Chapter 22
Beneficial Role of Plant Growth-Promoting Rhizobacteria in Bioremediation of Heavy Metal(loid)-Contaminated Agricultural Fields

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Abstract The synergy of plants and microbes is one of the most interesting parts of holobiont research that yet have to be unwrapped before we can understand its implications in agriculture. Environmental stresses on plant ecology have further added to our curiosity in this context. Microorganisms are key players in benefitting plant health. This chapter mainly covers heavy metal and metalloid (HM)-induced phytotoxicity in different crops. We will be describing the role of soil-dwelling plant growth-promoting rhizobacteria (PGPR) in the mitigation of HM-induced damages in plants. We will also consider more generally the influential role of these microbes in biotic stress tolerance and the agricultural adoption of PGPR-involved strategies to combat HMs, which will help us provide adequate food for the world's human population and the animals on which we depend for food, labor and companionship. Our starting point will be PGPR collected directly from the crop rhizosphere and associated with the lessening of HM content in crops, but excluding those intracellular endophytic microbes and those involved in PGPR-assisted phytoremediation. The principal rationale for these research efforts is to reduce the consumer's health risks that are directly associated with the mobilisation or immobilisation of HMs inside plant cells. These microbes are possibly the best candidates for bioremediation because of their resilience and ability to withstand high HM levels, their mediation of the limiting effects that recalcitrant metals exert upon plant's health, our successes of collaboration with the plants and microbes for biocontrol activities and microbial phytostimulation. This elaborative study covers the effect of 10 HMs (viz. Arsenic,

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Cadmium, Chromium, Cobalt, Copper, Lead, Manganese, Mercury, Nickel and Zinc) on crops and the HM-resistant PGPR discovered since 20 years. In addition, a general account of fundamental principles behind bacterial heavy metal resistance has been elaborated. Hence, this chapter will be of great interest especially to environmental microbiologists.

22.1 Introduction

The global food crisis is one of the discernible situations that necessitate substantial attention. Due to high population growth (especially in China and India, the top two populated countries in the world) with a proportionate decrease in cultivable land, this catastrophe is becoming more acute daily. Apart from natural sources, several unplanned anthropogenic activities are known to generate an additional burden that jeopardises the environment and its ecosystem, contaminating its different components including soil and groundwater (Sharma and Archana 2016; Liu and Ma 2020). Heavy metal(loid)s (HMs) are one of the recalcitrant contaminants in agricultural fields that degrade the soil quality affecting the growth and crop yield, causing severe to chronic phytotoxicity. This might be due in part to the selection pressure that HMs impose on the soil-dwelling microbiome involved in phytostimulation and maintaining soil-biogeochemical cycling. However, certain microorganisms with their unequivocal properties combat HMs, developing an array of active or passive resistance mechanisms to survive in such a harsh environment (Chen et al. 2016; Tiwari and Lata 2018; Kotoky et al. 2019). There are successful candidates among them that have been found to colonise the soil area around the rhizosphere and rhizoplane (root surface) in response to enriched soil nutrients including the attractants released as root exudates from host plants. Host root exudates provide nutrients and act as signaling molecules to the colonisers to establish effective plant-microbe interactions. These exudates take the foremost part in controlling the diversity and composition of plant-associated soil microbial communities (Steinauer et al. 2016).

Plant growth-promoting rhizobacteria (PGPR) are group of free-living rhizobacterial communities that competitively colonise around the root surfaces stimulating plant growth by secreting a variety of phytostimulating substances and preventing some causes of host's diseases in a sustainable manner (Kloepper 1978). Rhizobacterial plant growth-promoting (PGP) traits include 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity, phosphate solubilisation, indole-3-acetic acid (IAA) production, nitrogen fixation, siderophore production and many more. PGPR also protect plants from invading phytopathogens by secreting antibiotics, antifungal compounds, hydrocyanic acid (HCN), chitinase, etc. The PGPR strains with remarkable HM-withstanding property assist their immobile host to develop HM-tolerance for their combined survival in their contaminated habitat. These microbes are known as HM-resistant PGPR (HMR-PGPR). For several years, these PGPR strains have been isolated from the metal-contaminated rhizosphere of different crops including vegetables (Mitra et al. 2018a, b; Pramanik et al. 2017, 2018a, b; Khanna et al. 2019).

So, to ensure food security, the development of environmental cleanup methods is urgently needed to accomplish the reclamation of contaminated agricultural lands. Unlike the issue of organic pollutants, which sometimes seemed easier to resolve, mitigation of heavy metal contamination has been proving to be one of the more difficult tasks ever undertaken. Organic contaminants can be degraded. The metal pollutants are instead non-degradable in nature, and these contaminants can only be transformed into less toxic forms or removed by means that include accumulation and adsorption. Most of the conventional methods for remediation of heavy-metal-contaminated soil are physicochemical in nature which is expensive, ineffective, creates secondary pollutants and unsuitable for large areas (Quartacci et al. 2006). In this context, HM-resistant PGPR-induced bioremediation is one such approach which is inexpensive, effective, sustainable and ecofriendly. Unlike some non-PGPR microbial strains (Hu et al. 2007; Rehman et al. 2008; Muneer et al. 2009; Shakya et al. 2012; Liu et al. 2013; Davolos and Pietrangeli 2013) isolated from contaminated soil and groundwater, HM-resistant PGPR play a dual role in heavy metal bioremediation as well as plant growth promotion. Some of the non-PGPR strains have also been proven promising as potent bioremediators.

This chapter encompasses heavy metal and metalloid resistant plant growth-promoting rhizobacteria (HMR-PGPR), which are a functionally defined group of microorganisms, discovered during the last two decades that have been found to improve the growth of different crops across the world under different levels of HMs contamination. It covers latest information on diverse HMR-PGPR that exhibited various degrees of HM-resistance, different levels of release of plant growth-promoting substances and different capacities to accelerate plant growth by reducing HM stress-induced morpho-biochemical changes in the affected plants. A brief account of how biotic stress tolerance is facilitated by plant growth-promoting bacteria (PGPB), general HM resistant mechanisms, signaling cascades and genetically modified PGPR are also presented and discussed. Furthermore, we will provide some conclusions about the major obstacles to the application in HMR-PGPR in the field and future prospects of these strains. We will also discuss the times and places where non-HM resistant PGPR, metal-resistant plant growth-promoting bacteria (PGPB) and rhizobia have been advocated. Overall, this chapter is a substantial collection of information on heterogeneous microbial communities (especially HMR-PGPR) interacting with diverse hosts working in different soil types for crop improvement in a sustainable manner.

22.2 Heavy Metal(loid)-Induced Phytotoxicity in Crop Plants

The incessant spread and increasing levels of HMs in agricultural soils have caused severe impairment of crops which not only results in reduced yield but also a serious toxic threat to the crop consumers. Plants, being immobile, are unable to escape from this stressful environment and uptake bioavailable non-essential HM cations into their plant cells along with essential soil nutrients. These HMs, upon surpassing certain threshold levels, impose severe cellular damages with various unusual morphological manifestations. The threshold level of HMs to induce phytotoxicity highly depends on plant species or even a particular cultivar. The uptake, translocation and cellular compartmentalisation of heavy metals may be governed by perhaps only one or just a few genes (Ernst 1996). Moreover, this also depends on the cationic forms of HMs. The observable external changes include reduction of seed germination, changes in root-shoot length and changes in root-shoot fresh and dry weight that ultimately decrease plant biomass (Table 22.1). As the root is directly exposed to the soil HMs, the root is the first organ encountered by toxic HMs, and the toxic effects follow into the shoots and other aerial parts of the plants. Affected root growth results in the poor acquisition of essential nutrients, and thereby an insufficient supply of nutrients to the photosynthetic cells in the aerial parts. To date, the members of Poaceae are the most studied crops on which the phytotoxic effects of different HMs have been investigated (Fig. 22.1). The phytotoxic consequences of all the ten HMs (viz. arsenic, cadmium, chromium, cobalt, copper, lead, manganese, mercury, nickel and zinc) discussed here have been studied on Poaceae (Fig. 22.1). After Poaceae, the HM-phytotoxicity studies have focused mainly on members of Fabaceae, Solanaceae and Brassicaceae, as predominant crops (Fig. 22.1). The less-studied families in the context with HM phytotoxicity are Amaryllidaceae, Euphorbiaceae, Amaranthaceae, Rosaceae, Linaceae, Malvaceae, Asteraceae and Cucurbitaceae (Fig. 22.1).

Among HMs, arsenic (As) is considered as an analog of phosphate (P) that competes with P-transporters in the root plasma membrane (Meharg and Macnair 1992). Although As-tolerance has been identified in a number of plant species (Meharg and Macnair 1992), elevated As-level has been found to negatively affect rice, maize, black gram, soybean, mung bean, cucumber, sorghum, barley, mustard, broccoli, pea and Chinese cabbage (Table 22.1). Biochemical changes identified in these crops include a reduction in photosynthetic pigments (chlorophyll, carotenoids), increased accumulation of reactive oxygen species (ROS), membrane lipid peroxidation, inhibition of ATP formation, enhanced proline and protein content and increased abscisic acid (ABA) synthesis (Table 22.1). Furthermore, altered activities of various cellular enzymes including RuBisCO, amylase, protease, catalase, peroxidase and other antioxidant enzymes are evident (Stoeva et al. 2005; Srivastava et al. 2017; Ghosh et al. 2018; Dong et al. 2020; Chauhan et al. 2020). Besides, As-mediated induction of cell death in root tips, proteomic alteration and disruption

Table 22.1 Heavy metal(loid)-induced phytotoxicity in different crops

HMs	Crop	Phytotoxic effects[a]	References
As	*Oryza sativa* (Rice)	• Reduced root-shoot length, biomass and root hair • Increased accumulation of ROS and MDA • Damaged cortical cells and cellular structure • Reduction in RuBisCO activity, photosynthesis • Increased ABA synthesis and growth inhibition	Chauhan et al. (2020)
	Oryza sativa (Rice)	• Decreased rice biomass • Inhibition of root growth • Inhibition of RuBisCO and photosynthesis	Dong et al. (2020)
	Oryza sativa (Rice)	• Reduced seed germination • Decreased root-shoot elongation • Decreased amylase and protease activity • Increased antioxidant enzymes, MDA and proline	Ghosh et al. (2018)
	Vigna mungo (Black gram)	• Catalase activity decreased • Increased amount of lipid peroxidation • Peroxidase increased tremendously • Superoxide dismutase increased • Ascorbate peroxidase also increased • Reduction of photosynthetic pigments	Srivastava et al. (2017)
	Glycine max (Soybean)	• Inhibition of leaf development • Cell death in root tips • Decreased root-shoot biomass • Reduction in chlorophyll content • Increased membrane lipid peroxidation	Armendariz et al. (2016)
	Oryza sativa (Rice)	• Inhibition of ATP formation • Lowered the yield of rice grain • Increased oxidative stress	Syu et al. (2015)
	Phaseolus radiatus (Mung bean), *Cucumis sativus* (Cucumber), *Triticum aestivum* (Wheat), *Sorghum bicolor* (Sorghum), *Hordeum vulgare* (Barley), *Brassica campestris var. chinensis* (Chinese cabbage), *Brassica oleracea* (Broccoli),	• Inhibition of seed germination • Decreased seedling growth	Yoon et al. (2015)

(continued)

Table 22.1 (continued)

HMs	Crop	Phytotoxic effects[a]	References
	Brassica nigra (Mustard), *Pisum sativum* (Pea)		
	Oryza sativa (Rice)	• Stimulation of antioxidant enzymes • Increased accumulation of stress-responsive amino acids	Dave et al. (2013)
	Oryza sativa (Rice)	• Reduced seed germination • Stunted root-shoot growth • Inhibition of root formation at higher concentration	Shri et al. (2009)
	Zea mays (Maize)	• Proteomic alteration • Disruption of normal cellular function	Requejo and Tena (2006)
	Phaseolus vulgaris L. (Mung bean)	• Reduced growth, leaf gas exchange, water potential • Decreased protein and chlorophyll content • Root-shoot significantly reduced • Increased peroxidase activity and lipid peroxidation	Stoeva et al. (2005)
Cd	*Pisum sativum* (Pea)	• Reduced root-shoot length • Decreased fresh, dry weight, biomass • Increased proline, glycine betaine and soluble proteins, sugar content decreased • Chlorophyll ‘a’, ‘b’, carotenoid content decreased • Activities of antioxidant enzymes increased • Accumulation of phenols decreased	Sager et al. (2020)
	Oryza sativa (Rice)	• Reduced seed germination • Decreased root-shoot length • Decreased fresh and dry weight • Decreased amylase, total sugar, chlorophyll • Protease activity decreased • Increased total protein, antioxidant enzymes • Increased proline ad ethylene content	Mitra et al. (2018a)
	Oryza sativa (Rice)	• Reduced seed germination • Decreased root-shoot length • Decreased fresh and dry weight • Decreased amylase, total sugar, chlorophyll • Increased protease activity and total protein • Increased total protein, antioxidant enzymes • Increased proline ad ethylene content	Pramanik et al. (2018a)

(continued)

Table 22.1 (continued)

HMs	Crop	Phytotoxic effects[a]	References
	Solanum lycopersicum (Tomato) *Cucumis sativus* (Cucumber)	• Decreased root-shoot dry weight, decreased number of leaves • Total content of organic acid decreased • Activities of SOD and GR were depressed • CAT, APX activities, H_2O_2 were increased	Wu et al. (2015)
	Solanum tuberosum (Potato)	• Increased MDA content • Decreased chlorophyll content	Xu et al. (2013)
	Lactuca sativa (Lettuce)	• Decreased plant dry weight • Strong reduction of the maximum photochemical efficiency of PS II • Impairment of net CO_2 assimilation rate • Decrease in RuBisCO activity • Decreased efficiency of nutrient uptake and carbohydrate assimilation	Dias et al. (2013)
	Oryza sativa (Rice)	• Decreased root-shoot dry weight and biomass • Decreased chlorophyll content • Increased oxidative stress	Chou et al. (2011)
	Triticum aestivum (Wheat)	• Inhibition of root elongation	Cao et al. (2007)
	Phaseolus vulgaris (Mung bean)	• Decreased root-shoot length • Reduced dry weight and chlorophyll	Tripathi et al. (2005)
Co	*Triticum aestivum* (Wheat)	• Decreased growth, water content, osmotic potential • Reduced carbon assimilation rate, stomatal conductance, intercellular CO_2 concentrations, transpiration rate, photosynthetic capacity	Ozfidan-Konakci et al. (2020)
	Hordeum vulgare (barley) *Brassica napus* (Oilseed rape) *Lycopersicon esculentum* (Tomato)	• Decreased plant growth • Inhibition of plant shoot biomass	Li et al. (2009)
	Lycopersicon esculentum (Tomato)	• Decreased biomass, decreased concentration of Fe in different parts, chlorophyll, Hill reaction activity, catalase activity • Increased peroxidase, acid phosphatase, ribonuclease • Increased carbohydrate and phosphorus fractions in leaves	Chatterjee and Chatterjee (2003)
	Brassica oleracea (Cauliflower)	• Chlorosis on young leaves, a decrease in chlorophyll concentration • Restriction of translocation of P, S, Fe, Mn and Zn from roots to tops.	Chatterjee and Chatterjee (2000)

(continued)

Table 22.1 (continued)

HMs	Crop	Phytotoxic effects[a]	References
Cr	*Brassica napus* L. (Oilseed rape)	• Accumulation of reactive oxygen species, malondialdehyde • Antioxidant enzyme activities enhanced • Damaged the leaf and root ultra-structures	Gill et al. (2015)
	Vicia faba (Faba bean)	• Abberation of mitosis • Cr(VI)-induced disturbances of mitotic microtubules	Eleftheriou et al. (2015)
	Zea mays (maize)	• Decreased mitotic index, genomic template stability and soluble protein levels • Decreased growth-promoting hormones	Erturk et al. (2014)
	Pisum sativum (Pea)	• Growth inhibition, root deformations • DNA damage, cell cycle arrest and polyploidisation	Rodriguez et al. (2011)
	Oryza sativa (Rice)	• Root-shoot growth, leaf area, fresh and dry weight decreased • Grain weight and paddy yield decreased • Reduction in levels of nutrients in root and shoot	Sundaramoorthy et al. (2010)
	Lycopersicon esculentum (Tomato)	• Stunted growth, brownish, necrotic shoot and plant bending • Lethality observed in higher doses	Goupil et al. (2009)
	Pisum sativum (Pea)	• Chlorosis and wilting in leaves • SOD activity increased at lower Cr supply, decreased at higher Cr. • Significant reductions in Chl a and b • Monodehydroascorbate reductase activity significantly decreased	Pandey et al. (2009)
	Vigna mungo (Blackgram)	• Decreased germination percentage, root-shoot length, fresh & dry weight • Decreased total chromosome length, absolute chromosome length and average chromosome length of seedlings • Significant mutagenic effect on the root tip cells	Chidambaram et al. (2009)
	Brassica napus (Rapeseed)	• Plant growth inhibition • Genetic damage and DNA methylation	Labra et al. (2004)
Cu	*Linum usitatissimum* (Flax)	• Reduced plant height, diameter, fresh and dry biomass • Reduced chlorophyll contents in the leaves • Excess generation of reactive oxygen species • Increased activities of superoxide dismutase, peroxidase in the roots and leaves	Saleem et al. (2020)

(continued)

Table 22.1 (continued)

HMs	Crop	Phytotoxic effects[a]	References
	Brassica campestris ssp. *chinensis* Makino (Chinese cabbage)	• Decreased mineral nutrients, chlorophyll content • Increased MDA content and DNA methylation level	Zhou et al. (2017)
	Withania somnifera (Indian ginseng)	• Reduced leaf fresh weight, shoot length • Reduction in chlorophyll and carotenoid concentration • Increased lipid peroxidation, high $O_2^{-\bullet}$ and H_2O_2 content • Increased Ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase, glutathione-S-transferase, guaiacol-peroxidase activities in leaves	Khatun et al. (2008)
	Oryza sativa (Rice)	• Rice growth reduced • Grain yields decreased	Xu et al. (2006)
	Prunus cerasifera (peach rootstock)	• Reduced relative growth rate for both fresh and dry weight • Severe browning and necrosis • Increased total catalase, superoxide dismutase activity with the induction of *Sod* and *Cat* gene expression	Lombardi and Sebastiani (2005)
	Cucumis sativus (cucumber)	• Young expanding leaves exhibited a reduction in leaf area, while mature leaves showed reduced photosynthesis • Sucrose, starch content increased in both types of leaves • Net CO_2 assimilation decreased in mature leaves	Vinit-Dunand et al. (2002)
Hg	*Avena sativa* (Common oat)	• Decreased yield of aerial mass and roots • Increased contamination of Hg in soil increased N and K, but decreased P	Sadej et al. (2020)
	Triticum aestivum (Wheat)	• Roots of the plant were more affected as compared to the shoot • The malondialdehyde content increased in the roots • Significant decrease in root and shoot growth, content of chlorophyll and total soluble protein • Enzymatic antioxidants decreased	Sahu et al. (2012)
	Jatropha curcas (Physic nut)	• Loss of biomass, leaf area and growth • Reduction of net photosynthesis	Marrugo-Negrete et al. (2016)
	Brassica juncea (Indian mustard)	• Significant reduction in biomass, relative water content in leaves • Alteration of leaf cellular structure • Decreased number of palisade and spongy parenchyma cells • Reduced cell size and clotted depositions	Shiyab et al. (2009)

(continued)

Table 22.1 (continued)

HMs	Crop	Phytotoxic effects[a]	References
	Lycopersicon esculentum (Tomato)	• Decreased root-shoot growth • Decreased chlorophyll content in leaves • Enhancement of antioxidant enzyme activities, malondialdehyde formation, H_2O_2 content.	Cho and Park (2000)
Mn	*Triticum aestivum* (Wheat)	• Inhibited the uptake of other elements • Affected antioxidant enzymes	Faria et al. (2020)
	Glycine max (Soybean)	• Reduced CO_2 assimilation rate, stomatal conductance • Increased antioxidant enzymes in roots • Calcium travelled dramatically from the healthy to necrotic tissue under high Mn	Santos et al. (2017)
	Vigna unguiculata (Cowpea)	• Formation of brown spots in sensitive cultivars • Induction of callose formation and an enhanced release into the apoplast of phenols, peroxidases and other stress-related proteins • Proteins related to CO_2 fixation, stabilisation of the Mn cluster of the photosystem II, pathogenesis-response reactions were affected	Führs et al. (2008)
Ni	*Solanum lycopersicum* (Tomato)	• Inhibition of growth, biomass, impairment of photosynthesis, photosystem function, mineral homeostasis, root activity and osmotic balance • Increased ROS production in leaves and roots of tomato seedlings as compared with control plants	Jahan et al. (2020)
	Oryza sativa (Rice)	• Reduced the growth and yield of rice plants compared to the plants grown in normal soil without Ni stress • Reduced nutrient (NPK) content in rice straw and grain	Nazir et al. (2016)
	Zea mays (Maize)	• Seedling mortality at high Ni concentration • Inhibition of seedling growth and development • Leaves exhibited chlorosis and yellow spotting • Decreased the amount of soluble sugars in leaves	Nie et al. (2015)
	Vigna cylindrica (Catjang) *V. mungo* (Black gram) *V. radiata* (mung bean)	• Reduction in seed germination, fresh biomass • Drastic decline was observed for the formation of nodules and chlorophyll a and b contents	Ishtiaq and Mahmood (2012)

(continued)

Table 22.1 (continued)

HMs	Crop	Phytotoxic effects[a]	References
	Cicer arietinum (Chickpea)	• Decline in the seed germination, biomass and plant growth • Suppression of root nodules, roots and lateral roots • Reduction in chlorophyll content and development of chlorosis	Khan and Khan (2010)
	Hordeum vulgare (Barley)	• Decreased dry weight, which was more prominent in roots than in shoots • Interveinal chlorosis of younger leaves, necrosis of mature leaves and browning of the root system	Rahman et al. (2005)
Pb	*Lactuca sativa* (Lettuce)	• Decrease in shoot growth • Disturbed lettuce growth and net photosynthesis	Xiong et al. (2018)
	Vicia faba (Faba bean)	• Induction of lipid peroxidation and H_2O_2 generation in leaves • Overproduction of ROS resulting in bimolecular damage • Decreased chlorophyll content	Shahid et al. (2014)
	Glycine max (Soybean)	• Inhibitory effect on carbohydrate content • Starch was more reduced as compared to other carbohydrates • Carotenoids were less affected as compared to total chlorophyll • Reduction of protein content	Imtiyaz et al. (2014)
	Triticum aestivum (Wheat)	• Increased lipid peroxidation, enhanced soluble protein concentrations, accumulation of proline in roots • Enhanced Esterase activity • Inhibition of α-amylase activity • Antioxidant enzymes activities	Lamhamdi et al. (2011)
	Solanum lycopersicum (Tomato)	• Decreased calcium, magnesium, potassium phosphorus concentration in shoot and leafs • Decreased Na content in roots, shoots and leafs • Reduction in chlorophyll biosynthesis • Decreased root, shoot and leaf water contents	Akinci et al. (2010)
	Allium sativum (Garlic)	• Antioxidant enzymes increased in roots and shoots • Root-shoot growth were significantly inhibited	Liu et al. (2009)
	Phaseolus vulgaris (Mung bean)	• Decreased root-shoot length • Reduced dry weight and chlorophyll	Tripathi et al. (2005)
	Oryza sativa (Rice)	• Reduced chlorophyll in leaves, carotene, sugars, phenols, nonprotein	Chatterjee et al. (2004)

(continued)

Table 22.1 (continued)

HMs	Crop	Phytotoxic effects[a]	References
		nitrogen, protein, iron, manganese, copper, zinc, Hill reaction activity, peroxidase activity • Decreased plant dry weight and inhibition of root growth	
Zn	*Hordeum vulgare* (Barley)	• Reduction in the chlorophyll content • Decreased root-shoot biomass	Mossa et al. (2020)
	Solanum lycopersicum (Tomato)	• Generation of H_2O_2 and induction of oxidative stress • Reduction of stress-controlling enzymes (APX and SOD) in the root • Reduction in contents of Chl-a and T-Chl	Akanbi-Gada et al. (2019)
	Carthamus tinctorius (Safflower)	• Stunted growth, brownish roots, chlorosis on the leaves • Roots and shoots biomass production reduced significantly	Namdjoyan et al. (2017)
	Beta vulgaris (Sugar beet)	• Inward-rolled leaf edges, damaged and brownish root system, with short lateral roots • Decreased N, Mg, K and Mn concentrations in all plant parts • Significant decrease in the root/shoot ratio	Sagardoy et al. (2009)

[a] *ROS* Reactive oxygen species, *MDA* Malondialdehyde, *RuBisCO* Ribulose-1,5-bisphosphate carboxylase/oxygenase, *ABA* Abscisic acid, *SOD* Superoxide dismutase, *GR* Glutathione reductase, *CAT* Catalase, *APX* Ascorbate peroxidase

of normal cellular function have also been identified (Requejo and Tena 2006; Armendariz et al. 2016).

Likewise, phytotoxicity of other HMs reported almost parallel kinds of morpho-biochemical dysfunctions (Table 22.1). Studies of cadmium (Cd)-induced phytotoxicity have focused mainly on rice, wheat, tomato, potato, cucumber, pea, lettuce and mung bean (Table 22.1). An upsurge of ethylene content in rice seedlings has been noticed in response to Cd stress (Mitra et al. 2018a; Pramanik et al. 2018a) that is linked to increased accumulation of H_2O_2, leading to cell apoptosis (Chmielewska-Bak et al. 2014). Cobalt (Co), one of the naturally occurring HMs in the earth's crust, spreads through human activities as well, and that element is taken up by plants from the contaminated soil. However, information on Co-phytotoxicity is less available in the literature compared to As and Cd. Wheat, barley, oilseed rape, tomato and cauliflower have been studied so far to elucidate Co-induced phytotoxicity (Chatterjee and Chatterjee 2000, 2003; Li et al. 2009; Ozfidan-Konakci et al. 2020). Co was found to decrease plant growth, photosynthetic rate, water content, osmotic potential, stomatal conductance, transpiration rate and cause chlorosis that ultimately

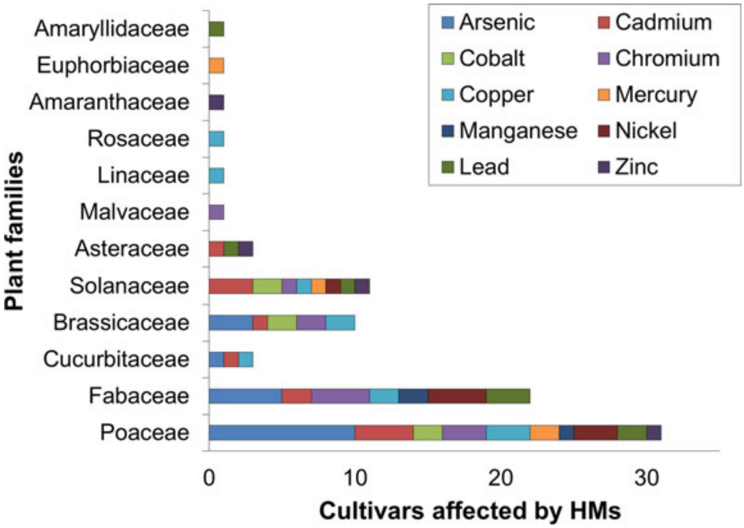

Fig. 22.1 Families of studied agricultural crops affected by heavy metal(loid)s

manifested as decreased plant biomass (Table 22.1). An exogenous application of $CoCl_2$ was shown to decrease plant ethylene levels compared to controls (Pramanik et al. 2017, 2018a). The number of phytotoxicity studies on chromium (Cr), copper (Cu), mercury (Hg), manganese (Mn), nickel (Ni), lead (Pb) and zinc (Zn) on the more common crop plants is also impressive, with reporting of various morpho-biochemical malfunctions in plants.

22.3 Role of Heavy Metal(loid) Resistant Plant Growth-Promoting Rhizobacteria in Crop Improvement

Soil, being the sink of nutrients for plants, is also the chief source of contaminants. The information summarised in Table 22.1 provides an idea of observed intensification of heavy metal contamination and consequences of the major HM contaminants on some common crops. Plants have developed their own natural mechanisms to regulate the uptake, translocation and accumulation of HMs, which is known as natural phytoremediation. In reality, plants are not the only warriors that are exposed to and affected by soil HMs, and indeed there similarly exist some close neighbors like the rhizospheric microbial community that also have direct or indirect influences on plant growth. Phytoremediation is one of the safest, eco-friendly technologies and is often triggered by plant growth-promoting bacteria (PGPB) as a response to accelerated HM uptake and accumulation in the plant cells (Ullah et al. 2015). This concept of designing and promoting bacteria-assisted phytoremediation

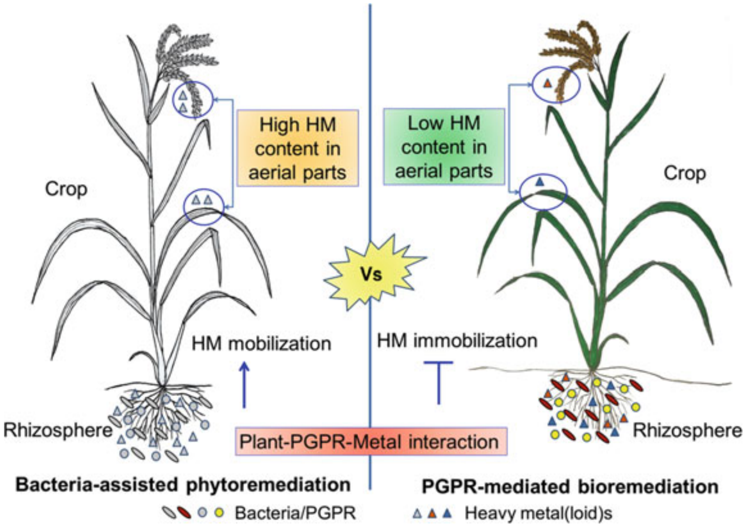

Fig. 22.2 Bacteria-assisted phytoremediation and PGPR-mediated bioremediation of heavy metal (loid)s

technology is not intended to be applied only in the case of agricultural crops that are consumed by humans, cattle or other animals to reduce the high chances of HM toxicity in the food chain (Fig. 22.2). Rather, the preferred usage of PGPR-mediated bioremediation would be in such cases where some specific group of PGPR reduce both the HM-induced phytotoxic effects and HM-uptake as well (Fig. 22.2). PGPR fall under a special group of fast-growing microorganisms which are a good instance of phytostimulating biological agents of natural occurrence. Since many years, soil microbiologists and environmentalists have been devoting their tireless efforts to isolate PGPR strains with greater efficiency of bioremediation and plant growth promotion, and to apply their discoveries about HM-contaminated soil for the benefit of sustainable agriculture (Table 22.2). Here, in this review, we will largely examine HM-resistant PGPR (involved in PGPR-mediated bioremediation) publications from the last two decades and present their results in brief (Table 22.2). We have considered only those HM-resistant PGPR strains which were tested for their plant growth-promoting activities on selected crops, with those microbes having been applied as bioinoculants either in laboratory conditions or in the field. It is evident from Table 22.2 that the phytotoxic effects mentioned in Table 22.1 have been significantly reduced by the use of HM-resistant PGPR.

One of the most vital and key representations of this chapter is the documentation of culture media for the isolation of HM-resistant PGPR. Proteobacteria seem to have been the most commonly isolated group from all the stated culture media. Yeast extract mannitol (YEM) medium has been the most preferable isolation medium, followed by Davis Mingioli (DM) medium with Cd (Fig. 22.3). From a critical

Table 22.2 Heavy metal(loid)-resistant PGPR including rhizobia discovered in the last two decades and their applications

PGPR	Associated crop	Media[a]	PGP traits[b]	MIC[c]/MBC/MTC/MRL/Highest tolerance	Plant growth promotion study performed on (plant)	Mode of study	Improvements in crops after PGPR inoculation	Reference
Enterobacter bugandensis TJ6	*Lactuca sativa* (Lettuce)	Urease screening agar plates	Urease, IAA, siderophore	(MIC-mg L^{-1}) Cd-400 Pb-1700	*L. sativa*	Hydroponic experiment in a glasshouse	• Compared with controls, inoculation with both strains significantly improved the root and shoot dry weight • Soluble protein and vitamin C content enhanced by both strains • Reduced Cd and Pb content in edible tissue. • Strain HD8 found more proficient in reduction of Cd and Pb uptake in lettuce than TJ6	Wang et al. (2020)
Bacillus megaterium HD8				Cd-700 Pb-2100				
Serratia marcescens SNB6	*Chrysopogon zizanioides* (Vetiver grass)	NM	Phosphate, IAA, siderophore	(MIC- ND) Cd	*C. zizanioides*	Pot experiment conducted in green house	• Improved the genes expression of (low molecular weight organic acids) LMWOAs, PGP traits, biomass • Improved the activities of antioxidant enzymes	Wu et al. (2020)

(continued)

Table 22.2 (continued)

PGPR	Associated crop	Media[a]	PGP traits[b]	MIC[c]/MBC/MTC/MRL/Highest tolerance	Plant growth promotion study performed on (plant)	Mode of study	Improvements in crops after PGPR inoculation	Reference
Agrobacterium fabrum SDW_6	*Zea mays* (Maize)	Dworkin and Foster (DF) nutrient 100 mg L^{-1} Cr	Phosphate, siderophore, IAA, potassium	(MIC- ND) Cr	*Z. mays*	Pot experiment	• Improvement in intake of N, P, K in leaves and in roots of maize after combined application of SDW_6 with 500 µM Fe • SDW_6 had better efficiency than SDW_{10} • Significantly enhanced of chlorophyll content • Enhancement of root-shoot dry weight, plant height, roots-shoot length in maize by SDW_6 strain	Danish et al. (2019)
Leclercia adecarboxylata SDW_{10}								
Serratia liquefaciens CL-1	*Amaranthus tricolor* (Elephant-head amaranth)	Luria–Bertani's (LB) supplemented with 3mM Cd	IAA, siderophore, ACCD	(High degree of resistance-mM) Cd-6.2 Pb-12.0 Cu-6.3	*Brassica napus* (Oil-seed rape)	Pot experiment	• Cell adsorption of Cd increased by strain CL-1 compared to strain X30 • Biomass, pH, polyamine content relative abundance of	Han et al. (2018)
Bacillus thuringiensis X30			IAA, ACCD	Cd-3.6 Pb-8.7 Cu-3.9				

							arginine decarboxylase-producing bacteria (ADPB) of rhizosphere soils, increased by strains • Both bacteria colonized oilseed rhizospheric soil • Both strains reduced Cd content of root • Cd translocation factor reduced significantly strain CL-1 than strain X30	
Azotobacter chroococcum CAZ3	*Capsicum annum* (Chilli)	Ashby's mannitol medium	IAA, siderophore, ACCD, ammonia	(Maximum tolerance-μg mL^{-1}) Cu-1400 Pb-2000	*Zea mays* (Maize)	Pot experiment	• CAZ3 strain improved growth, maize yield, presence of both metals • Levels of proline, malondialdehyde and antioxidant enzymes in foliage significantly reduced • Accumulated greatest quantities of metals in roots than other organs • In roots, shoots, kernels metal concentrations reduced	Rizvi and Khan (2018)

(continued)

Table 22.2 (continued)

PGPR	Associated crop	Media[a]	PGP traits[b]	MIC[c]/MBC/MTC/MRL/Highest tolerance	Plant growth promotion study performed on (plant)	Mode of study	Improvements in crops after PGPR inoculation	Reference
Enterobacter aerogenes K6	*Oryza sativa* (Rice)	Davis Mingioli (DM) medium with 1000 μg/mL Cd	Phosphate, IAA, siderophore, N_2, ACCD, HCN, ammonia	(High degree of resistance-μg/mL) Cd-4000 Pb-3800 As-1500	*O. sativa*	*In vitro* PGP experiment, *In vivo* root colonisation study	• Revealed growth promotion of rice seedling under Cd stress • Reducing oxidative stress (through antioxidants), stress ethylene by combined outcome of Cd resistance and PGP activities • 100% seed germination • Improved root length, shoot length, root weight, shoot weight • Strain K6 increased Chl-a, Chl-b and total chlorophyll content • In seedling tissues Cd uptake reduced	Pramanik et al. (2018a)

							• Colonisation of numerous bacterial cells around root surface	
Enterobacter K2	*Oryza sativa* (Rice)	Davis Mingioli (DM) medium with 500 µg/mL Cd	Phosphate, IAA, siderophore, N_2, NH_3, ACCD, HCN	(MIC- µg/mL) Cd-4000 Pb-4000 As-1200 Ni-600 Hg-40	*O. sativa*	*In vitro* PGP experiment in glass beaker	• Enhancement of germination percentage • Growth parameters (root length, shoot length and root-shoot biomass) increased significantly • Reduction of stress ethylene • Elongation of root increased by preventing senescence • Total chlorophyll content increased	Pramanik et al. (2018b)
Enterobacter asburiae S2	*Oryza sativa* (Rice)	Davis Mingioli (DM) medium with 1000 µg/ml Cd	Phosphate, IAA, N_2, ACCD	(MIC- µg/mL) Cd-3500 Pb-2500 As-1050	*O. sativa*	Pot experiment in growth chamber	• Germination percentage increased • Improvement in root-shoot length, fresh weight, dry weight • Significant reduction of Cd uptake, comparison to Cd treated	Mitra et al. (2018a)

(continued)

Table 22.2 (continued)

PGPR	Associated crop	Media[a]	PGP traits[b]	MIC[c]/MBC/MTC/MRL/Highest tolerance	Plant growth promotion study performed on (plant)	Mode of study	Improvements in crops after PGPR inoculation	Reference
							un-inoculated seedlings • Reduction of oxidative stress, stress ethylene	
Klebsiella michiganensis S8	*Oryza sativa* (Rice)	Davis Mingioli (DM) medium supplemented with 1000 μg/ml Cd	Phosphate, IAA, N_2, ACCD	(MIC- μg/mL) Cd- 3500 Pb- 3000 As- 1000	*O. sativa*	*In vitro* PGP experiment in glass beaker	• Revealed cadmium elimination proficiency • Good effect in seed germination percentage • Growth parameters (root-shoot length, fresh weight, dry weight) improved • Enhanced chlorophyll a, b and total chlorophyll content	Mitra et al. (2018b)
Klebsiella pneumoniae K5	*Oryza sativa* (Rice)	Davis Mingioli (DM) medium supplemented with Cd^{2+} (100–1000 μg/mL)	Phosphate, IAA, N_2, ACCD, NH_3, Siderophore	(MIC—μg/mL) Cd-4000 Pb-4000 As-1500	*O. sativa*	*In vitro* PGP experiment, *In vivo* root colonisation study	• Enhanced germination percentage, root-shoot length, root-shoot dry weight, seedling vigor index • Improved	Pramanik et al. (2017)

							antioxidant enzymatic activities • Increased α-amylase, total sugar, total protein, chlorophyll and proline content • Decreased stress ethylene and Cd content in seedlings	
R. leguminosarum bv. *viciae* SV15	Nodule of *Vicia faba* (Fava bean)	YEM medium	ND	(MIC -mM) Cu 0.5	*V. faba*	Hydroponic culture	• Co-inoculation treated sets with Cu increased root length, shoot dry weight • Reduced copper uptake in roots • in co-inoculated Cu treated plants, decrease antioxidative enzymes	Fatnassi et al. (2015)
Rhizobium sp. SV20				0.5				
Pseudomonas sp. SV23				1				
E. cloacae SV27				2				
Photobacterium sp. strain MELD1	*Phragmites australis* (Reed)	Luria Bertani (LB) and M9 minimal media plates	IAA	(MIC—mg. kg^{-1}) Hg—33	*Vigna unguiculata* ssp. *sesquipedalis* (Long yard bean)	In vivo experiment	• Significant improvement in biomass, root length, seed number • Helped in mercury uptake restricted to roots	Mathew et al. (2015)

(continued)

Table 22.2 (continued)

PGPR	Associated crop	Media[a]	PGP traits[b]	MIC[c]/MBC/MTC/MRL/Highest tolerance	Plant growth promotion study performed on (plant)	Mode of study	Improvements in crops after PGPR inoculation	Reference
Pseudomonas brassicacearum ssp. *brassicacearum* strain DBK11	*Brassica napus* (Indian mustard plant)	Medium 72- for tryptone casein soya agar Or Liquid medium 1 (DSMZ Medium 1a), 30°C	ND	(MIC- ND) Zn	*Brassica juncea* (Indian mustard plant)	Glasshouse pot experiment	• Root biomass increased after WSM1325 (B*R*o) inoculation compared to control • Plant growth higher with both bacterial strains inoculation • Co-inoculation of isolates, decreases metal toxicity, in plant growth • More Zn bioaccumulation, translocation showed significantly • B*RP*Zn set reduces Zn from soil	Adediran et al. (2015), Achouak et al. (2000)
Rhizobium leguminosarum bv. *trifolii* strain WSM1325	*Clover* sp. (Clover)							
Bradyrhizobium sp. YL-6	*Glycine max* (Soybean)	Modified YEM agars with 20 mg L^{-1} of Cd	IAA, siderophore, ACCD, phosphate	(MIC- mg L^{-1}) Cd -100	*G. max*, *Lolium multiflorum* (Italian ryegrass)	Pot experiment in glasshouse	• Enhanced shoot dry weight compared to uninoculated control in *L. multiflorum*	Guo and Chi (2014)

							• Increase photosynthetic pigments, mineral nutrients in both plants • Cd accumulation increased in *L. multiflorum* root, decreased in *G. max*	
Serratia sp. MSMC541	*Lupinus luteus* (Yellow Lupin)	YEM Agar 25 µg/mL congo red	ND	(MTC- mM) As-13.3 Cu-2.3 Pb-9.0 Zn-30 Cd-2.2	*L. luteus*	Pot experiment	• Increased shoot biomass • Plant tolerance to metals • Repressed metal translocation to shoot • Plant biomass improved	Aafi et al. (2012)
Agrobacterium radiobacter D14	*Pt. vittata* L. (Chinese brake)	Chemically defined medium with 800 (µmol/L) As (III)	IAA, siderophore	(MIC-mmol/L) As(III)-14 As(V)-150	*Populus deltoides* (Poplar)	Greenhouse pot experiment	• As uptake and translocation improved • Root-shoot growth enhanced • Plant dry weight increased • Chlorophyll, soluble protein content increased • Superoxide dismutase, catalase activity enhanced, malondialdehyde activity reduced	Wang et al. (2011)

(continued)

Table 22.2 (continued)

PGPR	Associated crop	Media[a]	PGP traits[b]	MIC[c]/MBC/MTC/MRL/Highest tolerance	Plant growth promotion study performed on (plant)	Mode of study	Improvements in crops after PGPR inoculation	Reference
Bacillus sp. PSB10	*Brassica campestris* (Mustard), *Lycopersicon esculentum* (Tomato)	Nutrient agar	Phosphate, siderophore, IAA, HCN, ammonia	(MIC-μg/mL) Cr-550	*Cicer arietinum* (Chickpea)	Open field experiment in pot	• Improved root-shoot length, nodule numbers, nodule dry weight, total dry weight • Enhanced seed yield, grain protein • Chromium uptake decreased	Wani and Khan (2010), Wani et al. (2007)
Bradyrhizobium sp. 750	*Lupinus* (Yellow Lupin) D.M.A.C. (Uppsala, Sweden)	NM	ND	(MTC-mM) As-2 Cd-<0.5 Cu -1.5 Pb-2 Zn-<1	*L. luteus*	In situ field experiment	• Zn accumulation higher than other HMs in roots, shoots • Strain 750 increased biomass, fixed nitrogen in soil • All strains improved biomass • Reduced metal accumulation in root shoot	Dary et al. (2010), Rodrı´guez-Llorente et al. (2010), Zurdo-Pineiro et al. (2007)
Pseudomonas sp. Az13	Rhizospheric region of legume plant	NM		MTC-mM As-4 Cd-1 Cu-4.5 Pb-5 Zn-3				
Ochrobactrum cytisi Azn6.2	*Medicago polymorpha* Nodules (Alfaalfa)	Tryptone yeast (TY) extract medium		MTC-mM As-8 Cd-1.5 Cu-3.5 Pb-6 Zn-10				

Burkholderia sp. RX232	*Salix caprea* (Goat willow)	Tryptic soy agar with $ZnSO_4$ (2 mmol l^{-1})	Siderophore, ACCD	(MIC-mmol/L) Cd-4 Zn-16	*S. caprea*	Greenhouse Pot experiment	• Helped in root growth • Significant reduction of HMs in roots	Kuffner et al. (2010)
Rhizobium sp. RP5	*Pisum sativum* (Pea plant)	Yeast extract mannitol (YEM) with $NiCl_2$ (0–350 μg. ml^{-1}) & $ZnCl_2$ (0–1500 μg.ml^{-1})	N_2, IAA, siderophore	(Tolerance-μg/mL) Ni-350 Zn-1500	*P.sativum*	Pot experiment	• Increased dry matter, nodule numbers, root-shoot N, leghemoglobin, seed yield, grain protein • Reduced HMs toxicity in plant organ	Wani et al. (2008a)
Rhizobium species RL9	*Lens esculenta* (Lentil)	Yeast extract mannitol medium	Siderophore, IAA	(Up to-μg/mL) concentration of Zn-400	*L. esculenta*	Pot experiment	• Enhanced dry weight, nodule numbers, nodule dry mass, growth, seed yield respect to uninoculated plants • Improved leghaemogloblin content, grain protein greater than uninoculated sets • Metal reduction noticed in plant tissue	Wani et al. (2008b)

(continued)

Table 22.2 (continued)

PGPR	Associated crop	Media[a]	PGP traits[b]	MIC[c]/MBC/MTC/MRL/Highest tolerance	Plant growth promotion study performed on (plant)	Mode of study	Improvements in crops after PGPR inoculation	Reference
Pseudomonas aeruginosa MKRh3	Rhizosphere samples of different plant species	King's B agar	IAA, siderophore, ACCD, phosphate	(MIC-mM) Cd-7	*Vigna mungo* (Black gram)	Pot experiment	• Significantly developed root-shoot length, root-shoot weight, plant growth, root branching • HM toxicity decreased • Cd accumulation lowered after inoculation	Ganesan (2008)
Bacillus subtilis strain SJ-101	Composite samples of rhizospheric soil	T-medium with (HMs) 1.0 mM each of Pb, Ni, Zn, Cr, Co, Cu	IAA, phosphate	(Maximum tolerance upto-mM) Ni-3.4	*Brassica juncea* (Indian mustard plant)	Pot experiment in open-field condition	• Plant growth promotion increased • Strain reduced phytoxicity by biosorption and bioaccumulation	Zaidi et al. (2006), Zaidi and Musarrat (2004)
Sinorhizobium meliloti strains Alf12	*Trifolium subterraneum* cv. *Nuba* (Sub clover), *Lotus corniculatus* (Birdsfoot trefoil), *Medicago sativa* (Alfalfa), *Vicia sativa* (Garden vetch)	Yeast Extract-Mannitol (YEM)	N_2	(MIC- ND)	*Medicago sativa* (Alfalfa)	Leonard jars were used for plant growth in growth chamber	• Healthier plants and N content increased • Symbiotic good effect noticed in contaminated soil • Nodulation and N_2 fixation similar to control	Carrasco et al. (2005)
S. meliloti Alf 2L4								
S. meliloti Med4D								

Mesorhizobium huakuii subsp. *rengei* B3	*Astragalus sinicus* (Chinese Milk Vetch)	NM	N_2	(MIC- ND) Cd	*A. sinicus*	Hydroponic experiment	• Nodule formation noticed • Synergetic relationship enhanced to accumulate Cd^{2+} in nodules 1.5-fold	Sriprang et al. (2003)
Proteus mirabilis T2Cr	Composite surface soil collected	Luria–Bertani (LB) media	IAA, phosphate, ACCD, siderophore	(MIC-ppm) Cr-90	*Zea mays* (Maize)	Pot experiment under room conditions	• Enhanced plant height, fresh weight, leaf area greater than control • Chlorophyll content improved by both strains compared to control • Isolates with salicylic acid application increased Cr tolerance by reducing metal uptake from root to shoot • Oxidative stress decreased by both strains with SA	Islam et al. (2016)
P. mirabilis CrP450				Cr-110				

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[a] *NM* Not mentioned

[b] *Urease* Urease activity, *IAA* Indole-3-acetic acid, *Siderophore* Siderophore production, *Phosphate* Phosphate solubilisation, *Potassium* Potassium solubilisation, *ACCD* 1-aminocyclopropane-1-carboxylic acid deaminase activity, N_2 Nitrogen fixation, *HCN* Hydrocyanic acid production, *Ammonia* Ammonia production, *ND* Not determined

[c] *MIC* Minimum inhibitory concentration, *MBC* Minimum bactericidal concentration, *MTC* Maximum/maximal tolerance/tolerable concentration

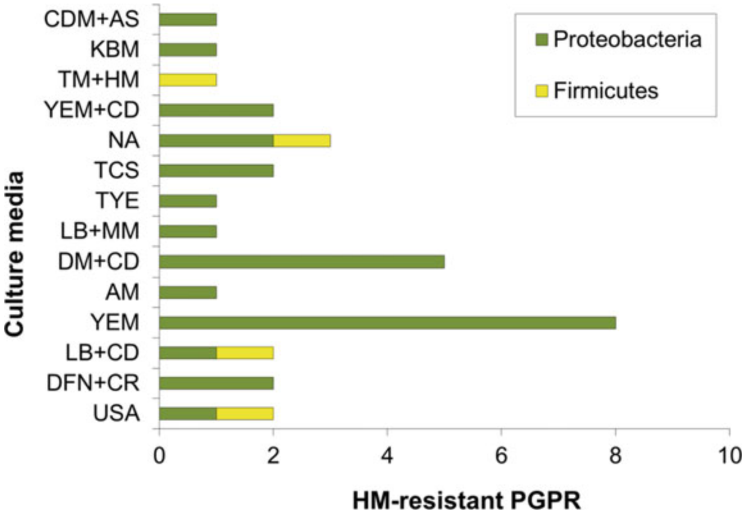

Fig. 22.3 Medium used for isolation of heavy metal(loid)-resistant PGPR. (*CDM* Chemically defined medium, *KBM* King's B medium, *TM+HM* T-medium with HM, *YEM+CD* Yeast extract mannitol with Cd, *NA* Nutrient agar, *TCS* Tryptone casein soya, *TYE* Tryptone yeast extract, *LB +MM* Luria–Bertani minmal media, *DM+CD* Davis Mingioli with Cd, *AM* Ashby's mannitol, *YEM* Yeast extract mannitol, *LB+CD* Luria–Bertani with Cd, *DFN+CR* Dworkin and Foster nutrient with Cr, *USA* Urease screening agar)

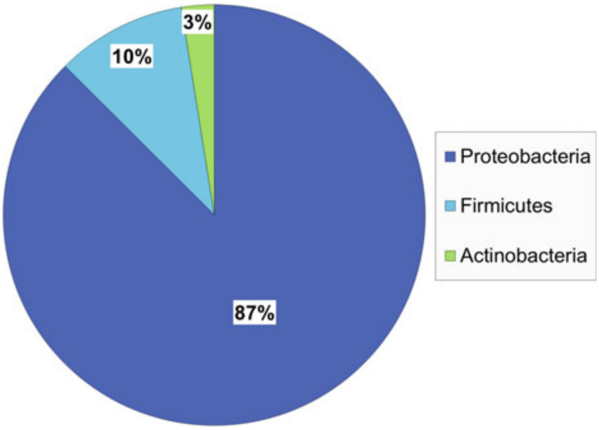

Fig. 22.4 Diversity and distribution of heavy metal(loid)-resistant PGPR

analysis of the information presented in Table 22.2, we find that the diversity of the HM-resistant PGPR community covers only three bacterial groups, i.e. proteobacteria, firmicutes and actinobacteria, and it is prominantly dominated by proteobacteria (Fig. 22.4). Furthermore, proteobacteria is the most abundant

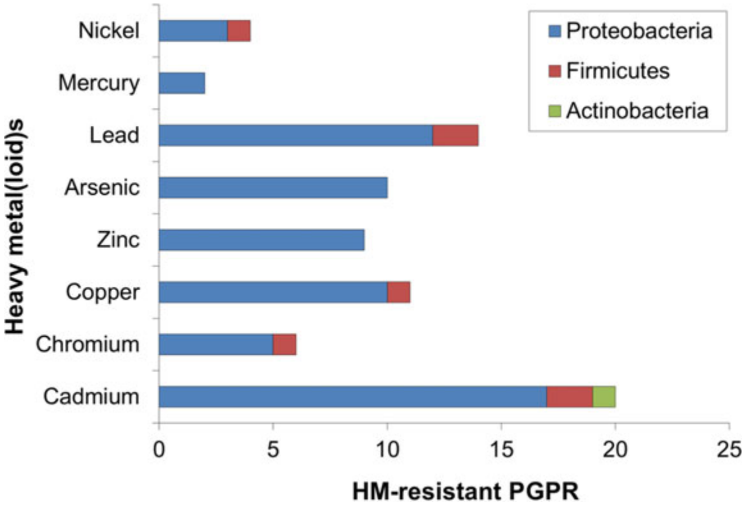

Fig. 22.5 Diversity and abundance of heavy metal(loid)-resistant PGPR

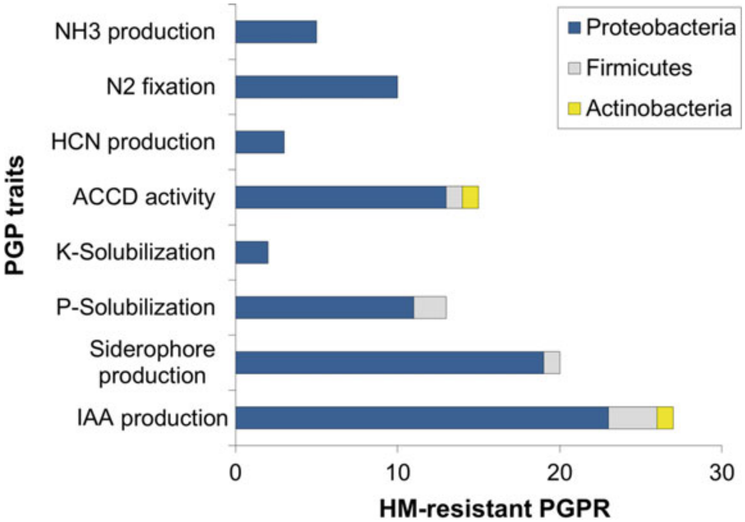

Fig. 22.6 Plant growth-promoting traits in heavy metal(loid)-resistant PGPR

PGPR member responsible for resistance to all the studied heavy metal(oid)s. Actinobacteria exhibit their remediational property only against Cd. The firmicutes are a set of PGPR sensitive to As, Hg and Zn (Fig. 22.5). Additionally, among the PGPR members, all the documented phenomenal PGP traits are mainly portrayed by the proteobacterial representatives, and actinobacterial agents are accountable only for their IAA and ACC deaminase producing capabilities (Fig. 22.6). Moreover, in case of firmicutes, they are the silent member in case of N_2 fixation, potassium solubilisation, ammonia and HCN production. However, the firmicutes have exhibited ACC activity, P-solubilisation, siderophore activity and IAA production (Fig. 22.6).

22.4 Genetically Modified Plant Growth-Promoting Rhizobacteria for Crop Enhancement

Natural components like the PGPR play an indispensable role in the advancement of sustainable agriculture and also serve as an imperishable treasure box for the environment. Considering the limitations of these natural bio-agents, the idea of using genetic modification approaches has attracted the attention of scientists with the goal of attaining greater desired efficiency. With the improvements achieved by genetically engineering PGPR, the heavy metal accumulating gene and the biocontrolling genes can be assembled to conduct enhanced bioremediation and potentially achieve biocontrol in the rhizospheric soil. In this context, for superior cadmium (Cd^{2+}) bioaccumulation purpose, the phytochelatin synthase gene (PCS_{AT}) from *Arabidopsis thaliana* was introduced into *Mesorhizobium huakuii* strain B3 and then set up as a symbiosis with *M. huakuii* strain B3 and *Astragalus sinicus,* whereupon a desired activity was noted accordingly (Sriprang et al. 2003). It was possible to carry out that project because the peptides like phytochelatins (PC) and metallothioneins (MT) exhibit high affinity towards a variety of heavy metals (Chaudhary and Shukla 2019). Furthermore, genetically transformed rhizobacterial strains demonstrated significant biocontrol potentiality over fungal phytopathogens (Sattiraju et al. 2019). In such cases, incorporation of a mini-Tn5 vector containing the complete operon for the biosynthesis of an antifungal metabolite phenazine- 1-carboxylic acid (PCA), within *Pseudomonas fluorescens* has been documented to accelerate the suppression of fungal diseases by the genetically engineered bacterial strain in comparison to the natural bacterial strain (Timms-Wilson et al. 2000). Similar kinds of approaches were reported from several studies where genetically engineered PGPR strains showed enhanced PGP traits as well as biocontrol efficiency (Bloemberg and Lugtenberg 2001) and can be exemplified by the integration of Cry-toxin-encoding *cry1Ac7* gene from *Bacillus thuringiensis*, chitinase-encoding *chiA* gene from *Serratia marcescens* and ACC deaminase-producing gene from *Enterobacter cloacae* into rhizobacterial strains like *Pseudomonas* sp. (Sattiraju et al. 2019). The relocation of *sss* gene from biocontrol strain *P. fluorescens* WCS365 to other *P. fluorescens* rhizobacterial strains was found to improve the competitive root colonising efficiency (Dekkers et al. 2000). Apart from the genetically modified PGPR, transgenic plants also display greater PGP traits, especially higher ACC deaminase activity and heavy metal accumulation (Zhuang et al. 2007; Stearns et al. 2005; Nie et al. 2002). However, genetically modified PGPB are considered less effective in terms of their survival and proliferation as compared to non-transformed versions of the same organisms; and this decreased fitness may be due to overburden of metabolic load by the expression of foreign genes (Glick 2020).

22.5 Plant Growth-Promoting Rhizobacteria in Biotic Stress Tolerance

The rhizosphere is a phenomenal environment where the plant-beneficial microbes especially the bacteria renowned as rhizobacteria, colonise and steadily perform several plant growth-promoting activities by means of facilitating nutrient availability and assimilation, and help conquer over disease-instigating microbes (Pérez-Montaño et al. 2014). The plant growth-promoting activities of these beneficial rhizobacteria include nitrogen fixation, solubilisation of minerals like phosphorus, production of ACC-deaminase and other plant growth regulators like auxins, gibberellins and cytokinins. Biocontrol properties are one of the key characteristic features of these PGPR (Kloepper 1978). Their antagonistic potentiality against phytopathogens is mainly categorised according to activities like the production of siderophores, lytic enzymes, antibiotics, bacteriocins, volatile organic compounds (VOC), hydrogen cyanide (HCN) and their ability to obstruct bacterial quorum sensing (Aloo et al. 2019; Pérez-Montaño et al. 2014; Kumar and Dubey 2012). Apart from these capabilities, PGPR also induce systemic resistance (ISR) proficiency which can help suppress pathogenicity that other microbes exhibit against host plants, and PGPR do as well improve the sustainability of agricultural systems (Beneduzi et al. 2012). Among the reported PGPR genera, *Pseudomonas* sp., *Bacillus* sp. and *Streptomyces* sp. are the warhorses in the avenue of biocontrol of phytopathogens (Table 22.3; Arrebola et al. 2019). Moreover, the rhizobacterial phyla involved in this job are dominated by proteobacteria, firmicutes and actinobacteria (Fig. 22.7). The bio-protecting efficiency of PGPR are not only restricted to countering the pathogenic microbial members of the rhizosphere community like fungi and bacteria, but are also promising as agents against metazoan phytopathogens like insects and nematodes (Table 22.3; Fig. 22.8).

The biological control of phytopathogens by the PGPR group of organisms does in many ways strengthen both plant and soil health. Rhizobacterial secretion of siderophores is among the mechanisms exhibited by the PGPR members that are antagonistic against other microoganisms. The actions of siderophores are based upon their chelation of iron which inhibits iron-dependent nutritional or energetic processes in those other microbes (Chaiharn et al. 2009). In iron-limiting soil environments, the binding of iron by siderophore-producing rhizobacteria can also boost up the availability of iron to those plants that are able to accumulate siderophore-bound iron (Tank et al. 2012). Apart from iron chelation, siderophores can bind with other heavy metals like Cd, Cu, Pb, Al and Zn which in turn diminishes the stress to plants that may be imposed by those other heavy metals

Table 22.3 Biocontrol activities of different PGPR

PGPR	Phylum	Pathogen	Reference
Fungi as phytopathogen			
Streptomyces sp.	Actinobacteria	*Fusarium oxysporum* *Fusarium* sp. *Gaeumannomyces* sp. *Phomopsis* sp. *Ulocladium* sp. *Rhizoctonia solani* *Colletotrichum* sp.	Suarez Moreno et al. (2019)
Pseudomonas aeruginosa	Proteobacteria	*Rhizopus microsporus* *Fusarium oxysporum* *Aspergillus niger* *Alternaria alternata* *Penicillium digitatum*	Uzair et al. (2018)
Azotobacter sp. *Pseudomonas* sp.	Proteobacteria Proteobacteria	*Helminthosporium* sp. *Fusarium* sp.	Bjelić et al. (2018)
Bacillus sp.	Firmicutes	*Fusarium culmorum* *F. oxysporum* *Monographella nivalis*	Przemieniecki et al. (2018)
Bacillus subtilis	Firmicutes	*Puccinia striiformis*	Reiss and Jørgensen (2017)
Burkholderia cenocepacia *Pseudomonas poae*	Proteobacteria Proteobacteria	*Alternaria alternata*	Ghosh et al. (2016a)
Burkholderia tropica *B. unamae* *B. cepacia*	Proteobacteria Proteobacteria Proteobacteria	*Alternaria alternata* *Rhizopus stolonifer* *Helminthosporium compactum*	Ghosh et al. (2016b)
Pseudomonas fluorescens	Proteobacteria	*Fusarium oxysporum*	Selvaraj et al. (2014)
Bacillus subtilis	Firmicutes	*Colletotrichum gloeosporioides*	Ashwini and Srividya (2014)
Bacillus simplex *B. subtilis*	Firmicutes Firmicutes	*Fusarium* sp.	Schwartz et al. (2013)
Bacillus sp.	Firmicutes	*Rhizoctonia solani*	Selva Kumar et al. (2013)
Brevibacillus laterosporus	Firmicutes	*Fusarium equiseti*	Prasanna et al. (2013)
Pseudomonas chlororaphis	Proteobacteria	*Fusarium oxysporum* *Rosellinia necatrix*	Calderón et al. (2013)
Pseudomonas chlororaphis	Proteobacteria	*Sclerotinia sclerotiorum* *Pythium aphanidermatum* *Macrophomina phaseolina* *Rhizoctonia solani* *Sclerotium rolfsii* *Fusarium oxysporum* *Alternaria solani* *Botryodiplodia theobromae*	Kumar and Dubey (2012)

(continued)

Table 22.3 (continued)

PGPR	Phylum	Pathogen	Reference
Rhizobium leguminosarum *Bacillus subtilis* *Pseudomonas* sp.	Proteobacteria Firmicutes Proteobacteria	*Macrophomina phaseolina* *Fusarium oxysporum* *F. solani* *Sclerotinia sclerotiorum* *Rhizoctonia solani*	Kumar (2012)
Bacillus antiquum	Firmicutes	*Macrophomonia phaseolina*	Gopalakrishnan et al. (2011)
Pseudomonas aeruginosa	Proteobacteria	*Aspergillus niger* *Helminthosporium* sp. *Fusarium oxysporium*	Hassanein et al. (2009)
Bacillus licheniformis	Firmicutes	*Gibberella saubinetii* *Aspergillus niger*	Xiao et al. (2009)
Rhizobium spp.	Proteobacteria	*Fusarium oxysporum*	Mazen et al. (2008)
Bacillus amyloliquefacines	Firmicutes	*Fusarium oxysporum*	Chen et al. (2007)
Rhizobium leguminosarum	Proteobacteria	*Pythium* spp.	Huang and Erickson (2007)
Pseudomonas fluorescens	Proteobacteria	*Pythium ultimum* *Rhizoctonia solani*	Andersen et al. (2003)
Rhizobium sp.	Proteobacteria	*Macrophomina phaseolina*	Deshwal et al. (2003)
Myxococcus sp.	Proteobacteria	*Cylindrocarpon* sp. *Fusarium oxysporum* *Phytophthora capsici* *Pythium ultimum* *Rhizoctonia* sp. *Sclerotinia minor* *Verticillium albo-atrum* *V. dahliae*	Bull et al. (2002)
Streptomyces sp.	Actinobacteria	*Pythium ultimum* *Fusarium oxysporum*	Castillo et al. (2002)
Pseudomonas fluorescens	Proteobacteria	*Fusarium oxysporum* f.sp. *ciceris*	Rangeshwaran and Prasad (2000)
Pseudomonas fluorescens	Proteobacteria	*Rhizoctonia solani*	Ligon et al. (2000)
Bacteria as phytopathogen			
Pseudomonas stutzeri *P. alcaligenes* *P. aeruginosa* *P. denitrificans* *P. syringae* *P. fluorescens*	Proteobacteria Proteobacteria Proteobacteria Proteobacteria Proteobacteria Proteobacteria	*Ralstonia solanacearum*	Mohammed et al. (2020)
Streptomyces sp.	Actinobacteria	*Burkholderia glumae*	Suarez Moreno et al. (2019)
Bacillus amyloliquefaciens	Firmicutes	*Ralstonia solanacearum*	Etesami and Alikhani (2017)

(continued)

Table 22.3 (continued)

PGPR	Phylum	Pathogen	Reference
Nematode as phytopathogen			
Pseudomonas aeruginosa *Burkholderia gladioli*	Proteobacteria Proteobacteria	*Meloidogyne incognita*	Khanna et al. (2019)
Pseudomonas fluorescens *Rhizobium leguminosarum*	Proteobacteria Proteobacteria	*Meloidogyne javanica*	Tabatabaei and Saeedizadeh (2017)
Bacillus velezensis *B. mojavensis*	Firmicutes Firmicutes	*Heterodera glycines*	Xiang et al. (2017)
Bacillus tequilensis *B. flexus*	Firmicutes Firmicutes	*Meloidogyne incognita*	Tiwari et al. (2017)
Bacillus sp. *Lysobacter* sp.	Firmicutes Proteobacteria	*Meloidogyne incognita*	Zhou et al. (2016)
Pseudomonas fluorescens *Bacillus Subtilis*	Proteobacteria Firmicutes	*Meloidogyne graminicola*	Priya (2015)
Pseudomonas fluorescens	Proteobacteria	*Helicotylenchus multicinctus*	Selvaraj et al. (2014)
Pseudomonads putida *P. fluorescens* *Serratia marcescens* *Bacillus amyloliquefaciens* *B. subtilis* *B. cereus*	Proteobacteria Proteobacteria Proteobacteria Firmicutes Firmicutes Firmicutes	*Meloidogyne incognita*	Almaghrabi et al. (2013)
Insect (Pest) as phytopathogen			
Pseudomonas protegens	Proteobacteria	*Galleria mellonella*	Bensidhoum et al. (2016)

(Ahemad and Kibret 2014). PGPR additionally produce various defensive lytic enzymes such as chitinase, glucanase, cellulase, protease, chitosanase, peroxidase, catalase, phenolic lyase, superoxide dismutase, etc. (Aloo et al. 2019) which can act to protect plants from the pathogens. Pathogens responsible for several plant diseases are directly liable for plant growth inhibition and these are mainly fungi and insects (Banerjee and Mandal 2019). The lytic enzymes like chitinase, chitosanase, glucanase and cellulases produced by PGPR act in a straight line biocontrol mechanism against the chitin and glucan cell wall components of those fungi and insects. Disease control management by the PGPR is additionally accomplished not only by means of antibiotics produced like zwittermicin, mycosubtilin, gramicidin S, polymyxin B, bacilysin, rhizocticins, etc. but also by bacteriocins (Saraf et al.

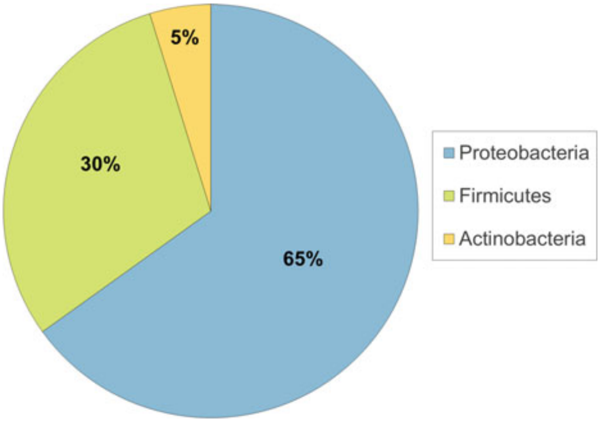

Fig. 22.7 Diversity and abundance of PGPR with biocontrol potentiality

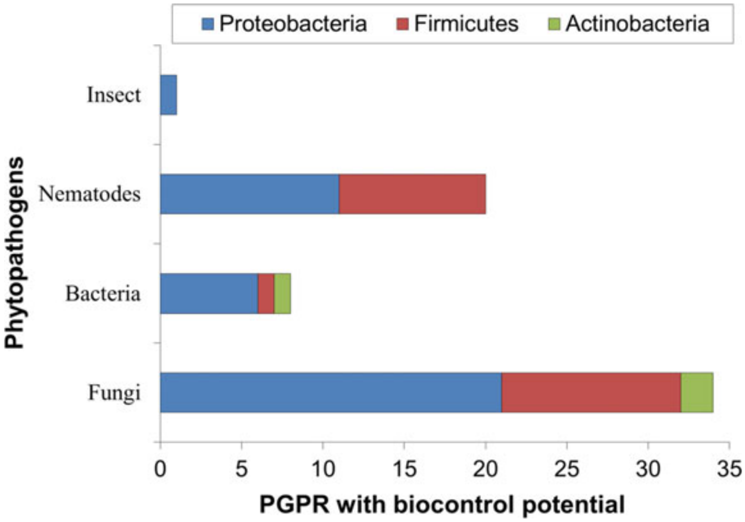

Fig. 22.8 Biocontrol proficiency of various PGPR against different phytopathogens

2014; Haggag 2008; Leclere et al. 2005; Chin-A-Woeng et al. 2003). Enhancement of plant defense mechanisms by a combination of ISR plus biocontrol ability was also validated by studies of several PGPR that produce VOCs (Shafi et al. 2017; Cao et al. 2011). The occurrence of such dual potentiality can be exemplified by VOCs like 2, 3-butanediol, isoprene and acetoin that are produced by different PGPR (Lee et al. 2015; Ryu et al. 2004). Plant pathogens can also be controlled by many PGPR via HCN production, a recognised VOC which disrupts the electron transport system that leads to blocking the energy supply of the pathogens (Patel and Minocheherhomji 2018).

In recent years, biocontrol has become an emerging and promising technological approach in developing sustainability in agriculture with optimism both for its comprehensive potentiality against various types of plant pathogens as well as its being an efficient alternative resource over chemical fungicides and pesticides. In addition, several PGPR have been documented for their ability to remediate heavy metals in agricultural fields. There are indeed many published reports on heavy metal remediation by the PGPR (Table 22.2); although reporting on the combinational effect of HM bioremediation cum biocontrol activity by PGPR is very scarce. Two such examples of combined activity by PGPR are *Alcaligenes* sp. and *Pseudomonas aeruginosa*, where nickel and manganese bioremediations were testified along with aptitude for biocontrol of phytopathogens like *Aspergillus niger, A. flavus, Fusarium oxysporum, Alternaria alternata, Cercospora arachichola* and *Metarhizium anisopliae* (Sayyed and Patel 2011). There is some justifiable optimism that the application of this kind of heavy metal remediating cum biocontrolling PGPR in agricultural fields will replace the usage of chemical pesticides and fertilisers, which in turn will decrease the bioaccumulation of hazardous chemicals into agronomic plants and passage of these contaminants further up the biological chain, leading to a more environmentally safe and affordable agriculture in terms of human welfare. However, the effective biocontrol property of PGPR against invading phytopathogens is subject to the considerations of soil type, host plant species and influential holobiont microbial community in the rhizosphere (Subrahmanyam et al. 2020).

22.6 Mechanism of Heavy Metal(loid) Resistance by Plant Growth-Promoting Rhizobacteria

Plant-associated HM-resistant PGPR are more profoundly present in heavy-metal-contaminated soil, as evidenced by many earlier publications (Pandey et al. 2010; Chen et al. 2016; Treesubsuntorn et al. 2018; Pramanik et al. 2017, 2018a, b; Mitra et al. 2018a, b). Such PGPR strains are known to develop resistance mechanisms in adaptation to the different HM ions present in their habitats (Table 22.4). The various known survival strategies which metal tolerant species have used to combat HMs are summarised in Table 22.4. These include active transport of metal ions (efflux/influx) by the presence of a group of specific membrane bound, cytoplasmic or periplasmic metal transporters (Nies 2003; Yang et al. 2019), production of biodegradable metal chelators like siderophores (Sinha and Mukherjee 2008; Dimkpa et al. 2008), intracellular bioaccumulation and biosorption (Chen et al. 2016; Treesubsuntorn et al. 2018; Pramanik et al. 2017, 2018a, b; Mitra et al. 2018a, b; Pal and Sengupta 2019), enzymatic oxidation and reduction metal transformations (Chatterjee et al. 2009; Pramanik et al. 2016; Ghosh et al. 2018; Kamaruzzaman et al. 2019), extracellular complexation by the secretion of extracellular polysaccharides (EPSs) (Gupta and Diwan 2017), etc. (Table 22.4). The genetic determinants of

Table 22.4 General mechanism of heavy metal(loid)-resistant PGPR including rhizobia

PGPR and Rhizobia	Heavy metal resistance	Proposed mechanism	References
Serratia marcescens S2I7	Cd(II)	Detoxification of Cd(II) by glutathione S-transferase (GST) mechanism and *czcD* gene-mediated protein	Kotoky et al. (2019)
Lysinibacillus varians KUBM17 *Pseudomonas putida* KUBM18	Cd(II), Pb (II)	Bioaccumulation of Cd(II) and Pb(II)	Pal and Sengupta (2019)
Caulobacter flavus RHGG3^{T}	Co(II), Cd (II), Zn(II)	Export of Co(II), Cd(II), Zn(II) metal cations from both cytoplasm and periplasmic space to outside of cell by efflux transporter protein encoded by several *czc* genes such as *czcA, czcB, czcC* and *czcD*. Another gene *znt* found to be involved in Cd(II) resistance encoded a Cd(II) exporting ATPase	Yang et al. (2019)
	Cu(II)	Cu(II) resistance by several efflux proteins encoded by different *cop* genes and also by multicopper oxidase protein encoded by *cueO*. Another gene system *cut* also found to be involved in Cu(II) resistance	
Bacillus cereus, *Bacillus aerius*, *Exiguobacterium profundum*	Cr(VI)	Reduction of Cr(VI) into Cr(III) and by adsorption of Cr(VI)	Kamaruzzaman et al. (2019)
Curtobacterium sp. GX_31, *Sphingomonas* sp. GX_15	Cd(II)	Biosorption of Cd(II) by physical entrapment, ion exchange and complexation on cell surface	Li et al. (2018)
Cupriavidus necator GX_5	Cd(II)	Bioaccumulation of Cd(II)	
Enterobacter sp. S2	Cd(II)	Bioaccumulation of Cd(II)	Mitra et al. (2018a)
Klebsiella michiganensis S8	Cd(II)	Cytosolic accumulation of cadmium	Mitra et al. (2018b)
Enterobacter aerogenes K6	Cd(II)	Bioaccumulation of Cd(II)	Pramanik et al. (2018a)
Bacillus aryabhattai MCC3374	As (III) and As (V)	Bioaccumulation, Biotransformation of As(V) to As(III) by arsenate reductase respectively	Ghosh et al. (2018)
Klebsiella pneumoniae K5	Cd(II)	Bioaccumulation of Cd^{2+} ions and biosorption of Cd^{2+} by negatively charged EPS	Pramanik et al. (2017)
Cellulosimicrobium funkei AR6	Cr(VI)	Bioreduction of Cr(VI) to Cr(III) without extracellular donor, immobilisation	Karthik et al. (2017a, b)

(continued)

Table 22.4 (continued)

PGPR and Rhizobia	Heavy metal resistance	Proposed mechanism	References
		of Cr(III) by cell wall, intracellular accumulation of Cr(III)	
Enterobacter sp. P36	Cu(II)	Cu(II) accumulation in bacterial cell	Sharaff et al. (2017)
Bacillus aryabhattai AB211	Cu(II)	Resitance by Cu(II) ion efflux system P-type ATPase (CopA), and copper resistance CopC/CopD protein	Bhattacharyya et al. (2017)
	Co(II), Zn (II), Cd(II)	Resitance due to Co(II)/Zn(II)/Cd (II) resistance protein CzcD and heavy metal resistance transcription regulatory protein HmrR. Zn(II) resistance also conferred by Sensor protein of zinc sigma-54-dependent two-component system and its regulatory protein	
	As(V) and As(III)	Arsenic resistance by arsenic efflux protein pump and arsenate reductase enzyme	
Enterobacter sp. EG16.	Cd(II)	Intracellular accumulation, biosorption by physical adsorption, ion-exchange and complexation on cell surface	Chen et al. (2016)
Bacillus flexus ASO-6	As (III) and As (V)	Oxidation of As(III) by arsenite oxidase encoded by *aoxB* gene	Das et al. (2016)
Rhizobium sp. ND2	Cr(VI)	Reduction of Cr(VI) to Cr(III), adsorption of chromium on cell wall	Karthik et al. (2016)
Raoultella sp. CrS2	Cr(VI)	Cr (VI) reduction by constitutive chromate reductase enzyme	Pramanik et al. (2016)
Bradyrhizobium japonicum	Pb(II), Ni (II)	Biosorption of Pb(II) and Ni(II) metal ions by amino, nitro functional groups present on bacterial cell wall	Seneviratne et al. (2016)
	Cu(II)	Biosorption of Cu(II) metal ions by alcoholic and amino functional groups present on bacterial cell wall	
Enterobacter cloacae HG 1 *Klebsiella pneumoniae* HG 3	Hg(II)	Mercury tolerance by EPS binding of mercury ions (hypothesised)	Gontia-Mishra et al. (2016)
Enterobacter ludwigii HG 2	Hg(II)	Mercury tolerance by *mer* operon (hypothesised)	
*Bacillus muralis*CA9 *B. muralis* CA16b *Bacillus simplex* CA15 *B. simplex* CA16a *B. simplex* CA22	Hg(II)	Reduction of Hg^{2+} into volatile Hg^0 by cytoplasmic mercuric reductase encoded by *merA* gene	Calzada Urquiza et al. (2016)

(continued)

Table 22.4 (continued)

PGPR and Rhizobia	Heavy metal resistance	Proposed mechanism	References
Bradyrhizobium japonicum E109	As (III) and As (V)	Bioaccumulation of As(III), reduction of As(V) to As(III) by arsenate reductase encoded by *arsC* gene and efflux by As(III) efflux pump encoded by *arsB* gene, oxidation of As(III), increased production of biofilm (possibly associated with resistance)	Armendariz et al. (2015)
Azospirillum brasilense Az39		Bioaccumulation of As(III), reduction of As(V) to As(III) by arsenate reductase encoded by *arsC* gene and efflux by As(III) efflux pump encoded by *arsB* gene, increased production of biofilm (possibly associated with resistance) Higher resistance to arsenic due to presence of two extra genes *arsH* and *Acr3* which encode NADPH:FMN oxide reductase and As(III) efflux protein respectively	
Rhizobium sp. CCNWSX0481 SV20, *Rhizobium leguminosarum* bv. *viciae* SV 15, *Pseudomonas* sp. SV23, *Enterobacter cloacae* SV27	Cu(II)	Bioaccumulation of Cu(II)	Fatnassi et al. (2015)
Pseudomonas spp. *Cronobacter* spp. *Bacillus* spp.	Hg(II)	Conversion of methyl mercury into Hg^{2+} ions in cell and conversion of toxic Hg^{2+} into less toxic form Hg_2S	Rafique et al. (2015)
Mesorhizobium amorphae 186	Cu(II)	Efflux of Cu(II) metal ions from cytoplasm to periplasmic space by P-type ATPase (CopA-6910), and CusAB detoxification of periplasm by exporting Cu(II) ions from periplasm to extracellular spaces	Hao et al. (2015)
Enterobacter cloacae AW1 *Pseudomonas fluorescens* AW2 *Pseudomonas putida* AW4 *Pseudomonas poae* AW5 *Pseudomonas poae* AW6	As (III) and As (V)	Bioaccumulation	Oller et al. (2013)

(continued)

Table 22.4 (continued)

PGPR and Rhizobia	Heavy metal resistance	Proposed mechanism	References
Pseudomonas aeruginosa OSG41	Cr(VI)	Bio-reduction of hexavalent chromium	Oves et al. (2013)
Rhizobium leguminosarum RL 9	Ni(II)	Metal adsorption/desorption	Wani and Khan (2013)
Pseudomonas aeruginosa WI-1	Pb(II)	Metallothionein (encoded by *bmtA* gene) mediated metal sequestration and intracellular bioaccumulation	Naik et al. (2011)
Sinorhizobium spp.	Zn(II), Cd (II), Pb(II), Cu(II)	Adsorption of heavy metal ions on cell surface, intracellular accumulation of heavy metal ions	Zribi et al. (2011)
Ochrobactrum cytisi Azn6.2	Cd(II), As (II), Zn(II), Cu(II)	Biosorption/ Desorption by lipopolysaccharides of cell wall	Rodríguez-Llorente et al. (2010)
Bacillus spp., *Achromobacter* spp., *Brevundimonas* spp., *Microbacterium* spp., *Ochrobactrum* spp. *Ensifer* spp. *Bosea* spp. *Sinorhizobium* spp. *Bordetella* sp. *Ancylobacter dichloromethanicum* As3-1b *Georgenia ferrireducens*As5-12 *Rhodococcus erythropolis*As5-4a	As (III) and As (V)	Reduction of As(V) into As(III) by arsenate reductase encoded by *ArsC* gene, efflux of As(III) by *ArsB* and *ArsA* genes which code for As(III) efflux pump and used proton motive force and AS(III) activated ATPase Another gene *ACR3* homologous to *ArsB* also codes for As(III) efflux protein in highly resistance strains Either one or both types of genes in combination confer resistance among these bacteria	Cavalca et al. (2010)
Mesorhizobium sp. RC1, *Mesorhizobium* sp. RC4	Cr(VI)	Reduction of Cr(VI)	Wani et al. (2009)
Cellulosimicrobium cellulans KUCr3	Cr(VI)	Reduction of Cr(VI)	Chatterjee et al. (2009)
Azotobacter chroococcum HKN-5 *Bacillus megaterium* HKP-1	Pb(II), Cd (II)	Adsorption of Pb^{2+} and Cd^{2+} on cell wall	Wu et al. (2009)
Enterobacter asburiae PSI3	Cd(II)	Complexation of metal by extracellularly secreted organic acids	Kavita et al. (2008)
Rhizobium sp. RP5	Zn(II), Ni (II)	Metal adsorption/desorption	Wani et al. (2008a)
Rhizobium leguminosarum RL 9	Zn(II)	Metal adsorption/desorption	Wani et al. (2008b)

(continued)

Table 22.4 (continued)

PGPR and Rhizobia	Heavy metal resistance	Proposed mechanism	References
Pseudomonas putida ARB86	Ni(II)	Absorption and accumulation of Ni in cells	Someya et al. (2007)
Bradyrhizobium sp. (vigna) RM8	Zn(II), Ni (II)	Metal adsorption/desorption	Wani et al. (2007)
Brevibacillus brevis B1	Zn(II)	Bioaccumulation and Biosorption	Vivas et al. (2006)
Pseudomonas aeruginosa sp. NBRI 4014 mutants	Cr, Cd(II), Ni	Bioaccumulation and internal sequestration by resistant enzymes	Gupta et al. (2004)
*Azospirillum lipoferum*137 *Agrobacterium radiobacter*10	Cd(II)	Accumulation of Cd	Belimov et al. (2004)
Azospirillum brasilense Sp245	Co(II)	Rapid adsorption of Co^{2+} on cell surface followed by rapid metabolic transformation	Kamnev et al. (2004)
Pseudomonas putida PNL-MK25	Cu(II)	Efflux of Cu(II) metal ions by P1-type ATPase (CueA)	Adaikkalam and Swarup (2002)
Serratia plymuthica Br-10	Cd(II)	Bioaccumulation	Carlot et al. (2002)

metal resistance can be localised either in chromosomal or extrachromosomal genetic elements.

Heavy metals most commonly exist in the form of cations which can form many unspecific complexes. Among all these, a few HM cations are important biological trace elements (such as Mn^{2+}, Zn^{2+}, Cu^{2+}, Ni^{2+}, Mo^{2+}, Co^{2+}) used in regulating several important biochemical reactions. The intracellular passage of different HMs is, in fact, governed by two opposite types of uptake systems. The first of these systems is constitutively expressed, fast, unspecific and uses a variety of substrates, while the second system is inducible, slow and highly specific for substrates (Nies 1999). The main driving force for the first system is an electrochemical gradient across the plasma membrane, and for the second system it is the energy generated by ATP hydrolysis (Nies and Silver 1995). The constitutive and unspecific nature of the first kind of system causes most of the HM-toxicity in bacteria as it continuously accumulates a heavy metal even if the cell already contains a high concentration of that same HM (Nies and Silver 1995). After a metal has been accumulated beyond threshold levels, HMs impart several toxic effects such as inhibition of enzyme actions due to the binding of Hg^{2+}, Cd^{2+} and Ag^{2+} to -SH groups, generation of oxidative stress and inhibition of the activity of sulphate and phosphate compounds by structurally related chromate and arsenate, respectively. Briefly, there are six widely known heavy metal resistance mechanisms in bacteria, they are: (1) exclusion of HMs by permeability barriers, (2) extracellular sequestration, (3) intracellular sequestration, (4) enzymatic detoxification of HMs, (5) active transport or efflux system of HMs and (6) reduction in HM sensitivity of cellular targets.

However, the details of many heavy metal resistance mechanisms used by PGPR are still to be fully explored, and we will have to unravel the genetic mysteries behind metal-PGPR interactions to effectively apply them for HM-bioremediation.

22.7 Constraints in the Application of Plant Growth-Promoting Rhizobacteria

Although the PGPR strains far discovered have proven promising in controlled laboratory conditions, their efficacy in reality is contingent on how they act in field conditions. During the last few decades, a number of PGPR strains have been discovered around the world but few reached the ultimate goal of having utility for farmers. In contrast to the laboratory, the reality of field work is one of non-optimal conditions that may or may not be favouarbale for the survival and proliferation of the PGPR strains (Glick 2020). The existence and growth of field-applied PGPR strains indeed depends on a vast range of adverse environmental factors that need to be overcome so that the microbes take part in assisting plant growth-promotion activities in contaminated soil (Fig. 22.9). It is not an easy task to achieve successful application of such PGPR strains even if they hold a bunch of potentially beneficial

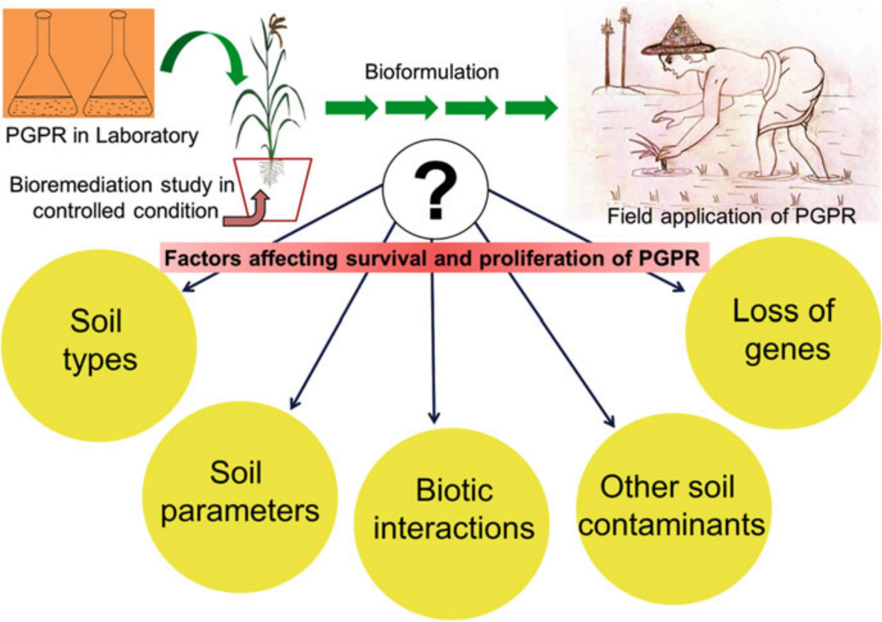

Fig. 22.9 Factors affecting survival and proliferation of PGPR

traits for the crop plants. Apart from following government-enforced guidelines, one of the major constraints in field application is soil type and it directly influences the survival and growth of the microbial communities (Fig. 22.9). To introduce a genetically engineered orgainsm, we need to give special attention to the fact that government legislation varies from country-to-country. Soil parameters such as compaction, oxygen content, pH and temperature are also crucial in this respect because they can affect the functioning of the microbes. In contrast to wild type indigenous strains, the genetically modified organisms are often less adaptive perhaps as a consequence of burdensome metabolic demands due to the expression and perhaps overexpression of foreign DNA (Glick 2020). In addition, PGPR strains often do not have equal abilities to compete with soil-borne phytopathogens and other antagonistic soil microbial communities, the PGPR strains sometimes do not have the capacities to tolerate a wide range of soil contaminants, and habituation to growing in nutrient-rich media under laboratory conditions may have resulted in functional loss of active genes that previously made the microbes suitable in contaminated rhizopshere environments (Glick 2020; Fig. 22.9).

22.8 Conclusion

Heavy metal(loid)-affected agricultural crops have benefitted for many years from the application of indigenous HM-resistant PGPR. Although there are a lot of constraints associated with the application of these microorganisms, their great diversity and natural abundance in contaminated soil offers a ray of hope as we explore their potential role in agriculture. Recent advancements in bioremediation strategies have given us cause for optimism. But, before field application, these PGPR should be verified for their degree of metal resistance, their level of plant growth-promoting traits, and obviously their ability to reduce HM-content in plant parts under controlled conditions. Henceforth, these PGPR are naturally dwelling microflora that should be isolated, enriched and applied for sustainable agriculture in HM-contaminated fields.

Contributing authors of this book chapter

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