Chapter 9
Cadmium Stress Tolerance in Plants and Role of Beneficial Soil Microorganisms

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Abstract Heavy metal stress triggers anomalies in the plant metabolic activity thereby reducing the yield potential of the crop plants. Cadmium (Cd) is one of the toxic heavy metals that is continuously added to the soil through natural as well as anthropogenic means and once taken up by plants can inhibit plant growth and development. Cd toxicity causes problem in uptake and metabolism of essential mineral elements as a result of reduced enzyme activity and protein synthesis. It has been observed that essential mineral nutrients and the available soil Cd show direct competition for the transport proteins. In addition, Cd alters with the sulfhydryl group of proteins resulting in reduced enzyme activity. Soilborne microorganisms include all actively metabolizing organisms directly or indirectly associated with the improvement of soil health and the existing flora. Among the soilborne beneficial microorganisms, arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) have been widely accepted for their growth-promoting role. Optimization of important physiological and biochemical processes in plants can be achieved by the soilborne microorganisms. Hence exploiting their unique properties including stress tolerance via synthesis of compatible

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solutes and phytohormones, biocontrol agents, etc. should be exploited. The present review discusses the role of beneficial soil microorganisms in alleviating the effects of Cd stress in crop plants.

Keywords Stress tolerance · Plant microbiome · Arbuscular mycorrhizal fungi · PGPR · Cadmium

9.1 Introduction

Soil solution forms the key component for healthy plant growth and inhibiting microbes, and any alteration in its physical, chemical, and biological characteristics will have direct influence on the existing flora. Likewise, interactions triggered due to metal pollution affect the bioavailability of essential nutrients (Nazar et al. 2012; Ahmad et al. 2015; Kamran et al. 2015). Some plants modulate metal accumulation using various transporters either via active or passive mechanisms resulting in net change in the soil pH around root, i.e., rhizosphere. Alterations in the rhizosphere soil pH majorly affect the bioavailability of the pH-dependent nutrients in addition to the toxic metal ions (Hinsinger et al. 2006). As a common view, soil contains nutrients as well as toxic metals which often display interactions at precipitation, absorption, and the complex formations with the important organic compounds (Pantazis et al. 2007; Chibuike and Obiora 2014). Root secretions or exudates considerably influence Cadmium (Cd) bioavailability and its toxicity due to alterations in the pH, chelation, redox state, intensity, and the activity of soil microbes. It has been observed that the optimal availability of root-secreted organic substances like oxalic acid, citric acid, etc. in the rhizosphere has a key role in reducing the absorption of toxic metals like Cd by formation of metal-chelate complex.

Growth of plants is determined by several factors, and excess presence of a particular factor can create alterations in normal developmental and metabolic processes. Stresses, including biotic and abiotic, impart deleterious effects on the crop growth and hence result in significant yield losses. Between the abiotic stress factors, the presence of heavy metals in agricultural soils has been observed to restrict growth of major food crops. Cd is one of the toxic heavy metals easily taken up by plants and obstructs the metabolic processes. The most accepted reasons for the increased concentration of Cd in soils have been the greater usage of chemical fertilizers, sewage wastewater for irrigation, and rapid industrialization. All these sources result in triggering harmful effects on soil-plant environment system. Cd has been ranked among seven most toxic substances and the key reason for the alarming toxicity of being its prolonged lifetime in soil. It has been observed that the concentration of Cd in soils considered as suitable for normal growth is less than 0.5 mg kg^{-1} of soil (Vahter et al. 1991). Cd is considered as a non-essential element for the crop plants; however, it has high mobility between soil and plant system, thereby entering the food chain resulting in significant damage to plants as well as animals including humans. Different threshold levels for Cd accumulation in plants have been determined in crops like cereals (0.013–0.22 mg kg^{-1}) and grasses (0.07–0.27 mg kg^{-1}) (Kabata-Pendias and Pendias 2001). There are considerable evidences that excessive use of phosphate fertilizers or phosphorites also results in heavy accumulation of Cd in soils resulting in alteration of growth (Abd_Allah et al. 2015; Ahmad et al. 2015). It has been observed that accumulation of Cd causes several physiological, biochemical, and genetic alterations which are more often reflected on the structural makeup of the plant (Feng et al. 2010). Plants grown on Cd-rich soils display altered nutrient uptake, photosynthetic restrictions, hampered enzyme activity, altered stomatal functioning, and declined tissue water content (Abd_Allah et al. 2015; Hashem et al. 2016a, b). Moreover, excess Cd translocation into plants has been observed to reduce the activity of enzymes of carbon metabolism hence the productivity and biomass accumulation (Mobin and Khan 2007; Hashem et al. 2016a, b, c). Plants exhibiting higher intake of Cd and other heavy metals show greater generation of free radicals including superoxide, hydrogen peroxide, and hydroxyl due to the direct effect on the activity of the radical generating pathways mediated by enzymes like NADPH oxidase (Sirhindi et al. 2016). Cd hampers the cellular redox balance, thereby leading to obstructions in the normal functional patterns of major metabolic pathways (Ahmad et al. 2018; Alyemeni et al. 2017). In addition, the accumulated free radicals in Cd stress lead to enhancement in the rate of lipid peroxidation, and hence oxidative damage to plant tissue is initiated (Abd_Allah et al. 2015; Per et al. 2016).

For counteracting the negative effects triggered by Cd accumulation, numerous mechanisms are initiated, and these include greater synthesis and accumulation of compatible solutes, phytochelatins, upregulation of the antioxidant system, and effective partitioning of the toxic ions (Hashem et al. 2016a, b, c; Alyemeni et al. 2017). Antioxidant system neutralizes the toxic radicals to prevent oxidative damage to key molecules, and on the contrary, phytochelatins bring chelation of toxic metal ions thereby proving much effective by preventing the initiation of toxic effects of metal ions (Ahmad et al. 2018). Osmolytes, antioxidants, and phytochelatins in combination bring modulation of metabolic pathways by maintaining the tissue water content and structural integrity and preventing radical generation, respectively (Nazar et al. 2012). So, the net effect of Cd in soil-plant relationship is its influence on the physiological and biochemical processes primarily by affecting the enzyme activity, mineral nutrition and assimilation, photosynthesis, antioxidant metabolism, and redox homeostasis (Ahmad et al. 2018; Chiboub et al. 2018). In the first part of the present review, the growth and metabolic alterations triggered by Cd are addressed followed by the role of existing soil microorganisms in the amelioration of metal-induced effects focusing primarily on the importance of beneficial microorganisms in the alleviation of Cd toxicity and its ill effects.

9.2 Mechanisms of Uptake, Transport, and Accumulation of Cd

Uptake, transport, and accumulation or partitioning of Cd in plants have been studied in somewhat up to comparable levels. With the induction of Cd stress, plants have been observed to experience restriction on the uptake of other mineral elements by competing for the transport protein at the membrane levels (Nazar et al. 2012; Ahmad et al. 2018; Abd_Allah et al. 2017). Transport proteins including ABC and natural resistance-associated macrophage protein have been observed to carry out the transport of Cd ions in plants and their expression get upregulated in plant species exposed to Cd stress (Sarwar et al. 2010). Besides the activation of Cd transport proteins, the partitioning of accumulated Cd into various organs plays an important role in determining the intensity of Cd toxicity in plants under question. Several factors controlling the Cd uptake, accumulation, and toxicity include the concentration and availability of Cd in rhizosphere, symplastic or apoplastic space of Cd transport within the plant tissues, loading and translocation via xylem, and the accumulated Cd within vacuoles as cadmium-phytochelatin complex. In addition to the transport proteins and other mechanisms depicted above, the cation-exchange capacity of the cell walls of root tissues is also a key determining factor in the net uptake of heavy metal(loid)s. In the simplest way, greater action-exchange capacity reflects greater metal adsorption in the cellular walls, thereby making them easily available for the membrane transport with a significant reduction in efflux of metal ions. Such high ion-exchange capacity trigger metal accumulation in cellular components, including the cytoplasm, and severely affects metal tolerance potential of plants (Singh et al. 2015a).

In general, it can be quoted that transport proteins carrying out metal transport may be either general or specific. For example, among the key general metal ion transporters, NRAMP represents an important group of transporters which are transmembrane proteins implemented in transport and homeostasis of metal ions and are considered as responsible for the transport of Fe^{2+}, Cd^{2+}, Mn^{2+}, Cu^{2+}, Ni^{2+}, Zn^{2+}, and Co^{2+} ions (Nevo and Nelson (2006). More precisely, the transporters that mediate transport of one ion may also carry the other ions as has been observed for uptake and transport of zinc (Zn) and Cd (Wong and Cobbett 2009). P1B-ATPase (HMA) – a specific metal ion transporter – is involved in the translocation of ions specifically Cd and Zn out of the cytoplasm into the vacuole, thereby reflecting to their efflux mechanism. It has been suggested that the efflux or export metal ion transporters are much more selective as compared to the ones involved in the import function (Kramer et al. 2007; Singh et al. 2015a). Overexpression of the exporter proteins derived from metal hyper-accumulators has been observed to improve tolerance of yeast to Cd and Zn (Papoyan and Kochian 2004). Such transporters are considered as potential candidates for exploitation as agents of improving Cd stress tolerance in plants. Expression of an iron transporter gene (IRT1), zinc-regulated transporter/IRT-related proteins (ZIP), can help in the removal of Cd from polluted soils. However, in *Arabidopsis* IRT1 transporters have affinity for a range of ions including Cd, manganese (Mn), Fe, and Zn (Korshunova et al. 1999). In addition to this action, the well-characterized proteins known as diffusion facilitator transporters are implicated in the vacuolar sequestration and transport of toxic metal ions (such as Zn, Cd, cobalt (Co), nickel (Ni), etc.) from the cytoplasm into the outer cellular compartments (Montanini et al. 2007). The isotopes of natural resistance-associated macrophage protein, i.e., NRAMP3 and NRAMP4, have been studied to mediate the efflux of cadmium from the vacuole (Thomine et al. 2003), and the overexpression of *NRAMP3* and *NRAMP4* in *Arabidopsis* resulted in greater Cd sensitivity due to disturbance caused in the Fe homeostasis after its release from the vacuole in addition to Cd. Beneficial soil microbes have the potential to restrict the uptake of Cd to upper plant parts (Abd_Allah et al. 2015; Hashem et al. 2016a).

9.3 Cd Toxicity in Plants

The effect of heavy metals in altering the soil characteristics is now well established; the influence of these metals on the essential mineral nutrition has been observed leading to impeded plant growth and development. The effects may vary with the concentration of metal and the type of existing plant species encountered. Recent studies of Abd_Allah et al. (2015) have demonstrated restricted growth in Cd-stressed *Helianthus annuus* and *Sesamum indium* L. due to impaired lipid metabolism and uptake of nutrients, respectively. While comparing the Cd tolerance in rice accessions, Ueno et al. (2009) noticed considerable variations in the concentration of Cd in shoot ultimately displaying completely vibrant tolerance potential (Fig. 9.1). Genotypes of the same species display considerable differences in the Cd metal tolerance (Khan and Khan 2014; Asgher et al. 2014; Alyemeni et al. 2017; Ahmad et al. 2018). These differences may be attributed to the inherent differential capacity of different species and varieties for Cd accumulation and partitioning in root and shoot and also on the ability to restrict Cd in roots. In *Glycine max*, De Sousa and Sodek (2003) observed the induction of the alanine aminotransferase and hexokinase activity after the plants were exposed to Cd (10 μM) resulting in improved tolerance due to greater production of reduced glutathione (GSH). Restricted functioning of the transport proteins in Cd-treated plants results in increased affinity for the sulfhydryl groups of enzymes, for example, the activity of H^+ - ATPase decreased significantly in the roots of papilionaceous plants due to Cd contrary to cucurbitaceous plants reflecting higher metal tolerance (Chetty et al. 1980; Janicka-Russak et al. 2012).

In addition, accumulation of Cd has been observed to impair the structural stability of DNA by inducing breaks in strands, causing oxidative damage, and also leads to chromosomal aberrations with increased programmed cell death (Tuteja et al. 2009). Cd has been reported to trigger cytotoxic as well as genotoxic effects in *Vicia faba* resulting in exchange of sister chromatids, and hence persistent DNA damage can occur (Unyayar et al. 2010). In connection to this, the protective mechanisms like osmolytes, phytochelatins, and antioxidant system have been essential in

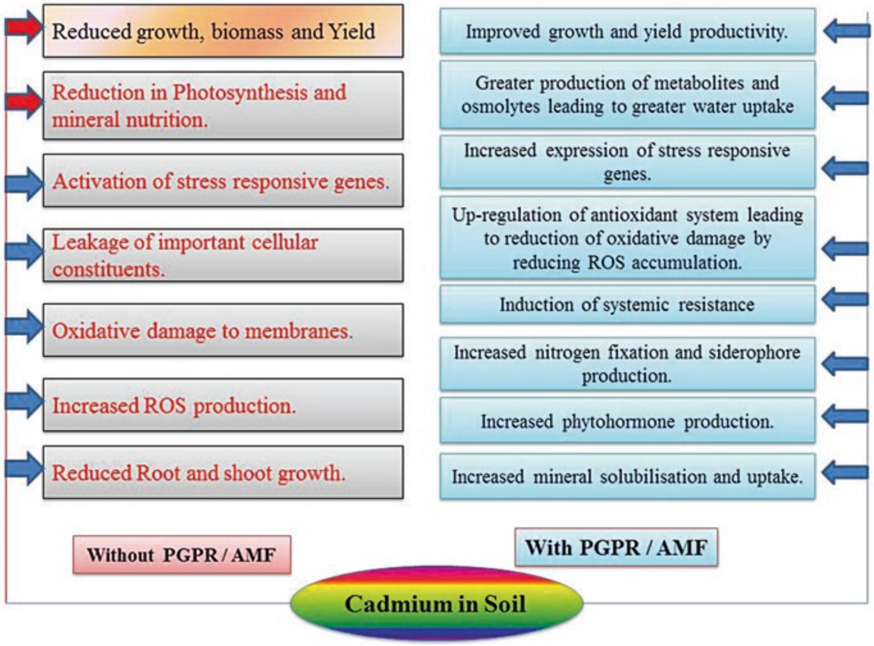

Fig. 9.1 Skeleton diagram describing the mechanisms involved in remediation and alleviation of adverse impact of cadmium stress by rhizosphere microorganisms

averting the genotoxic stress as observed in several crops subjected to Cd stress (Emamverdian et al. 2015). Future studies are required to unravel the exact mechanisms of protection from genotoxic effects of Cd and other metals. Thorough understanding about the cross talk between different protective molecules can be handy in strengthening our knowledge about signaling cascades and the apoptotic pathways involved in such conditions. While screening *Brassica juncea*, Blanvillain et al. (2009) identified a chromatin remodeling factor, i.e., OXS3, as key factor for improved Cd stress tolerance. Contrarily, OXS3 mutants exhibit extra sensitivity to Cd treatment which is usually overcome by its subsequent overexpression thereby leading to the protection of DNA (Verbruggen et al. 2009). No doubt plants tend to chelate most of Cd taken up; however, accumulated Cd is sequestered into the vacuole involving the active participation of transporters, e.g., CAX2 or CAX4 acting as Cd/H antiporters. Besides it has been confirmed that *Nicotiana tabacum* overexpressing the *Arabidopsis* tonoplast Cd/H antiporter exhibit greater tolerance to cadmium stress (Korenkov et al. 2007).

Most of the nutrients including nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), etc. are mobile within the plant system, i.e., in xylem and phloem tissues, compared to calcium (Ca), boron (B), sugars, etc. Heavy metals like Cd may compete with ions like Ca and Mg at the membrane level (Llamas et al. 2000) resulting in its uptake by the cation transport system (employed in the uptake of essential elements, e.g., transporters belonging to ZIP and NRAMP families and Ca channels (Perfus-Barbeoch et al. 2002)). Competition occurring between nutrients and the existing toxic heavy metals for the binding sites in different cellular compartments can affect the distribution of toxic metals, for example, absorption of Cd through Ca ion channel hampers the plant-water relationship (Perfus-Barbeoch et al. 2002) imparting hindrances in metabolism by inducing stomatal closure, lowered transpiration, and chlorophyll metabolism, hence restricting photosynthesis. Reduced uptake of sulfur (S) in *B. juncea* cultivars under Cd treatment restricts photosynthesis and growth (Asgher et al. 2014; Ahmad et al. 2015). Similarly, in chickpea, Cd stress reduces the uptake of key mineral nutrients leading to increased oxidative damage and growth restrictions. Reduced photosynthesis due to Cd stress has been attributed to the reduction in the activity of enzymes of the Calvin cycle, photosynthetic electron transport chain, PSII activity, CO_2 concentration, expression of Rubisco, and uptake and translocation of key mineral nutrients (Asgher et al. 2014; Per et al. 2016). Cd stress increased DNA polymorphism in rice and possibility of occurrence of breaks in the DNA (Aina et al. 2007). Cd affects the antioxidant system of plants and induces oxidative damage to key metabolic pathways (Hashem et al. 2015; Abd_Allah et al. 2015, 2017). Partly such negative effects of Cd can be ascribed to low mineral availability in the contaminated soils. Cd brings alteration in the protein conformation after binding with the sulfhydryl and carboxylic groups of proteins. According to the study of Yoshihara et al. (2006), exposure of tobacco to Cd stress induces iron deficiency by significantly increasing the expression of *NtFRO*1 and *NtIRT*1 in the roots. Transcription factors including *FIT*, *AtbHLH38,* and *AtbHLH39*, which belong to helix-loop-helix group, get upregulated in plants exposed to Cd stress for protecting the iron homeostasis. In *Arabidopsis*, overexpression of *FIT* either with *AtbHLH38* or *AtbHLH39* activates the expression of *MTP3*, *HMA3*, *IRT2,* and *IREG2* involved in the detoxification of heavy metals and further enhanced the expression of nicotianamine coding NAS1 and NAS2 genes thereby contributing to iron homeostasis.

9.4 Soil Microorganisms: PGPR and AMF

Already as mentioned above, plant development primarily depends on the characteristics of the rhizosphere soil, the existing environment, and lesser on the plant species. A galaxy of microflora interacting with their immediate neighbors for one or the other beneficial or neutral associations inhabit Earth. Species belonging to different bacterial and fungal genera form the vital components of soil. Among the key biotic activities is the nutrient turnover so as to make it sustainable for increased crop production (Hameed et al. 2014). Soil microorganisms bring positive changes in growth by mediating the mobilization of key nutrients and inducing the synthesis of endogenous plant growth regulators (Hashem et al. 2014; Abd_Allah et al. 2015), modulating the concentration of polyamines (Hashem et al. 2014; Upadhyay et al. 2012), inhibiting the growth of phytopathogens, improving soil structure, and removing the toxic heavy metals and xenobiotic compounds including pesticides (through sequestration) (Hayat et al. 2010; Singh et al. 2015a, b). It has been accepted that bacteria are inhabiting in the rhizosphere, i.e., rhizobacteria are the most versatile agents in transforming, mobilizing, and solubilizing the key mineral nutrients (Oteino et al. 2015). In connection to this, the rhizobacteria and arbuscular mycorrhizal fungi (AMF) are considered as the dominant driving forces for nutrient recycling and hence soil fertility (Li et al. 2017). Exploitation of soil microorganisms for remediation of toxic metals has been under intense research (Ma et al. 2016). The main aim of all the integrative biotechnological or agricultural approaches employed for improving crop production via biological means is gaining ground in the current era. In connection to this, rigorous research practices have been initiated worldwide with greater emphasis on exploring a range of rhizobacteria possessing novel traits like heavy metal elimination (Ma et al. 2011; Wood et al. 2016), pesticide degradation (Ahemad and Khan 2012a), salt tolerance (Upadhyay et al. 2012), and control of phytopathogens and insects along with the key plant growth controlling properties like phytohormone (Tank and Saraf 2010; Upadhyay et al. 2012), siderophore (Nadeem et al. 2014), 1-aminocyclopropane-1-carboxylate, hydrogen cyanate, and ammonia production in addition to nitrogenase activity, antioxidant enzymes (Stefan et al. 2013), and phosphate solubilization (Hashem et al. 2014) etc.

Plant growth-promoting rhizobacteria (PGPR) include both symbiotic and non-symbiotic bacterial strains, and key examples for symbiotic ones include rhizobia, while non-symbiotic ones are *Bacillus*, *Klebsiella*, *Pseudomonas*, *Azospirillum*, and *Azotobacter,* and AMF are being exploited worldwide as the bio-inoculants for promoting the growth and development of plants under a wide range of environmental stresses including heavy metals (Wani and Khan 2010; Abd_Allah et al. 2015; Hashem et al. 2016a, b, c), herbicides (Ahemad and Khan 2011a), salinity (Mayak et al. 2004; Alqarawi et al. 2014; Bharti et al. 2016), water stress (Alwhibi et al. 2017), insecticides (Ahemad and Khan 2011b), fungicides (Ahemad and Khan 2012b), etc. In mycorrhiza "myco" means "fungus" and "rhiza" means "root"; therefore it means fungi infecting roots (Hameed et al. 2014). AMF improve nutrient absorption, water holding capacity, and stress tolerance (Alqarawi et al. 2014; Candido et al. 2015). Nearly 250 species of AMF have been identified (Kruger et al. 2012). AMF isolates have been classified within six major genera under order *Glomales* also referred as *Zygomycota* (Ahanger et al. 2014). Advancement in the molecular techniques has enabled the direct identification of the AMF isolates infecting roots or rhizosphere, and the confirmation of the genetic diversity occurring within the different species has also been confirmed (Kruger et al. 2012). Therefore, both PGPR and AMF must have (1) efficiency to colonize roots and (2) potential to mediate growth promotion by modifying the metabolism (3) and must multiply and compete efficiently with the existing microbiota.

Despite having enormously available research findings on PGPR-AMF-induced stress mitigation, the exact mechanisms underlying plant growth promotion are not fully known. It has been observed that both PGPR and AMF exhibit beneficial properties for regulating the growth and development of plants positively (Khan et al. 2009; Hameed et al. 2014; Santoyo et al. 2016; Meena et al. 2017).

To be accurate rhizosphere can be the zone of soil, which is surrounding the plant root system, and rhizobacteria and AMF refer to cluster of microorganisms competently colonizing the roots (Kloepper et al. 1991). It has been reported quite often that plant roots synthesize and release an array of chemical compounds into the rhizospheric soils, which act as attractants for a wide variety of soil microorganisms (Walker et al. 2003). These exudates bring modification in the physical as well as chemical properties of the soil, therefore, determining the structure of existing soil microbial populace residing in immediate vicinity of the root surface (Baetz and Martinoia 2014). It must be pointed out here that some exudates repel microorganisms, while some attract which may vary with the composition of exudates, often dependent on the physiological status in addition to the type of plant and microbe species involved (Kang et al. 2010). Nardi et al. (2000) have suggested that exudates inhibit the growth of competing plant species as well and favor the symbiotic associations. However, the inhabiting beneficial microorganisms modify the root developmental patterns and mediate exchange of nutrients by making significant increase in the production of exudates (Neumann et al. 2014).

9.5 Plant Growth Promotion by PGPR and AMF Under Cd Stress

As already discussed PGPR and AMF trigger plant growth promotion by the alteration of the whole microbial community existing in the rhizosphere niche. Generally, the rhizospheric microorganisms (PGPR and AMF) improve plant growth by direct or indirect mechanisms. Enhancing the nutrient acquisition including N and P, modulating the endogenous hormone levels, and improving the enzyme activity are included in direct growth-promoting mechanisms while acting as biocontrol agents resulting in the reduction of the inhibitory effects the pathogens are involved in indirect mechanisms (Ahanger et al. 2014). However, both direct and indirect beneficial mechanisms are triggered in plants exposed to different stresses with specificity of response exhibiting certain degree of variation with type of stress imposed. Reports available depicting the beneficial role of soil bacteria and fungi in amelioration of different stresses have been described by various researchers all over the world (Al-karaki et al. 2004; Yedidia et al. 2001; Gamalero et al. 2009; Garg and Singla 2012; Gholamhoseini et al. 2013; Hameed et al. 2014; Hashem et al. 2014, 2015, 2016a, b, c; Yang et al. 2015; Abd_Allah et al. 2015, 2017; Wu and Zou 2017; Scagel and Bryla 2017; Mitra et al. 2018a, b) (Table 9.1). In the following sections, beneficial role of soil PGPR and AMF in growth regulation under metal stress will be discussed with special attention on Cd stress (Fig. 9.1).

Table 9.1 The effect of microbes on Cd stress of plants

Microorganisms	Plants	References
Bacillus amyloliquefaciens SAY09	*Arabidopsis*	Zhou et al. (2017)
Pseudomonas aeruginosa Burkholderia gladioli	Tomato	Kanika et al.
Agrobacterium fabrum, Stenotrophomonas maltophilia	Wheat	Zafar-Ul-Hye et al. (2018)
Enterobacter sp.	Rice	Mitra et al. (2018a, b)
Bacillus, Klebsiella, Leifsonia, Enterobacter	Maize	Ahmad et al.
Enterobacter aerogenes	Rice	Pramanik et al. (2018)
Burkholderia sp. D54	Tomato	Wei et al. (2018)
Burkholderia cepacia CS8	*Catharanthus roseus*	Khan et al. (2018)
Klebsiella michiganensis MCC3089	Rice	Mitra et al. (2018a, b)

9.6 Soil Microbes and Mineral Nutrition

Soil microbes including PGPR and AMF regulate the uptake of mineral ions in the host plants under normal and environmental extremes. Among the key mineral elements, the uptake of which is mediated by associated microbes, are N, P, Mg, S, etc. Nitrogen-fixing bacteria make the nitrogen available to plants for absorption and subsequent assimilation, while phosphate-solubilizing microbes preferentially assist in P uptake. Biologically fixed N accounts for at least two-thirds of the total fixed N even under extreme conditions like high temperature, salinity, metal stress, etc. (Raymond et al. 2004). Microorganisms including rhizobia, cyanobacteria, *Gluconacetobacter diazotrophicus, Azotobacter*, and *Azospirillum* may enter either in symbiotic or non-symbiotic relation with the host plant. Chen et al. (2003) have shown that soybean treated with Cd (10 and 20 mg kg^{-1} soil) exhibited a significant reduction in the nitrogen fixation by reducing the number of nodules resulting in considerable decline in the nitrogen assimilation. The specific type of nitrogen fixation genes (*nif* and fix genes) controls nitrogen fixation (Kim and Rees 1994). *Leucaena leucocephala* grown on metal-contaminated soils showed significant recovery in the decline of N assimilation by the presence of native rhizobia (Rangel et al. 2017). On the other hand, inorganic phosphate solubilization mediated by the associated bacteria involves the release of certain organic acids by the bacteria into the soil leading to solubilization of the complex phosphate compounds into orthophosphate, thereby making it easily available to plants for absorption and assimilation. Oteino et al. (2015) have demonstrated that endophytic bacteria have the potential to produce gluconic acid which initiates the solubilization of insoluble phosphate, thereby leading to significant improvement in growth of *Pisum sativum* L. Recently, Korir et al. (2017) reported that co-inoculation of rhizobia and other PGPR improved growth of common bean by increasing the uptake and assimilation of nitrogen and phosphorus. Greater uptake of minerals was found to be regulated by the impact of inoculants on the gene expression. In addition to N and phosphate assimilation, the homeostasis of other elements, including Zn, Ca, Mn, and Fe, has been observed to show close linkage with the Cd toxicity and tolerance (Wu et al. 2012; Zhai et al. 2016). Cd stress affects the transport proteins and PGPR, and associated beneficial microorganisms may have a key role in the modulation of their activity and expression; however, experimental studies confirming this are not available. It should be noted here that excess phosphate supplementation leads to disastrous effects on the soil fertility and plant growth due to considerably excessive accumulation of Cd. However, improving phosphate solubilization using PGPR is safe for the environment and plants. In this context phosphate-solubilizing microbes make the availability of P to the plants (Khan et al. 2006). Among the key phosphate-solubilizing microorganisms are *Bacillus, Beijerinckia, Rhizobium, Azotobacter, Enterobacter, Microbacterium, Flavobacterium, Pseudomonas, Serratia,* etc. making P availability easy for plants via the involvement of various mechanisms (Zaidi et al. 2009). It has been observed that bacterial strains show both phosphate solubilization and mineralization functions (Tao et al. 2008). Phosphate-solubilizing bacteria (PSB) are exclusively found in various soil types, and the performance of particular strain depends on the environmental factors (Ahemad and Khan 2012a, b). It should be noted here that the positive effects of the PSB either alone or with rhizobia under stress conditions have been reported by many workers (Zaidi and Khan 2005; Ahemad and Khan 2011a, b, 2012a, b; Poonguzhali et al. 2008; Chen et al. 2008; Zaidi et al. 2009).

9.7 Soil Microbes and Antioxidant System

It is well established that crop plants growing under stressed environmental conditions show upregulated antioxidant defense system for the protection of major cellular pathways from the free radical-triggered oxidative damage (Mittler 2002; Hashem et al. 2015). Antioxidant system includes enzymatic and non-enzymatic components working coordinately for bringing the stability to metabolism. Strengthening the antioxidant system with the help of soil beneficial microorganisms helps plants to neutralize the toxic ROS quickly and keep metabolism at optimal level (Abd_Allah et al. 2015; Alwhibi et al. 2017). Inoculation of Cd-resistant PGPR to stressed (50 μM $CdCl_2$) *Sulla coronaria* reduced the oxidative damage by upregulating the activity of antioxidant enzymes, SOD, APX, SOD, and GPOX (Chiboub et al. 2018) proving the beneficial impact of PGPR in protection of *S. coronaria* from heavy metals. Increased activity of antioxidant enzymes due to rhizobia and PGPR strains in metal-stressed *Vicia faba* reduces the oxidative damage by decreasing the accumulation of free radicals (Fatnassi et al. 2015).

Plants grown in Cd-contaminated soils show considerable increase in the generation and accumulation of free radicals such as superoxide, H_2O_2, and hydroxyl, leading to increased lipid peroxidation (Ouariti et al. 1997; Hossain et al. 2006; Ahmad et al. 2011, 2015; Abd_Allah et al. 2015, 2017). Metal stress-induced peroxidation of lipids is widely accepted as one of the important damaging aspects and a determining factor of the magnitude of environmental stress. The inoculation of AMF has been observed to improve the structural integrity of membranes by improving the polyunsaturated lipid components of the membranes (Alqarawi et al. 2014; Abd_Allah et al. 2015). It is established that the membrane lipids are very much sensitive to ROS and initiate their oxidation causing the accumulation of peroxide radicals. Cd stress-induced peroxidation of membrane lipids causes membranes to loose their functional integrity resulting in leakage of essential elements (Djebali et al. 2005). In addition to this, Cd and other stress factors triggered ROS accumulation and the lipoxygenase activity, deteriorating the membranes and other cellular components (Djebali et al. 2005). In rice, Kuo and Kao (2004) also demonstrated an increase in the production of H_2O_2 resulting in oxidative stress and reduced growth.

Barley root tips displayed a considerable increase in the expression of lipoxygenase activity after exposure to Cd resulting in membrane damage (Tamas et al. 2009). Zhang et al. (2014) have demonstrated a significant increase in the expression of antioxidant coding genes in *Populus* under Cd stress. In another study with *Chlorella vulgaris*, Cheng et al. (2016) have demonstrated that activity of SOD, CAT, POD, and GR increased with treatment of Cd resulting in the prevention of oxidative damage to some extent. Not only in plants Cd uptake by animals, including fishes like *Takifugu obscurus,* has been reported to improve the gene expression of important antioxidant genes and their isozymes including *CAT1*, *Cu/Zn-SOD*, *Mn-SOD,* and GR (Kim et al. 2010). The improving antioxidant system can prove exceptionally beneficial in promoting growth via protection of major metabolic processes. In context to this, increasing the indigenous antioxidant defense system has been the key target of present research for protecting the maximum crops from metal damage, and exploiting the potential of soil microbes is one such strategy (Fig. 9.1).

9.8 Soil Microbes and Osmolytes

The accumulation of osmotic solutes under different stresses including metal stress has been reported (Ahmad et al. 2015). The accumulation of osmolytes leads to osmoregulation and protection of major plant assimilatory pathways. Among the most important solutes are proline, glycine betaine, sugars, etc. The accumulation of solutes tends to bring the turgor maintenance via increased water uptake under stress by maintaining the water potential of tissue well below that of soil solution (Tester and Davenport 2003). Osmolytes maintain the ionic balance between vacuoles and cytoplasm. More importantly they do not hinder the normal metabolic reactions if accumulated in large concentrations (Zhifang and Loescher 2003). It has been reported that accumulation of osmolytes is proportional to change in the external osmolality, which varies with species, thereby leading to protection of key cellular structures and the maintenance of the osmotic balance for continuous water influx (Hasegawa et al. 2000). Though the majority of the compatible solutes implicated in osmoregulation are organic in nature, essential inorganic ion such as K^+

also serves as a major osmolyte (Yokoi et al. 2002). The type and concentration of solute accumulated vary with the type of stress and the species. Accumulated osmolytes may be simple sugars like fructose and glucose, sugar alcohols or complex sugars like trehalose and raffinose, quaternary amino acid derivatives like proline and glycine betaine, tertiary amines, and sulfonium compounds like choline (Yokoi et al. 2002). Among the main functions of osmolytes are the maintenance of cellular water status and the protection of subcellular structures, membranes, and proteins (Ashraf and Foolad 2007). It is now widely accepted that osmolytes including proline, glycine betaine, and sugars mediate ROS scavenging and signaling under stressful conditions (Kathuria et al. 2009; Szabados and Savoure 2010). Plants showing greater accumulation of glycine betaine have been reported to exhibit maintained activity of PSII complex and carboxylase activity of RUBISCO, thereby leading to improved photosynthetic efficiency (Papageorgiou and Murata 1995; Tian et al. 2017).

There are increasing research reports that crop cultivars exhibiting greater synthesis and accumulation of osmolytes are more efficient to combat stress as compared to the low accumulating mutants. Plants having increased expression of proline and glycine betaine coding genes accumulate significant concentrations of proline and glycine betaine (Verdoy et al. 2006; Giri 2011). Transgenic *Medicago truncatula* overexpressing delta(1)-pyrroline-5-carboxylate synthetase shows greater osmotic stress tolerance (Verdoy et al. 2006). Khan et al. (2015) reported that greater proline accumulation imparts Cd stress tolerance to *B. juncea*. Therefore, from the above brief discussion, it can be concluded that greater accumulation of compatible solutes is one of the key mechanisms or adaptations to combat stresses like Cd toxicity. PGPR and AMF inoculation increases the accumulation of proline, glycine betaine, and sugars in different crop plants resulting in growth regulation (Dimkpa et al. 2009; Abd_Allah et al. 2015; Vurukonda et al. 2016).

Increased accumulation of proline and other metabolites was observed in *Bacopa monnieri* after inoculation of PGPR (Bharti et al. 2013); similarly *Pseudomonas pseudoalcaligenes* colonizing rice seedlings resulted in enhanced synthesis of glycine betaine and glycine betaine-like quaternary compounds resulting in improved stress tolerance (Jha et al. 2011). It has been reported that inoculation of VOC-emitting *Bacillus subtilis* GB03 to *Arabidopsis* promoted the synthesis and accumulation of glycine betaine and its immediate precursor choline imparting greater stress tolerance (Zhang et al. 2010). However, it shall be noted that very scanty reports are available regarding the impact of soil microbes on the growth and tolerance of plants under Cd stress. Inoculation of *Pseudomonas putida* (ATCC 39213) to *Eruca sativa* declined the uptake of Cd (Kamran et al. 2015) and Ni (Kamran et al. 2016) by improving the accumulation of osmolytes. Haneef et al. (2014) have demonstrated reduced oxidative damage to *Plantago ovata* by the inoculation of AMF and *Azotobacter* via increased accumulation of osmolytes including proline. In *Cajanus cajan* inoculation of AMF improves growth and N metabolism by enhancing the accumulation of trehalose in the presence of Cd (Garg and Chandel 2011).

9.9 Soil Microbes and Phytohormone Production Under Cd Stress

Generally, it may be said that the phytohormones like indole acetic acid (IAA) synthesized by the rhizobacteria may interfere with the developmental processes of host plant altering the endogenous pool (Glick 2014). No doubt increase in endogenous concentration of hormones may initiate reciprocal signaling resulting in impeded gene expression; however, their role in initiating and regulating the rhizobacteria-AMF-plant interactions cannot be neglected (Spaepen and Vanderleyden 2011). Generally, plant hormones regulate so many processes including cell division and differentiation, germination, ripening, signaling, vegetative growth, root formation and development, and response to numerous biotic and abiotic stresses (Ahmad et al. 2011). It has been observed that the bacteria-derived phytohormones, e.g., IAA, result in increased root growth by enhancing the surface area and length of roots, thereby mediating improved growth of plants by improving the access to mineral nutrients. In addition to this, the root cell walls get loosened due to IAA facilitating increase in exudation, thereby providing nutrients for supporting microbes in rhizosphere (Glick 2014; Spaepen and Vanderleyden 2011). In *Leucaena leucocephala*, PGPR inoculation improved production of organic acids, IAA, siderophore production, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, and $Ca_3(PO_4)_2$ solubilization resulting in improved Zn and Cd tolerance (Rangel et al. 2017). Kotoky et al. (2019) reported enhanced growth of rice by IAA producing PGPR strain of *Serratia marcescens* even in the presence of high Cd concentrations. The synthesis of phytohormones by the microbes inhabiting the plants has been observed from times.

Another important phytohormone is ethylene which has been reported to get accumulated under stresses like waterlogging, salinity, heavy metal, drought, etc. resulting in significant decline in growth (Asgher et al. 2014; Khan et al. 2015). High concentration of ethylene induces defoliation, thereby reducing the crop performance (Bhattacharyya and Jha 2012). PGPR possessing ACC deaminase enzymes promote growth and development of plants by reducing the endogenous levels of ethylene to normal level (Zahir et al. 2008). *Achromobacter, Bacillus, Pseudomonas, Agrobacterium, Azospirillum, Burkholderia, Serratia,* and *Rhizobium* strains have been reported to show ACC deaminase activity (Nadeem et al. 2007; Kang et al. 2010; Glick 2014; Singh et al. 2015c). In general, phytohormones have been observed to mediate the signaling under metal stresses (Bak et al. 2014). The PGPR strains displaying ACC deaminase activity help host plants to prevent damage of several stresses including phytopathogenesis, heavy metals, radiation, salinity, temperature, and flooding (Glick 2014). Enhancement in the rhizobial nodulation and uptake of essential nutrients like N, P, and K in addition to healthy AMF colonization have been observed in crops infected by the ACC deaminase producing PGPR strains (Shaharoona et al. 2008; Glick 2014). In *Arabidopsis*, Zhou et al. (2017) demonstrated that inoculation with *Bacillus amyloliquefaciens* SAY09 improves Cd stress tolerance by regulating the synthesis of abscisic acid, IAA, and gibberellic acid resulting in optimizing signaling events.

9.10 Conclusion

The soil rhizospheric microflora including PGPR and AMF are much beneficial for the healthy maintenance of growth of plants, and most of them have been recognized for their beneficial role in regulating the growth and development of plants. PGPR and AMF benefit plants by enhancing the mobility of key nutrients into the plants concomitant with the reduction or restriction of toxic ions including metals. The beneficial role of soil microorganisms in ameliorating the ill effects of stresses via the modulations in the key defense mechanisms is now an obvious established fact. Future research shall remain focused to unravel the exact mechanism of soil microorganisms bringing amelioration of the metal stress. Making integration between the physiological, biochemical, molecular, and genetic approaches will be handy in identifying the key regulatory mechanisms induced by rhizospheric microorganisms in driving various known structural and functional integrities within the host plants for improved metal stress tolerance.

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