella pneumoniae T22, *Klebsiella oxytoca* N53, *Bacillus subtilis* T23, *Acinetobacter lwoffii* T24, and *Citrobacter freundii* N52	*Triticum aestivum*	As(III) oxidation and plant growth promotion	Qamar et al. (2017)
Rhizobium radiobacter strain VBCK1062	*V. radiata*	Production of exopolysaccharide (EPS) and As(V) sequestration	Deepika et al. (2016)
Brevundimonas diminuta	*Oryza sativa*	Phytostabilization of As	Singh et al. (2016)
Bacillus flexus ASO6	*O. sativa*	As oxidation and plant growth promotion	Das et al. (2016)
Streptomyces sp.	*O. sativa*	As methylation	Kuramata et al. (2015)
Pseudomonas sp. P1III2, *Delftia* sp. P2III5, *Bacillus* sp. MPV12, *Variovorax* sp. P4III4, *Pseudoxanthomonas* sp. P4V6	*Pteris vittata*	As removal and production of siderophore and indoleacetic acid (IAA)	Lampis et al. (2015)
Pantoea sp. strain (EA106)	*O. sativa*	As oxidation and plant growth promotion	Lakshmanan et al. (2015)
Bacillus flexus ASO-6	*O. sativa*	Production of siderophore, IAA, 1-aminocyclopropane-1 carboxylic acid (ACC)-deaminase and solubilization of phosphate, improved seed germination, and reduced As accumulation in grains	Das et al. (2015)
Pseudomonas fluorescens	*Solanum lycopersicum*	Phosphate solubilization and siderophore production	Ghosh et al. (2015)
Brevibacterium, Rahnella, Pseudomonas, Rhodococcus, Microbacterium, Paenibacillus	*Zea mays*	As oxidation, production of siderophore, IAA, ACC-deaminase, and solubilization of phosphate	Shagol et al. (2014)
Alcaligenes sp.	*Helianthus annuus*	Production of ACC- deaminase, siderophore, and IAA	Cavalca et al. (2013)
Staphylococcus arlettae strain NBRIEAG-6	*Brassica juncea* (L.) Czern. Var. R-46	Production of IAA, siderophores, and ACC- deaminase	Srivastava et al. (2013)

(continued)

Table 8.3 (continued)

Bacterial class	Beneficiary plant	Mechanism	References
Pseudomonas, Comamonas, Stenotrophomonas	*Pteris vittata*	As solubilization	Ghosh et al. (2011)
Bacillus, Achromobacter, Brevundimonas, Microbacterium, Ochrobactrum	*Cirsium arvense* (L.)	As oxidation and plant growth promotion	Cavalca et al. (2010)

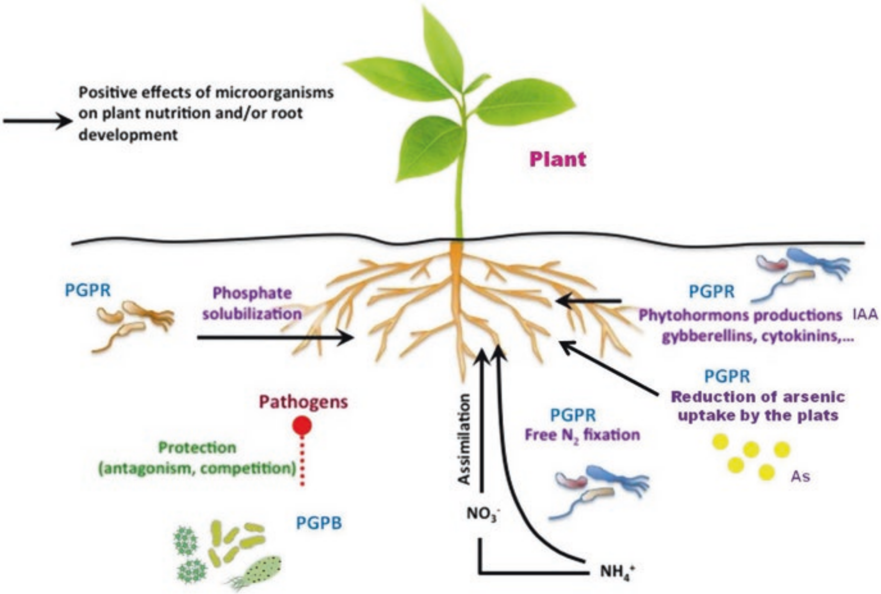

Fig. 8.3 Beneficial effects of metal-resistant and plant growth promoting bacteria

in soil, or by inducing systemic resistance (ISR) against wide-ranging root pathogens in the rhizosphere. Out of the many resistance mechanisms acquired by rhizobacteria, salicylic acid-dependent SAR pathway or jasmonic acid and ethylene perception from the plant are the most evident ones (Beneduzi et al. 2012). Arsenic-resistant PGPR's might be useful in framing new amalgamations, leading to a more efficient use for phytostabilization and improvement of cropping systems (Gupta et al. 2015).

8.5.2 Arbuscular Mycorrhizal Fungi

Arbuscular mycorrhizal fungi (AMF) are ubiquitous in nature and establish important symbiotic relationships with most terrestrial plants even in heavy metal–contaminated environments (Sun et al. 2016). Moreover, plant compatibility with mycorrhizal fungi is a generalized and primordial phenomenon. Arbuscular mycorrhizas are characterized by the formation of highly branched and unique structures called arbuscules, which help plants to capture nutrients such as phosphorus, carbon, sulfur, nitrogen, and other micronutrients from soil (Gianinazzi-Pearson 1996).

However, AMF are widespread in different regions of the world; they are influenced by As concentrations and seasonal variations. A variety of species have been identified, belonging to the genus *Acaulospora*, *Glomus*, *Gigaspora*, *Westerdykella*, *Trichoderma*, *Rhizopus*, *Lasiodiplodia*, *Paraglomus*, *Rhizophagus*, etc. (Table 8.4). Arbuscular mycorrhizal fungi belonging to the phylum *Glomeromycota* form a symbiotic association with more than 80% of terrestrial plants. The predominance

Table 8.4 Arsenic-resistant and plant growth promoting fungi

Fungi	Beneficiary plant	Mechanism	References
Acaulospora morrowiae, Rhizophagus clarus, Gigaspora albida, Paraglomus occultum	*Leucaena leucocephala*	As phytostabilization	Schneider et al. (2017)
Rhizoglomus intraradices and *Glomus etunicatum*	*T. aestivum*	Reduced translocation of As to grains, and higher activities of the antioxidant enzymes	Sharma et al. (2017)
Aspergillus oryzae, Fusarium sp., *Aspergillus nidulans, Rhizomucor variabilis, Emericella* sp.	*Calendula, Withania,* and *Avena sativa* plants	As bioaccumulation and biovolatilization	Singh et al. (2015)
Glomus etunicatum, Acaulospora morrowiae, Gigaspora gigantea, Acaulospora sp.	*Acacia mangium, Crotalaria juncea, Enterolobium contortisiliquum, Stizolobium aterrimum*	Phytoprotective effect and phytoremediation of As contaminated soil	de Melo et al. (2014)
Acaulospora morrowiae, Glomus clarum, Gigaspora albida	*L. leucocephala*	As removal from the soil and phytoextraction	Schneider et al. (2013b)
Westerdykella, Trichoderma, Rhizopus, Lasiodiplodia	*O. sativa* and *Pisum sativum*	Improved soil nutrient content and enhanced plant growth	Srivastava et al. (2012)
Glomus mosseae, Glomus intraradices, Glomus etunicatum	*Pityrogramma calomelanos, Tagetes erecta, Melastoma malabathricum*	Improved growth and As accumulation	Jankong and Visoottiviseth (2008)
Glomus mosseae	*S. lycopersicum, Medicago sativa Linn., Z. mays* L., *M. truncatula*	Enhancing phosphorus nutrition and restricting root As uptake	Liu et al. (2005); Chen et al. (2007); Xia et al. (2007); Xu et al. (2008)

of these species indicates their high tolerance to excess As; nevertheless, As contamination adversely affects the diversity and function of AMF (Schneider et al. 2013a; Sun et al. 2016). Dominant plant species present in As-contaminated sites are habitually colonized by AMF, which is indicative of their central role in mitigating heavy metal stress in plants. Arbuscular mycorrhizal fungi improve the tolerance of host plants to As in contaminated soils by performing two different roles in phytoremediation: one being phytoextraction and another phytostabilization (de Melo et al. 2014; Krishnamoorthy et al. 2015).

8.6 Plant Growth Promoting Microorganisms in Extenuating Arsenic Toxicity

8.6.1 Precipitation, Binding, or Chelation of Arsenic in the Rhizosphere

The biochemical and molecular mechanisms of plant-microbe interactions in As stressed soils can change metal bioavailability in soil through various mechanisms such as acidification, precipitation, chelation, complexation, and redox reactions. The microbial activities are known to enhance the mobility of metals by forming metal/mineral complexes, intracellular binding, electron transfer by enzymes in the rhizosphere (redox reactions), etc. The microbes present in the As-contaminated soils have evolved resistance strategies to tolerate considerably high concentrations of metals. The extensive research on the metal-resistant PGPM have shown many possibilities to improve plant growth by alleviating metal toxicity, and improving restoration by mobilization/transformation of metals in soil (Rajkumar et al. 2012; Tak et al. 2013; Ma et al. 2016).

8.6.2 Root Colonization

Rhizobacteria provide nutrients to the plant by habituating the soil surrounding the roots of the beneficiary plant. In turn, the plant creates and maintains root nodules for rhizobacteria, thereby providing a proper place and conditions for the bacteria to be alive and active. This colonization makes the soil, surrounding the plant, more rich in terms of nutrients. The effectiveness of PGPR has often been attributed to their ability to colonize plant roots. Bacterial colonization into plant roots is a series of a process involving various steps. It defines the ability of the bacteria to survive and multiply in the region surrounding the roots in response to the plant exudates, to attach with the root surface, and to colonize developing a root system. There could be multifactorial phenomenon contributing the process of colonization, viz. chemotaxis to root exudates, cell motility, production of pili or fimbriae, quorum sensing, etc. (Ma et al. 2016).

In case of AMF, the process of colonization takes place in a way different to that in bacteria. The plant-microbe interaction starts with the signal exchange and recognition between host plants and AMF before they come into physical contact. Signal recognition has been proposed to help in cellular adaptation in fungi required for the functional compatibility between the plant and fungal cells. This finely tuned recognition processes help in establishing molecular coordination between the two. The recognition signal from the host plant helps in inducing hyphal branching followed by the formation of appressoria at the root surface during the early hours of contact. Metabolites exuded by plant roots specifically enhance spore germination and fungal growth which helps the fungus to invade the root. Fungal development is limited to the outer root tissues, while hyphae quickly enter the inner cortical cells of host plant where they differentiate into the highly ramified arbuscules (Gianinazzi-Pearson 1996).

This proves that the successful colonization forms an important part of the plant-microbe relationship. It not only helps in the exchange of nutrients but also limits the uptake of harmful chemicals and heavy metals like As to the plant tissues and prevents the rate and extent of pathogen colonization in roots, thereby helping the plants to grow and propagate at high concentrations of As (Jog et al. 2014; Mallick et al. 2014).

8.6.3 Facilitating Resource Acquisition

8.6.3.1 Nitrogen Fixation

Nitrogen is an imperative nutrient to all life forms; however, gaseous nitrogen remains unavailable to the plants due to the high energy required to break the triple bonds present between the two atoms. Rhizobacteria, through nitrogen fixation, are able to convert gaseous nitrogen to ammonia, and making it available to the host plant (Ullah and Bano 2015). This is one of the most mutualistic relationships between a microbe and the plant taking place in soil, where the host plant provides the bacteria with amino acids for the production of ammonia. The enzyme involved in the process of nitrogen fixation is called nitrogenase, while the oxygen is provided by a protein called leghemoglobin, which is produced within the nodules (Vejan et al. 2016). A wide range of PGPR is present in nature and belongs to the genera: *Rhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Bradyrhizobium*, and *Frankia* (Masson-Boivin et al. 2009). Although the presence of As adversely affects the process of biological nitrogen fixation, the As-resistant microbes have all managed to cope up with such extreme conditions, hence providing the plants with the requited nitrogen even in the presence of As.

8.6.3.2 Phosphate Solubilization

Plant growth promoting rhizobacteria solubilize insoluble phosphorus in the soil and increase the accessibility of unavailable nutrients to plants. Phosphorus, a key element required for the nutrition of plants, is abundantly present in soil, but its insoluble nature makes it inaccessible to plants. The two soluble forms of phosphate, i.e., monobasic ($H_2PO_4^-$) and diabasic (HPO_4^-) ions, are readily absorbed by the plants. Rhizobacteria may employ one of the following mechanisms to facilitate the conversion of insoluble forms of phosphorus to soluble forms: release of compounds, for example, organic acid anions to dissolve minerals; production of extracellular enzymes like phosphatases for phosphate solubilization; release of phosphate during substrate degradation, etc. (Kumar et al. 2010). Phosphate solubilizing rhizobacteria are included in the *genera Rhodococcus*, *Bacillus*, *Serratia*, *Erwinia*, *Flavobacterium*, *Arthrobacter*, *Pseudomonas*, *Beijerinckia*, *Burkholderia*, *Microbacterium*, *Rhizobium*, and *Enterobacter*, and are extensively studied to improve plant growth and yield responses. Further, the application of phosphate solubilizing bacteria has also been reported to show many beneficial effects when employed with other metal-resistant rhizospheric microbes for the increased productivity and stability of plants in contaminated soils (Tian et al. 2014).

8.6.3.3 Siderophore Production

The plant's nutritional requirements of iron are satisfied by specific microorganisms which have evolved precise pathways that employ low molecular weight iron chelators termed siderophores. Siderophores are small peptidic molecules secreted to solubilize iron from their surrounding environments, forming a complex called ferric-siderophore that can move by diffusion (Glick 2012). Siderophores can chelate ferric ion with high affinity, allowing its solubilization and extraction from most mineral or organic complexes. In soil, siderophore production activity plays a central role in determining the ability of different microorganisms to improve plant development (Arora et al. 2013). Microbial siderophores enhance iron uptake by plants that are able to recognize the bacterial ferric-siderophore complex. The highly competitive conditions in the root environment help the plants to selectively use iron for their growth. Siderophore-forming microbes also selectively inhibit the growth of other soil-borne fungal and bacterial pathogens through the release of iron-chelating substances (Dwivedi and Johri 2003). Siderophore-producing bacteria have been extensively studied belonging to the genera *Bradyrhizobium*, *Pseudomonas*, *Rhizobium*, *Serratia*, and *Streptomyces* (Sujatha and Ammani 2013). Siderophore-producing metal-resistant microbes are also identified which serve a dual role in soil; they are actively engaged in providing nutrients and helping the plants to survive in heavy metal–contaminated soil (Wani and Khan 2013).

8.6.4 Modulating Phytohormones

A wide range of microorganisms has been found in the rhizosphere which is capable of producing plant growth regulating substances. Plant growth promoting microorganisms produce phytohormones such as auxin(s), cytokinin(s), gibberellin(s), and ethylene, which affect cell proliferation with a subsequent increase in nutrient and water uptake.

8.6.4.1 Cytokinin

Several PGPMs of the genera *Azotobacter*, *Rhizobium*, *Rhodospirillum*, *Pseudomonas*, *Bacillus*, and *Paenibacillus* are known which can produce cytokinins (Glick 2012). However, a detailed understanding of the role of bacterial-synthesized hormones is still unclear; it is believed to provide exogenous and purified hormones to growing plants.

8.6.4.2 Gibberellin

Gibberellin is another hormone actively engaged in regulating plant growth and influencing various developmental processes including stem elongation, germination, dormancy breaking, flowering, sex expression, enzyme induction, and leaf and fruit senescence. Many bacterial species have been identified contributing to the production of this hormone in the soil, thereby promoting plant growth (Glick 2012).

8.6.4.3 Auxin

Although several naturally occurring plant growth regulators, indole-3-acetic acid (IAA) is by far the most common as well as the most studied auxin and much of the scientific concern, exerting a positive effect on root growth. It is evident that up to 80% of root colonizing rhizobacteria can synthesize IAA to stimulate cell proliferation and enhance the uptake of minerals and nutrients from the soil (Gupta et al. 2015). Indole-3-acetic acid not only affects plant cell division, extension, and differentiation but also provides resistance to stressful conditions. An array of metabolically active PGPRs like *Pseudomonas*, *Rhizobium*, *Bradyrhizobium*, *Agrobacterium*, *Enterobacter*, and *Klebsiella* are known to promote root growth in various plant species (Shilev 2013).

8.6.4.4 Ethylene

Ethylene is a key phytohormone having a wide range of biological activities. It affects plant growth and development by promoting root initiation, fruit ripening, seed germination, leaf abscission, and synthesis of other plant hormones, while inhibiting root elongation and wilting (Glick et al. 2007). The enzyme ACC is a prerequisite for ethylene production which is reported to improve dry weight, grain yield, straw production, and nitrogen content in different plant species (Glick 2012; Gupta et al. 2015). Currently, bacterial strains exhibiting ACC deaminase activity have been identified in a wide range of genera such as *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia*, and *Rhizobium* (Kang et al. 2010).

8.6.5 Reducing Oxidative Stress/ Improving Antioxidant Potential

Arsenic induces toxicity in plants that has been linked to the production of reactive oxygen species (ROS), thereby inducing lipid peroxidation and damage to nucleic acids and proteins (Aksakal and Esim 2015; Chandrakar et al. 2016; Chandrakar et al. 2017). Production of ROS in plants is regulated by antioxidative enzymes which remove free radicals thereby protecting the cells from oxidative damage. In the presence of metal-resistant PGPM, the oxidative stress decreases to a considerable level, owing to the reduced uptake of As, thereby balancing the levels of antioxidative enzymes required in the cell (Mishra et al. 2013; Talukdar and Talukdar 2013).

8.6.6 Induced Systemic Resistance

Plant growth promoting microorganisms are capable of controlling diseases that are caused by inhabiting pathogenic bacteria and fungi. The disease is suppressed through Induced Systemic Resistance (ISR) against a broad spectrum of plant pathogens and the production of antibacterial/antifungal metabolites. The production of antibiotics is considered to be one of the most powerful and studied biocontrol mechanisms of PGPR against phytopathogens. The microbial metabolites produced in the rhizosphere help in the reduction of diseases of fungal, bacterial, and/or viral origin, and in some instances even damage caused by insects and nematodes (Choudhary et al. 2007). Beneficial microbes also induce signaling pathways within the plant to stimulate the production of hormones involved in plants defense responses against a variety of pathogens (Haas et al. 2002). A number of bacterial components like lipopolysaccharides (LPS), siderophores, cyclic lipopeptides, and some volatiles are known to encourage ISR, which have now been commercialized to increase the resistance of host plant (Ongena et al. 2004; Ryu et al. 2004). This has led to the genetic modification of many bacterial strains to develop as a bioinoculant to improve plant growth and disease resistance of agricultural crops.

8.6.7 Reducing Arsenic Absorption and Translocation

Metal-resistant PGPR and AMF, particularly those isolated from metalliferous sites, are capable of boosting plant growth by reducing As absorption, changing available As through alteration of soil pH, and by affecting As translocation (Rajkumar et al. 2012). Moreover, As accumulation in plant tissues is more likely to be associated with the availability of As in the soil. The presence of microbial population is known to significantly decrease the uptake and accumulation of As in plant tissues even in the As rich soil, may be due to the microbial uptake of a metalloid. It is well established that the presence of the beneficial bacteria/fungi not only colonizes the roots of the plants but also decreases the uptake of As in tissues, thereby helping the plants to grow and propagate at high concentrations of As (Wani and Khan 2013; Mallick et al. 2014; Selamat et al. 2014).

8.6.8 Enhancing Plant Growth and Biomass

Certain bacterial strains synthesize a wide spectrum of multifunctional exopolysaccharide (EPS) in response to the heavy metals. Exopolysaccharide is a mode of protecting bacteria from desiccation, environmental stress, and plant defense responses in plant-microbe interactions (Limoli et al. 2015). This class of polysaccharide also helps plants to flourish in As stressed soil in many different ways. Production of EPS is known to assist in biofilm formation, attachment to plant surface, root colonization, holding free phosphorus in soils, cation binding including Na^+, circulating essential nutrients to the plant for proper growth and development, and protecting it from the attack of foreign pathogens (Vu et al. 2009; Gupta et al. 2015). This indicates the importance of PGPR producing EPS in promoting plant growth and biomass production by establishing beneficial interactions, satisfying environmental stress. and providing defense response during the infection process.

8.6.9 Improving Plant Establishment in Contaminated Soils

The association of As-resistant PGPMs with the roots opens new ways in securing the host plant not only against As but also from the deleterious effects of other cross contaminating heavy metals. The metal-resistant systems in bacteria/fungi enable them to limit the availability of metals to plants by producing and transporting inorganic phosphate and other growth-promoting substances from the soil. Further, the efflux of As from the host plant is absorbed by the microbes residing in the roots, thereby ensures reabsorption of As decreasing the overall metal concentration of the soil. The AMF may also act as a filter to maintain low plant As levels while maintaining an adequate supply of phosphorus to the host (Liu et al. 2005; Chen et al. 2007; Xia et al. 2007; Xu et al. 2008).

8.7 Microbial Technologies for the Alleviation of Arsenic Effects in Plants

8.7.1 Enzyme Technology

Among biological agents, enzymes have a great potential to effectively transform and detoxify environmental pollutants (Rao et al. 2010). Biocatalysts may serve as an alternate method for As remediation, and recently, there has been increasing interest in their potential applications. Enzymes could provide a more specific and clean way of dealing with the toxic metalloid, As (Dhankher et al. 2002; Bahar et al. 2012). Many microorganisms are known to produce enzymes involved in As detoxification, which could be successfully extracted and used for the remediation purposes. Enzymes in their immobilized forms are drawing significant attention for potential applications in As removal due to the reducing operational expenses and the increased process utilization of the enzymes (Talat et al. 2009). Typically, immobilized enzymes have greater thermal and operational stability at various pH values, ionic strengths and are more resistant to denaturation than the soluble native form of the enzyme (Bayramoglu et al. 2013). Similarly, immobilized biocatalyst displays the property of recycling and offer continued activity and stability for being reused many times (Eş et al. 2015).

However, the use of nanoparticle as supporting material for immobilized enzymes of microbial origin is drawing great attention to other materials. It provides many advantages such as the higher surface area that allows greater enzyme loading, higher stability and lower mass transfer resistance (Ho et al. 2008; Ansari and Husain 2012). The selectivity and increased activity of the immobilized enzymes could be utilized on a large scale for the improved As removal from soil and treatment process.

8.7.2 Genetic Engineering

The severity of the As contamination had raised an alarming situation demanding immediate attention and novel methods of remediation. The method of genetic engineering could be a potential strategy to overcome the drawbacks of this toxic metalloid. Many studies have been undertaken for the improvement of As methylation and detoxification abilities of the microbes by successful expression of the target gene (Qin et al. 2006; Yuan et al. 2008; Chen et al. 2014; Huang et al. 2015). These recombinant bacteria had 10-fold increase in response and resistance toward As and showed the successful transformation of inorganic As into less toxic organoarsenicals when compared to wild-type strains (Liu et al. 2011). This demonstrates the potential application of genetically engineered microorganisms as an efficient strategy for As bioremediation from contaminated soil (Liu et al. 2011), thereby reducing its translocation and accumulation in food stuff (Chen et al. 2013).

8.8 Conclusions and Prospects

The uniqueness of microorganisms and their often unpredictable nature and biosynthetic competences have made them promising candidates for solving As stress in different plant species. The conscientious use of indigenous microorganisms with the advanced technologies and modern techniques would attract economic, social, and environmental benefits which would provide an efficient way to protect the ecosystem. Microbial populations are known to affect As mobility and availability to the plant and therefore have potential to enhance phytoremediation processes. The advances in exploring and utilizing the significance of As-resistant rhizobacteria and AMF would be the simplest phenomenon to protect crops from As, as they may prevent the transport of As from root to shoot, thereby decreasing its uptake by plants. There is an urgent need to improve our understanding of the mechanisms involved in the transfer and mobilization of As by PGPRs and AMF, and to conduct research on the selection of microbial isolates from the rhizosphere of plants growing on As-contaminated soils for specific restoration programs.

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