

Chapter 9

Role of Plant-Microorganism Interactions in Plant Tolerance to Arsenic



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Abstract In this chapter, the review of the newest reports on plant-microbe interactions in plant tolerance to arsenic (As) is presented in two aspects. One is the bacteria effect on regulation of As availability in growth environment of the plant, and the second is direct influence of them on plant organism tolerance to As. The role of As oxidization or reduction mechanisms which were developed by microbes colonizing soil or water in plant tolerance to As is discussed. The meaning of rhizospheric bacteria contribution to bioavailability of elements such as phosphorus, iron, silicon or As, by mineral solubilization, as well as the significance of the bacteria siderophores in plant As tolerance is also explained. As and Fe released from iron(III) arsenate by symbiotic bacteria of As-hyperaccumulator fern, *Pteris vittata*, are not omitted. The role of As-resistant representatives of plant growth-promoting bacteria (PGPB) group in the reduction of As uptake by plants from contaminated soil is also described. Considering novel aspects of plant-microbe interactions under As stress, the content of this chapter refines previous knowledge about plant physiology in terms of As tolerance and in the field of As-resistant plant-microbe model application in environment remediation.

Keywords Metalloids · Phytoremediation · Plant-microbe interaction · *Pteris vittata* · Soil pollution

9.1 Introduction

In the environment, besides herbivores, plants are exposed to different biotic factors, both beneficial and pathogenic such as insects, nematodes, fungi, bacteria, archaea or viruses (Coats and Rumpho 2014; Müller et al. 2016; Busby et al. 2017). They interact with plant affecting its metabolism and development (Martin et al.

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2016; Martin et al. 2017). There are long-term symbiotic interactions, bringing bidirectional benefits (mutualism), exploiting one side of the relation (parasitism) or mutualistic and detrimental for both sides of interrelationship at the same time (Martin et al. 2017). Since plants colonized terrestrial environment, they have evolved a variety of interrelationships with actively selected microorganisms, what seemed to be the most beneficial way to provide poorly soluble nutrients and protect from toxins in environment deficient in water, main solvent and transporter, comparing to previous habitat (Bulgarelli et al. 2013; Zgadzaj et al. 2016; Martin et al. 2017). The common pathway of symbiotic signalling is shared by all plants of endosymbiotic interrelationship with fungi and bacteria, including *Actinobacteria*, from rhizosphere (Martin et al. 2017). Chitin-based signalling molecules secreted by symbiotic fungi and rhizobia, which are detected by receptor-like kinases, activate the signalling pathway of plant host, and this mechanism is common regardless of plant species, genus or family (Martin et al. 2017). That process, although similar to an infection, leads to bidirectional mutualistic benefits and also modifications of hormone activity and such organs as root development towards colonization by determined microorganisms (Martin et al. 2017). Establishing mutualistic interrelationships, such as mycorrhizae or bacteria-host plant relation, can be crucial in case of exposition to different environmental biotic and abiotic stress factors, enhancing plant resistance to metals and metalloids by sequestering them into roots and by protecting these other organs from translocation of uptaken toxic ions or molecules (Garg et al. 2015), on the other hand. It is worth to emphasize, that recently microbial symbionts interacting with plants were distinguished into two groups and are investigated as endophytes or rhizospheric microorganisms.

9.2 Microbial-Mediated Arsenic Transformations in Plant Symbionts

Amongst potentially harmful substances, arsenic (As) contamination is one of the major environmental problems affecting plants (Zhao et al. 2009; Gupta and Khan 2015; Latowski and Kowalczyk 2016). Its uptake by the plants causes damage to natural plant ecosystems and crops as well, ceasing by this continuity of agriculture production. Arsenic causes a variety of damages to nucleic acids, proteins, membranes and other cell compounds (Gupta and Khan 2015). In environment, there are different speciations of this element existing, including organic and inorganic compounds, and it is commonly known that those inorganic, such as arsenite and arsenate, are more toxic to living organisms, including plants (Gupta and Khan 2015; Latowski and Kowalczyk 2016). The toxic effect also depends on valency state of As in given compound (III state of oxidation in arsenite or V state of oxidation in arsenate). Arsenic toxicity effects to plants are mainly due to As(III) because As(V) is immediately reduced to As(III) by arsenate reductase when absorbed into the cell

(Hu et al. 2013; Jia et al. 2014). On the other hand, in the external environment, which is rhizosphere, arsenite is oxidized to arsenate either by arsenite-oxidizing microbes (Hu et al. 2013). It was confirmed by several studies that As processing is strongly influenced by microbial activity in addition to chemical transformations in soils or water (Xu et al. 2007; Wang et al. 2011a, b; Hu et al. 2013; Jia et al. 2014; Han et al. 2017b). On the other hand, little is known about interactions between As-resistant plant endosymbionts and root and rhizosphere microbes, particularly on As oxidation and reduction in terms of plant uptake, acquisition, transformation and tolerance to As.

Arsenic transport into plant cells is facilitated, as it is recognized and bound by phosphate or silicon transporters. So far, there are no results explaining what are interactive effects of As and Si to plants (Hu et al. 2013; Schneider et al. 2013); however it was reported that presence of silicon facilitates forming iron plaque on root surface of rice and other wetland plants, thus building barrier for As uptake or space for transformations of As (oxidation/reduction reactions) (Awasthi et al. 2017). In plant roots, arsenate is quickly reduced to arsenite and can outflow back to the soil (Xu et al. 2007; Hu et al. 2013) where under aerobic conditions, it is oxidized rapidly again to arsenate by arsenite-oxidizing microbes. It is worth to notice that As(V) is much stronger bound with soil particles such as ferrihydrite, aluminosilicates or aluminium hydroxides than As(III), and thus oxidation of As(III) to As_{in}(V) is one of the most significant factors decreasing As bioavailability to plants. It is also known that iron plaque can bind As(V) even four times easier than As(III) (Blute et al. 2004). Studies on rice (*Oryza sativa*), grown on submerged areas deficient in oxygen, revealed that As uptake by roots is strongly dependent on microbial oxidization of As(III) to As(V) in combination with root radial oxygen loss (ROL) and availability of organic matter, such as addition of extra rice straw (Jia et al. 2014). Rice cultivars with higher ROL demonstrated lower As uptake than those with lower ROL. The enhancement of this rhizospheric effect on the abundance of the As(III) oxidase gene (*aroA*-like) was greater than on the As(V) reductase gene (*arsC*) and As(V) respiratory reductase gene (*arrA*). The direct effect was As(III) oxidation and sequestration in the rhizosphere, protecting the plant from the uptake of As(III), which intoxicate plant much easier than As(V). These rhizospheric processes, together with the addition of rice straw and growth stage dependently, influenced the rhizospheric population of bacteria, which therefore was dominated by α -, β - and γ -*Proteobacteria*. Mentioned proteobacteria inhabiting rhizosphere are both As(III)-oxidizing, with *arsC* and *arrA* gene representatives including *Enterobacteriales*, *Rhizobiales*, *Sphingomonadales*, *Burkholderiales* and *Xanthomonadales*, and also As(V)-reducing with *aroA*-like sequences, such as *Phyllobacteriaceae*, *Bradyrhizobiaceae*, *Methylobacteriaceae*, *Rhizobiaceae*, *Burkholderiaceae*, *Comamonadaceae* and also seven unidentified mainly rhizospheric clusters (Jia et al. 2014). Recent studies on As hyperaccumulator fern, *Pteris vittata*, demonstrated that about 50% of the tissue microbiota consists of mentioned above α -, β - and γ -*Proteobacteria* species, but the half is dominated

by *Bacteroidetes* and *Firmicutes* (Han et al. 2017a). The important role of the plant organism microbiota was proved e.g. by experiments performed by Mathews et al. in 2010, when under aerobic conditions after 24 h of incubation of 0.1 mM As(III) solution with unsterilized plant samples, considerable amount of the arsenite was oxidized to As(V), while oxidization was not observed in control without plants or with plants sterilized (Mathews et al. 2010).

9.3 Element Availability and Role of Siderophores

Plants and microorganisms involved in biogeochemical element cycles have to deal with reduced access to sufficient nutrients bound in forms of insoluble minerals (Sharma and Sohn 2009; Han et al. 2017b). It is commonly known that mycorrhizal interaction of fungi with plant brings to plant increase of water and nutrient uptake, which is significant concerning such macroelements like P or N, especially in low-fertility soils (Bais et al. 2006; Schneider et al. 2013; Garg et al. 2015).

In terrestrial environments P and As(V), which are chemically P homologue, often bind with Fe. Another factor limiting element availability to plants is pH; the more alkaline, the less mobile are metals and metalloids. *P. vittata* fern, a model plant organism which Han with the team broadly researches currently (Chen et al. 2016; Han et al. 2016a; Han et al. 2016b; Han et al. 2017a; Han et al. 2017b), as a hyperaccumulator of As had to evolve mechanisms to mobilize nutrients, and As as well, from insoluble minerals in rhizosphere soils and also translocation and detoxification pathways (Chen et al. 2016; Han et al. 2016b; Han et al. 2017b). Obtaining nutrients such as P or Fe by plants is possible, e.g. by excretion to rhizosphere substances such as organic acids, decreasing pH of the microenvironment and thus increasing the concentration of soluble P compounds (Han et al. 2017b; Liu et al. 2017a). Besides plant exudates, also microorganisms play a significant role in mineral solubilization (Han et al. 2017b). In soil different elements, including Fe and As, coexist. Under nutrient deficiency bacteria developed an efficient pathway of their harvest by producing siderophores, low-molecular-mass molecules enhancing Fe uptake (Liu et al. 2015; Han et al. 2017b; Liu et al. 2017a; Liu et al. 2017b) divided by chemical structure into three groups: catecholates, hydroxamates and carboxylates (Liu et al. 2016). The ability of elements such as phosphorus and metals or metalloid uptake and transformation is species- and genotype-specific, and this concerns microorganisms (including bacteria and fungi) and plants as well (Garg and Aggarwal 2012; Garg and Bhandari 2012). Siderophores besides other ions such as Cd^{2+} , Cu^{2+} , Ni^{2+} , Pb^{2+} , Zn^{2+} , Mn^{3+} , Co^{3+} , Al^{3+} , Th^{4+} , U^{4+} and Pu^{4+} (Ahmed and Holmström 2014) release Fe^{3+} , As^{5+} and P^{5+} from minerals, thus making them available and facilitating their uptake also to plant roots (Azeem et al. 2014; Han et al. 2016a). However, microbial activity within rhizome space and on the root surface can also determine species of As in iron plaque coating roots, i.e. in the direct vicinity of the plant tissues. *Acidovorax* and *Hydrogenophaga* genera colonizing iron plaque were reported to be involved in oxidation of As(III) bound within,

decreasing uptake, hence total As concentration in the rice roots (from 30 mg kg⁻¹ to about 1 mg kg⁻¹) straw (from 8 mg kg⁻¹ to 1 mg kg⁻¹) and grain (from 23 mg kg⁻¹, to 10 mg kg⁻¹) (Hu et al. 2015). Ghosh with the team (Ghosh et al. 2011; Ghosh et al. 2015) proved that release of ions from iron(III) arsenate (FeAsO₄) is observed, when As-resistant bacteria producing siderophores and isolated from *P. vittata* rhizosphere are present in the direct environment. What is more, some strains, like *Pseudomonas* PG12 isolated from studied fern and producing catechol type of siderophores, can thus enhance biomass growth and are more efficient than fungal siderophores. Research performed by Liu et al. (2016) indicated that *Pseudomonas* PG012 siderophore was more effective in promoting FeAsO₄ dissolution and Fe and As plant uptake, than fungal-siderophore desferrioxamine B (DFOB). Assays performed on *P. vittata* with DFOB demonstrated that DFOB treatment caused uptake and accumulation of mainly As(V) in roots inhibiting its reduction and transport to other organs, whereas bacterial PG12 siderophore treatment resulted in more efficient uptake of As(V) from soil and then its reduction to As(III) and translocation to rhizome and fronds (Liu et al. 2016). Accumulation of As(III) is typical for this fern (Wang et al. 2011a) and beneficial for potential phytoremediation, as above-ground organs are easy to remove from the ground surface. What is interesting, in pot experiments performed on pigeon pea (*Cajanus cajan*) and pea (*Pisum sativum*) under As stress (30 or 60 mg kg⁻¹ dry soil), in which arbuscular mycorrhiza with *Funneliformis mosseae* was investigated in terms of protective for plant role towards As toxicity, demonstrated two important aspects of plant-microbial interactions. Besides beneficial effects of inoculation with mycorrhizal *F. mosseae* enhancing As tolerance of tested plants, the important role played rhizospheric bacteria *Sinorhizobium fredii* AR-4 (inoculated to pigeon pea) and *Rhizobium leguminosarum* bv. *viciae* strain PRH-1 (inoculated to pea). Those endophytic bacterial strains are reported to fix nitrogen and nodulate legumes (Mora et al. 2014). Pretreatment of sterilized seeds with mentioned strains facilitated fertilization of plants by fixing nitrogen from rhizosphere under stress conditions (As contamination). Interaction of inoculates with germinating seeds and forming organs resulted in increase of P, N and K uptake and, on the other hand, decrease of As uptake, thus diminishing its deleterious effect towards seedlings, as concentration of As after 75 days after sowing was up to about 22% lower in leaves and roots of As-treated plants comparing to uninoculated ones (Garg et al. 2015).

9.4 Plant Growth-Promoting Bacteria Under Arsenic Stress

It is commonly known that community of microbes inhabiting rhizosphere influence coexisting plants. There is a variety of phenomena and processes ranging from biochemical to ecological level, which indirectly or directly cause-effect to plant organisms. Recently research focus on beneficial aspects of them, as so far microorganisms were supposed to be mainly pathogens.

One of the protective roles of microorganisms colonizing rhizosphere is just occupying an environmental niche, potential habitat for pathogens. A consequence is competing and limiting indispensable nutrients, such as discussed P or Fe, for pathogen growth. Direct important benefit for plant organism is mitigation or even elimination of additional stress factor, what can be crucial to survive and develop in the environment with overlapping endangerments exposure. Rhizospheric bacteria can limit pathogen reproduction by synthesizing signal components, lytic enzymes, antibiotics or other toxins for potential pathogens and alter plant defence or induce mechanisms of resistance (Bais et al. 2006; Coats and Rumpho 2014). Several research proved that metal(loid)-resistant microorganisms colonizing rhizosphere and/or becoming plant endosymbionts, besides chemical transformation of molecules or ions thus being “alive targets”, can promote growth of plant (plant growth-promoting bacteria, PGPB) (Wang et al. 2011a, b; Liu et al. 2015; Han et al. 2016b; Liu et al. 2017b). Experimental studies on poplar (*Populus deltoides*), rice (*O. sativa*) and ferns *P. vittata* or *Vigna radiata* demonstrated that presence of symbiotic bacteria in rhizosphere or within plant tissues not only induces plant growth-promoting effect but also conduces As transformation and detoxification (Mathews et al. 2010; Liu et al. 2015; Han et al. 2016a; Singh et al. 2016; Batool et al. 2017; Liu et al. 2017b; Das and Sarkar 2018). Such parameters as germination percentage, biomass growth, chlorophyll, carotenoid and soluble protein or sugar content, indole-3-acetic acid (IAA) synthesis, the activities of ACC deaminase and oxidative stress enzymes like superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and the malondialdehyde (MDA) concentrations were controlled to determine As stress of plant organisms treated or untreated with different microbial isolates (Mathews et al. 2010; Zhu et al. 2014; Hu et al. 2015; Liu et al. 2015; Han et al. 2016a; Singh et al. 2016; Batool et al. 2017; Liu et al. 2017b).

Inoculation of poplar cuttings pot cultures with isolate *Agrobacterium radiobacter* D14 strain isolated from *P. vittata* rhizosphere contaminated with As resulted in an increase of soluble sugar content in leaves of plants from As-treated cultures in comparison with control assays without As although both types of plants were treated with tested bacterium strain. What is interesting, without inoculation with the D14 strain, the sugar content increased only at a low concentration of As (150 mg kg⁻¹soil), whereas the activity of D14 in inoculated assays resulted in an increase of sugar content also at a high concentration of As (300 mg kg⁻¹). Arsenic contamination caused a decrease of chlorophyll content, but in the presence of microorganisms, chlorophyll contents were higher compared with samples uninoculated (34). Both experiments on rice and poplar plants (Wang et al. 2011b; Pandey et al. 2013) demonstrated increased activity of investigated enzymes, except for POD in poplar tissues. POD activity in poplar was decreased along with the increasing concentration of As, despite inoculation with D14 (Wang et al. 2011b). In experiments on rice (*O. sativa*), inoculation of plants with As-resistant AsSP9 strain increased amylase and protease activity (from 0.001 mg/g d.w./min up to 0.002 for

amylase and 0.002 to 0.0025 mg/g d.w./min for protease, respectively) (Pandey et al. 2013). In lower concentration of As, i.e. 150 mg kg⁻¹ without D14 inoculation, SOD activity was increased in response to stress factor, but the higher the concentration of As in the environment, the higher the enzyme activity inhibition observed. However, inoculation with bacteria diminished the effect of As toxicity and facilitates SOD activity even under high concentration of As, i.e. 300 mg kg⁻¹, whereas without bacteria under such condition, SOD was strongly inhibited (Wang et al. 2011b). What is important, the increased activity of enzymes was correlated with the increased percentage of germination and relative root elongation in presence of As. Moreover, biomass amount, i.e. dry mass weight and plant height in presence of endosymbiotic bacteria, was significantly increasing and was comparable with respective parameters measured in control plants grown without As. The most putative explanation of this mechanism is that the effective availability of the As is decreased by bacterial immobilization or exclusion which in a consequence reduces the inhibitory effect of this stress factor. What is more, this mechanism was observed only in the case of bacterial strains which are plant symbionts and As resistant, results obtained from experiments on non-symbiotic As-resistant species or strains did not demonstrate beneficial effect to investigated parameters of treated plants (Pandey et al. 2013).

Production of IAA by bacteria, causes auxin stimulated root cell division, which is an additional factor promoting the growth of a plant (Lehmann et al. 2010). It was reported that isolates of *P. multifida* and *P. vittata* are capable of synthesizing up to 36.5 mg L⁻¹ and 18.5 mg L⁻¹ of IAA, respectively (Zhu et al. 2014). Soil symbiont of chickpea (*Cicer arietinum* L.), *Acinetobacter* sp. nbri05 strain, produced IAA on level up to 60.93 µg mg⁻¹ of fresh cell weight. These results allow concluding that additional content in a toxic environment of a compound stimulating root elongation facilitates plant development and on the other hand can therefore enhance and accelerate As uptake (Srivastava and Singh 2014), which may be useful in terms of application in phytoremediation.

The level of lipid peroxidation, which indicates stress factor exposure, is usually estimated by malondialdehyde (MDA) concentration which is the product of peroxidized polyunsaturated fatty acids of the lipid membrane (Kong et al. 2016). MDA concentration was measured in experiments performed on chickpea, pea, pigeon pea, poplar and rice treated with different concentrations of As(III) and As(V) and inoculated with microbial symbiotic organisms, bacteria and fungi as well (Wang et al. 2011b; Pandey et al. 2013; Srivastava and Singh 2014; Garg et al. 2015). The decrease of measured MDA content was observed in all cases if As-treated plants were inoculated. Each concentration of MDA determined in above-ground parts of plant, i.e. shoot for chickpea, pea and pigeon pea or leaves for poplar as well as in roots of rice, chickpea, pea, pigeon pea and poplar (details: Table 9.1), independently on concentration or state of oxidation of As provided in particular study, was significantly decreased (Wang et al. 2011b; Pandey et al. 2013; Srivastava and Singh 2014; Garg et al. 2015).

Table 9.1 Microorganism-host plant interaction characteristics and growth promoting-like activity review

Source	Host	Activity/property of given As-resistant endosymbiont in terms of potential growth promotion				
		Mineral solubilization	Siderophores	As acquisition	Inoculate effect on biomass	Host pigments content
		Species: <i>Pseudomonas</i> sp. (strains PG4, 5, 6, 9, 10, 12, 16), <i>Comamonas</i> sp. and				
<i>Pteris vittata</i> (Ghosh et al. 2011; Ghosh et al. 2015)	tomato seedlings	increase bioavailability of Fe ³⁺ and As ⁵⁺ from FeAsO ₄	+, catecholate type (<i>Pseudomonas</i>)	As(V) uptake, reduction to As(III), translocation to rhizome and fronds	increase comparing to uninoculated under As stress 1.7 times higher due to P solubilization (PG6 strain) and 44% higher shoot biomass	no data
		Types: <i>Firmicutes</i> , <i>Actinobacteria</i> , <i>Proteobacteria</i>				
<i>P. vittata</i> , <i>P. multifida</i> (Zhu et al. 2014)	<i>P. vittata</i> , <i>P. multifida</i>	no P solubilization	+, synthesized by five strains isolated from <i>P. multifida</i> , from three up to five units determined as [(Ar - A As)/Ar] * 100	As(V) uptake, reduction to As(III) by arsenate reductase/As(III) oxidation to As(V) by arsenite oxidase (PV, dependent on concentration of As(III) in environment and correlated with As tolerance; PM, not dependent, not correlated); retain of As(III) in endophytes: PV the higher the outer concentration lower; PM endophytes, the lower the outer conc. higher	no data	no data

Soluble sugars	Enzymes of oxidative stress activity			IAA production	ACC deaminase production	MDA production	other
	SOD	CAT	POD				
<i>Stenotrophomonas</i> sp.							
no data	no data	no data	no data	no data	no data	no data	
no data	no data	no data	no data	+, 0.3–18.5 mg L ⁻¹ (<i>P. vittata</i> isolates) 0.36–36.5 mg L ⁻¹ (<i>P. multifida</i> isolates), higher in <i>P. multifida</i>	no data	no data	

(continued)

Table 9.1 (continued)

Source	Host	Activity/property of given As-resistant endosymbiont in terms of potential growth promotion				
		Mineral solubilization	Siderophores	As acquisition	Inoculate effect on biomass	Host pigments content
		Species: <i>Agrobacterium radiobacter</i> D14 strain				
<i>P. vittata</i> (Wang et al. 2011b)	<i>Populus deltoides</i>			As translocation from roots to shoots, translocation ratio [(stems+leaves)/roots] 0.8, higher than the uninoculated treatments (0.5). 45% As translocated from roots to the above-ground tissues (19.2% more than uninoculated plants)	increase of roots, stems, leaves inoculated comparing to uninoculated, 150 mg g ⁻¹ treatment, stems weight comparable with untreated with As; 150 mg g ⁻¹ and 300 mg g ⁻¹ treatment, leaves biomass about 26% increase comparing with untreated with As	increase of content in plants inoculated (leaves) comparing to uninoculated (under As 150 mg g ⁻¹ and 300 mg g ⁻¹ treatment); inoculation of plants untreated with As does not affect the chlorophyll content
		Species: <i>Bacillus</i> sp. AsSP9 strain, <i>Kocuria flava</i> AB402 strain, <i>Bacillus vietnamensis</i>				
slag disposal site (<i>Bacillus</i> sp. AsSP9 strain) <i>Ceriops decandra</i> mangrove tree (<i>Kocuria flava</i> AB402, <i>Bacillus vietnamensis</i> AB403) (Pandey et al. 2013; Mallick et al. 2018)	<i>Oryza sativa</i>	no data	+ (<i>Bacillus</i> sp. AsSP9 strain)	As retain in biofilm by extracellular polymeric substance (EPS) (<i>K. flava</i> AB402, <i>B. vietnamensis</i> AB403 strain)	increase 3 times comparing to uninoculated plants and reached about 4/5 mass controls without As and inoculate (<i>Bacillus</i> sp. AsSP9 strain); increase of root and shoot length with <i>K. flava</i> AB402, <i>B. vietnamensis</i> AB403 strain, AB402 effect stronger than AB403 effect	no data (<i>Bacillus</i> sp. AsSP9 strain), increase with <i>K. flava</i> AB402, <i>B. vietnamensis</i> AB403 strain, AB402 effect stronger than AB403, chlorophyll content with AB403 comparable to control (uninoculated, untreated with As)

Soluble sugars	Enzymes of oxidative stress activity			IAA production	ACC deaminase production	MDA production	other
	SOD	CAT	POD				
increase of content in plants inoculated (leaves) comparing to uninoculated (under As 150 mg g ⁻¹ and 300 mg g ⁻¹ treatment)	increase after inoculation: up to 31%, roots; up to 51%, leaves	increase after inoculation: up to 98%, roots; 1.42 times, leaves)	decrease: up to 31%, roots; up to 50%, leaves	no data	no data	decrease comparing to uninoculated plants, roots, up to 16%; leaves, up to 30%	soluble proteins: decrease along with increasing As concentration; increase after inoculation comparing to uninoculated plants treated and untreated with AAs, more efficient in leaves comparing to roots
AB403 strain							
no data	no data	+	no data	no data	+(<i>Bacillus</i> sp. AsSP9 strain)	decreased up to about 33% (<i>Bacillus</i> sp. AsSP9 strain)	AsSP9: increased amylase (from 0.001 up to 0.002m/g d.w./mm.) and protease (0.002 to 0.0025 m/g d.w./min)

(continued)

Table 9.1 (continued)

Source	Host	Activity/property of given As-resistant endosymbiont in terms of potential growth promotion				
		Mineral solubilization	Siderophores	As acquisition	Inoculate effect on biomass	Host pigments content
<i>Acinetobacter lwoffii</i>						
soil (Das and Sarkar 2018)	<i>Vigna radiata</i>	+, negatively correlated with increasing As concentration	+	arsenic content in the plant differentiation in time, in the first 15 days of As treatment, the highest concentration of As observed in roots; after the next 15 days, arsenic in high concentration in leaves	growth of the plant is inhibited by arsenic presence comparing to control; in bacteria- and arsenic-treated plants, growth is not significantly different from control	decrease of chlorophyll and carotenoid concentration in As-treated plants comparing to control; plants As-treated and inoculated – about two times higher concentration of chlorophyll comparing to control and about 25% higher content of carotenoids than control
Genus: <i>Acinetobacter</i> sp						
soil (Srivastava and Singh 2014)	<i>Cicer arietinum</i> chickpea	phosphate solubilization up to 213.88 $\mu\text{g mL}^{-1}$	+	As uptake in inoculated plants decreased: up to 66% (shoots), 44% (fruit cover), 64% (fruit)	4.3 times increase of inoculated As-treated than uninoculated As-treated plants, shoot length 31%, root length 18% higher comparing to control untreated with inoculum and As	chlorophyll, 20% increase (1.19 mg g^{-1} to 1.43 mg g^{-1}) comparing to uninoculated As-treated plants, comparable to control; carotenoids, 9% decrease comparing to uninoculated As-treated plants

Soluble sugars	Enzymes of oxidative stress activity			IAA production	ACC deaminase production	MDA production	other
	SOD	CAT	POD				
no data	no data	no data	no data	+, increase with concentration of As from 204 $\mu\text{g/L}^{-1}$ (control) to 325 $\mu\text{g/L}$ (100 mg of As L^{-1}), but at 1000 mg of As L^{-1} decreased to 32 $\mu\text{g L}^{-1}$	no data	inoculation effected with 13–20% decreased MDA concentration comparing to uninoculated As-treated plants; MDA concentrations in control plants 36%–40% lower than in uninoculated As-treated plants	formation of biofilm observed
+, lactose, sucrose	no data	+	no data	+, 60.93 $\mu\text{g mg}^{-1}$ (fresh weight)	5.77 $\mu\text{M } \alpha\text{KB mg}^{-1} \text{h}^{-1}$	about 70% content decrease in shoots and 52% decrease in roots of As-treated and inoculated plants comparing to control without As and inoculate	

(continued)

Table 9.1 (continued)

Source	Host	Activity/property of given As-resistant endosymbiont in terms of potential growth promotion				
		Mineral solubilization	Siderophores	As acquisition	Inoculate effect on biomass	Host pigments content
		<i>Cryptococcus</i> sp., <i>Rhodotorula</i> sp., <i>Exophiala</i> sp., <i>Trichosporon</i> sp., <i>Cystobasidium</i> sp.				
<i>Tithonia diversifolia</i> , <i>Flaveria angustifolia</i> , <i>Sphaeralcea angustifolia</i> , <i>Prosopis</i> sp., <i>Bahia absinthifolia</i> , <i>Sphaeralcea</i> (Ramos-Garza et al. 2015)	<i>Brassica juncea</i>	-	+, despite iron abundance synthesized by 8 amongst 31 isolated strains from 1 up to 2.53 units determined as $[(Ar - As)/Ar] * 100$	arsenate reduction by 51.6% of isolated rhizospheric strains, reduction from 10% up to 40% of As(V) 0.15 mmol L ⁻¹ present in solution; none capable to oxidize arsenite; no data about influence on uptake by plant	increase of seed germination percentage by <i>Rhodotorula</i> sp. and <i>Cystobasidium</i> sp. up to 96.6% (all attempts demonstrated >70% germination; conditions without As; increase of seedlings height more than two times comparing to control; conditions without As)	no data

ACC 1-aminocyclopropane-1-carboxylate, CAT catalase, IAA indole-3-acetic acid, MDA “+”, presence of compound observed; “-”, no product observed

Soluble sugars	Enzymes of oxidative stress activity			IAA production	ACC deaminase production	MDA production	other
	SOD	CAT	POD				
no data	no data	no data	no data	+, three strains: <i>Cystobasidium</i> sp. representative ($6.8 \mu\text{g mL}^{-1}$), two <i>Rhodotorula mucilaginosa</i> strains (9.02 and $9.61 \mu\text{g mL}^{-1}$), both capable to produce siderophores)	no data	no data	

malondialdehyde, *POD* peroxidase, *SOD* superoxide dismutase

9.5 Concluding Remarks

Review of recent reports on microorganism-plant interactions showed that the cooperation between microbes and plants particularly under stress condition is beneficial or even indispensable. These interrelationships are intensively explored last years, starting from screening and discovering organisms involved in different interactions, via isolation of microbes, and their characteristics and analyses of their effect on plant physiology, ending with molecular signalling pathways underlying the interrelationship in terms of its beneficial role for both involved sides, however focusing on the plant. Research in this relatively novel topic joins interests of microbiology and plant biochemistry and physiology.

In all discussed cases, experiments comparing physiological and biochemical properties and/or activity of microbial inoculates in treated and in untreated plants exposed to As stress demonstrated, that the presence of As-resistant microorganisms brings irrefutable benefits to colonized plant (Table 9.1). Investigation of such parameters as total biomass of leaves, shoots and roots, as well as fronds or rhizomes (*Pteris* genus) of plant organism interacting with primarily bacteria but also fungi including yeasts under As exposure demonstrated that beyond plant or symbiotic microorganism genus/species, each interrelationship results in increase of physiological potential of studied plant to diminish efficiently deleterious As effect, survive and grow, comparing to plants uninoculated with microorganisms. In several cases studied plants even reached the extent of measured parameters comparable to controls without As and microorganisms.

It was proved that endosymbionts and beneficial rhizosphere bacteria support nutrient uptake by plant releasing such elements as P or Fe from insoluble minerals, thus enabling their sequestration (usually facilitated by siderophores) and transport into root tissue. Another benefit for the plant is that activity of microorganisms efficiently involved in oxidation/reduction of As(III)/As(V) reactions functionally decreases the concentration of As available for plant or contributes its efflux from tissues.

Biochemical analyses of enzyme activity increasing physiologically under stress conditions, such as SOD, CAT and POD, demonstrated that the activity of the enzymes protecting cells from oxidative stress, except for POD activity, increases with the concentration of As(III) or As(V) plant exposure; however when the concentration of As exceeds critical value (depending on species and other factors), inhibition of the activity starts. Colonization of rhizosphere and plant tissues with rhizospheric and endosymbiotic bacteria expands the range of the concentration and decreases the value of the concentration-deactivating enzyme. On the other hand, microorganisms efficiently synthesize compounds such as IAA or ACC deaminase, which support root cell division and nitrogen uptake by the plant, thus directly contributing to plant development. The biodiversity of microorganisms, amongst which there are representatives of bacteria and fungi including yeasts (Ramos-Garza et al. 2015), creating unique and specific for their host microbiomes indicate, that they are responsible for a variety of functions supporting plant organism like another higher organism.

Reviewed results reflect previous knowledge about the role of rhizospheric and endosymbiotic microbes of plants, especially in terms of As uptake, transformation and translocation within tissues and beneficial effect on plant physiology under stress conditions, such as As contamination, therefore changing the significance of those microorganisms towards plant organism, including human interests in terms of potential bio-phytoremediation application.

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