Cadmium Stress Management in Plants: Prospects of Plant Growth-Promoting Rhizobacteria

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Abstract

Cadmium (Cd) pollution in agricultural soils has become a great concern for global food security and the environment. Cd is a nonessential heavy metal and a group-I carcinogen. Excessive uses of phosphate fertilizers, dispersal of municipal waste, sewage sludge disposal and atmospheric deposition have polluted agricultural soils with cadmium. Accumulation of Cd in crops may cause severe damages to plant growth and agricultural productivity. Human beings get exposed to cadmium toxicity through the food chain. In recent times, plant growth-promoting rhizobacteria (PGPR)-mediated Cd detoxification in plants emerged as an excellent alternative to physicochemical approaches as it is economical and environmentally sustainable. Generally, PGPR enhances plant growth by nitrogen fixation, producing phytohormones, ACC deaminase (ACCD), siderophores, and solubilizing inorganic or organic phosphates. PGPR enhance Cd bioremediation through different mechanisms, such as biosorption, complexation, chelation, sequestration and biotransformation. The application of Cd resistant PGPR to alleviate Cd stress in plants has an exciting prospect, and early findings look promising for boosting food security, especially in contaminated soil, for the increasing global population.

Keywords

ACC deaminase • Bioremediation • Cadmium • Detoxification • Immobilization • Plant growth promoting rhizobacteria (PGPR) • Siderophore

Abbreviations

ABC	ATP-binding cassette
ACC	1-Aminocyclopropane-1-carboxylic acid
ACCD	1-Aminocyclopropane-1-carboxylic acid
APX	Ascorbate peroxidase
ASA	Ascorbic acid
CAT	Catalase
CAX	Cation/proton exchangers
CDF	Cation Diffusion Facilitator
CBA	Capsule Biogenesis/Assembly
Cd	Cadmium
Czc	Cobalt/zinc/cadmium
DHAR	Dehydroascorbate reductase
EPS	Exopolysaccharide
GPX	Glutathione peroxidise
GR	Glutathione reductase
GSH	Glutathione (reduced)
H_2O_2	Hydrogen peroxide
IAA	Indole Acetic Acid
IARC	International Agency for Research on Cancer
IRT	Iron-Regulated Transporter
LCT	Lysosomal Cystine Transporter
MDHAR	Monodehydroascorbate reductase
MT	Metallothionein
NRAMP	Natural Resistance-Associated Macrophage Protein
PC	Phytochelatin
PEPCase	Phosphoenolpyruvate carboxylase
PGPR	Plant Growth Promoting Rhizobacteria
POX	Peroxidase
Q_A	A bound primary plastoquinone
Q_B	A secondary plastoquinone

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S. Roy et al. (eds.), *Plant Stress: Challenges and Management in the New Decade*,
Advances in Science, Technology & Innovation, https://doi.org/10.1007/978-3-030-95365-2_15

RuBisCo	Ribulose-1, 5-bisphosphate carboxylase
ROS	Reactive Oxygen Species
SAM	*S*-Adenosyl-1-methionine
SOD	Superoxide dismutase
TF	Transfer Factor
WHO	World Health Organization
ZIP	ZRT-IRT-like Proteins

1 Introduction

Agricultural soil health deteriorated considerably in the last few decades due to heavy metal contamination in soil. In general, heavy metals are found in the earth's crust; however, heavy metal contamination is mainly the consequence of increased industrial activities, combustion of coal and petroleum products, mining, smelting, use of agrochemicals (e.g. fertilizers) and disputed agricultural practices, such as the release of industrial effluents, municipal wastes and sewage sludge in agricultural soils. Atmospheric deposition, geogenic activities such as weathering, leaching and volcanism have also contributed to heavy metal pollution to a great extent (Kubier et al. 2019; Singh et al. 2021). Heavy metals are non-biodegradable; most show toxicity even at a low concentration and accumulate in the soil. Consequently, they adversely impact the functions of all the living entities present there and eventually invade the food chain via edible crops and pose a major threat to human well-being and food safety (Kumar 2012; Sharma and Archana 2016).

Heavy metals may be classified as a group of metals that have a high atomic weight and high density (>5 g cm^{-3}) (Nies 1999). They may be essential in trace amounts (e.g. Mn, Cu, Fe and Zn) or nonessential with no known physiological role (e.g. Cd, Hg, As and Pb) (Shanmugaraj et al. 2019). Cadmium (Cd) is highly mobile in soils and is the most toxic nonessential metal with a long biologic half-life. Cadmium is a trace element in the earth's crust (0.2 mg/kg) and generally occurs as oxides, sulfides, and carbonates in zinc, lead, and copper ores. In the past, cadmium was used mainly in metal electroplating, pigments and stabilizers for plastics. In recent decades, the use of cadmium has been growing up for its application in cadmium-nickel batteries, the modern electronics and communication industry, and the power industry. Cadmium is also released into the environment, naturally through volcanic activity and weathering, but mostly it is released into the environment through municipal waste incineration, fossil fuel combustion and smelting. Use of phosphate fertilizers and pesticides, irrigation with municipal waste, and sewage sludge are mainly liable for agricultural soil contamination with cadmium (Fig. 1). Cadmium content in agricultural soils ranges between 0.01 and 1 mg kg^{-1}, averaging 0.36 mg kg^{-1} worldwide (WHO 2000; Kubier et al. 2019). The World Health Organization (WHO) has recommended a guideline value of 3 µg/L for cadmium in drinking water (WHO 2010).

Chronic Cd exposure causes kidney damage, respiratory disorders, cardiovascular disorder, hypertension, cerebral infarction, disorders in glucose, calcium and vitamin-D metabolism, bone lesions, osteoporosis, and diabetes in humans. Cadmium also has embryotoxic, teratogenic and carcinogenic effects. It has been reported in several studies that the lung, kidney, breast and prostate are the primary target organs for Cd carcinogenicity. The first documented chronic cadmium poisoning incidence was the Itai-Itai disease that occurred in Japan in the 1950s. Cadmium is toxic to living beings even at a low level, and has been classified as a Group-I carcinogen to humans by International Agency for Research on Cancer (IARC) in 1993 (WHO 2000; Hu et al. 2016; Khan et al. 2017b). Cadmium entry into the human body takes place mainly through the dietary intake (e.g. cereals, vegetables) and bio-accumulates in different organs as it is non-degradable, persistent, and has a biological half-life of 10–35 years. In comparison to other cereals, the accumulation of cadmium in rice is much higher and, therefore, increases the health risk in manifold of the rice-consuming population of the world (Hu et al. 2016; Kubier et al. 2019).

Besides animal toxicity, cadmium exhibits phytotoxicity even at a low concentration. Cadmium is easily absorbed by roots of crop plants, especially rice and other cereals and leafy vegetables, during cultivation in Cd-polluted soil and can be translocated to the aerial parts. Cadmium accumulation in plant parts severely damages crop productivity (Bolan et al. 2014). Cadmium toxicity triggers diverse morphological, physio-biochemical, and molecular disturbances in plants, such as stunting overall plant growth, wilting, senescence, reduced photosynthesis, reduced pigment synthesis, leaf chlorosis, inhibition of seed germination, interference in nutrient uptake and disruption in the electron transport chain. Cadmium stimulated oxidative stress may also injure plasma membranes and a variety of different biological molecules, such as nucleic acids and proteins, by generating an excessive amount of reactive oxygen species (ROS) (Gallego et al. 2012; Roy et al. 2016; Moradi et al. 2019; El Rasafi et al. 2020).

Many traditional methods, such as soil dressing, soil removal, chemical washing, soil liming, electrochemical treatment, reverse osmosis, biochar amendment, bio-slurries and other agronomic approaches, are used for cadmium-contaminated soil remediation. These conventional physicochemical Cd remediation methods are usually expensive, require high maintenance and skilled labour, and typically cause harm to the soil in the long run by the

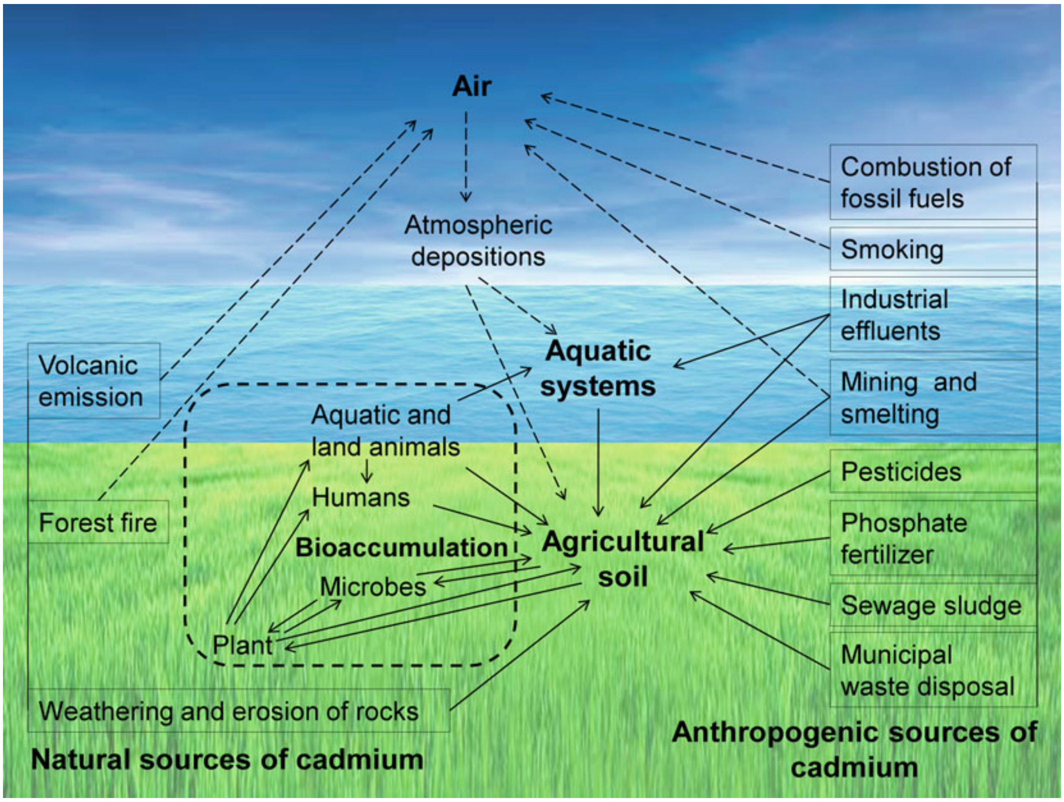

Fig. 1 Sources of cadmium in agricultural soil

resultant secondary toxic products (Volesky 2001; Vinod and Sashidhar 2011; Singh and Gadi 2012). Phytoremediation through hyperaccumulator plants is a possible alternative technique for the bioremediation of contaminated sites. However, they have little practical value in the heavy metal toxicity alleviation from the soil due to their slow growth rate and small biomass (Blaylock et al. 1997; Kayser et al. 2000).

Bioremediation involving microorganisms has attracted increasing interest in recent years (Dixit et al. 2015). The free-living rhizospheric bacteria that assist in plant growth and development are generally regarded as plant growth-promoting rhizobacteria (PGPR). The approach of using PGPR to alleviate heavy metal stress, including cadmium, is environment-friendly and inexpensive. PGPR also promote plant growth by producing growth promoters (Kloepper et al. 1980; Pramanik et al. 2017; Abbas et al. 2018). Microbial remediation of heavy metal toxicity involves bioadsorption, bioaccumulation, complexation, precipitation and biotransformation. PGPR like *Bacillus subtilis*, *Burkholderia gladioli*, *Citrobacter* spp., *Enterobacter aerogenes* and *Pseudomonas* spp., have been found effective in mitigating Cd toxicity in plants (Kumar 2012; Pramanik et al. 2018; Khanna et al. 2019a; Halim et al. 2020). In this chapter, we summarized Cd uptake, its toxicity and plant response to cadmium stress. Furthermore, we have discussed Cd tolerance strategies found in PGPR and the different PGPR mechanisms involved in Cd detoxification in plants.

2 Cadmium Uptake and Transport in Plants

Cadmium is readily taken into the inside of plant root and then translocated to the aerial plant parts. The uptake of Cd in the higher plants is regulated by diverse aspects of soil and plant characteristics, such as soil type, soil pH, presence of organic matter, Cd availability, plant species, and their genotypes, plant age and growth stage, presence of organic matter, mineral elements, and nutrients. The adsorption and complexation of Cd with soil minerals regulate its mobilization and bioavailability in soil. An increase in soil pH and organic matter stimulates Cd immobilization in soil mainly through precipitation and chelation. Cd ions could be absorbed by root cell transmembrane carriers, meant for uptake of essential micronutrients, such as Ca^{2+}, Fe^{2+}, Mg^{2+}, Cu^{2+} and Zn^{2+} (Dalcorso et al. 2008; El Rasafi et al. 2020; Halim et al. 2020). The presence of Zn in ample amount in soil decreases Cd uptake by plants as both of them use the same route to gain entry into the root cell. It is worth noting that modulation of soil conditions through soil management approaches can significantly change the bioavailability of Cd (Hu et al. 2016). The quotient of Cd concentration in the plant to that in the soil defines the Cd transfer factor (TF), which ranges between 0.01 and 0.3 (Smolders 2001). Plant root cell walls can transport cadmium to the xylem through passive transport (diffusion) (Redjala et al. 2011). Cd can be transported symplastically in root cortical cells through membrane transporters, such as zinc transporter [ZIP], iron transporter [IRT]) and metals pumping ATPase (Gallego et al. 2012; Wu et al. 2015; Yamaguchi et al. 2011; Sebastian and Prasad 2018). Also, natural resistance-associated macrophage protein (NRAMP) family, cation/proton exchangers (CAX), P-type ATPase, lysosomal cystine transporter (LCT) family and ATP-binding cassette (ABC) transporters distribute Cd in different plants parts (Gallego et al. 2012; Song et al. 2017; El Rasafi et al. 2020). Cd ions are chelated to organic molecules and distributed to different parts of the plant body through xylem and phloem translocation after xylem loading via apoplast or symplast route (Dalcorso et al. 2008).

3 Phytotoxicity of Cadmium

Due to the toxic effects of Cd, plants and other living beings have no use for it. However, a few diatoms present in seawater utilize Cd in the enzyme Cd-carbonic anhydrase (Lane and Morel 2000). In plants, the bioaccumulation of Cd causes severe toxicity symptoms, such as reduced photosynthesis, chlorosis, wilting, altered enzyme activities, altered membrane functioning, stunted growth and development, and finally, plant death. However, the severity of Cd toxicity depends on plant species and their genotypes (Shanmugaraj et al. 2019). Cd binding with sulfhydryl groups in proteins, due to its high affinity for it, interferes with protein configuration, inhibits enzymatic activities and their regulation (Hall and Brown 2002). Also, Cd^{2+} ions can displace chemically identical cations, such as Cu^{2+}, Ca^{2+}, Zn^{2+} and Fe^{2+}, from catalytic sites of enzymes. The released free ions increase the oxidative stress and could cause damage by the Fenton reaction triggered by free Fe/Cu ions (Roy et al. 2016).

3.1 Effect on Plant Root

Roots accumulate more Cd, like other heavy metals, than above-ground parts and show initial symptoms of Cd toxicity (Singh and Shah 2015). Cd interferes with the micronutrient (Ca, Mg, Zn, K, P and Fe) uptake by the roots and thus, disturbs the plant-water balance. Cd^{+2} ions mainly bind with the negatively charged components of the cell walls of the root. Exposure to Cd inhibits root growth and lateral root formation but stimulates root hair formation (Benavides et al. 2005; Daud et al. 2009). Cd could disrupt the growth and elongation of the root in a dose-dependent manner, as seen in soybean (Sahile et al. 2021). The reduction of root length, decline in root surface area and swelling of root diameter affect the nutrient uptake capacity of roots. Cd forms a callus-like structure in the root through enlargement of parenchyma cells and unorganized cell differentiation (Halim et al. 2020). Cd stress changes the appearance of the root system, and the roots become rigid, necrotic, decomposing, twisted, and mucilaginous. Browning of the root is commonly associated with cd stress (Rascio and Navari-Izzo 2011; Abbas et al. 2017). In tomato plants, roots become thick and sturdy under Cd stress (Chaffei et al. 2004). Cd stress injures the DNA and the nucleoli in the root-cap and root tip cells (Seth et al. 2008). Also, prolonged exposure to Cd could increase the nucleus number in the differentiated root cells and disrupt the mitotic index, induce chromosomal anomaly, irregular mitotic behaviour, and affect micronucleus formation when exposed to Cd (Fusconi et al. 2006; Shanmugaraj et al. 2019).

3.2 Effect on Photosynthetic Apparatus

When a plant counters Cd contamination in its vicinity, it affects photosynthetic growth parameters, such as total chlorophyll and carotenoid contents, photochemical efficacy, and intensity of photosynthesis. Cd exposure causes leaf roll, damages chlorophyll content in old leaves and inhibits biosynthesis of chlorophyll in newer ones to cause leaf chlorosis (He et al. 2008; Xue et al. 2013). In several economically important crops, such as *Pisum sativum*, *Zea mays*, Hordeum vulgare, *Brassica juncea*, *Triticum* and *Oryza sativa*, inhibition of photosynthesis due to a short and long period of Cd exposure was well documented (Ci et al. 2010; Popova et al. 2012; Irfan et al. 2014; Pramanik et al. 2018; Almuwayhi 2021). Cd toxicity also triggers stomatal closing and, subsequently, a reduction in photosynthetic activity in higher plants. Cd strongly binds with several proteins involved in photosystems I (PSI) and II (PSII). Cd toxicity also injures the light-harvesting complex (Küpper et al. 2007; Haider et al. 2021). Ribulose-1, 5-bisphosphate carboxylase (RuBisCo), and phosphoenolpyruvate carboxylase (PEPCase) are essential enzymes for CO_2 fixation during photosynthesis. Cd replaces cofactor Mg^{+2}, needed for the carboxylation step of Calvin cycle, of enzyme RuBisCo and inhibits its activity. It also decreases the activity of PEPCase (Siedlecka et al. 1998; Tran and Popova 2013). Cd toxicity also reduces the e^{-} flow from Q_A to Q_B by altering the Q_B binding site. Cd ions can bind competitively at Ca-binding sites and replace Ca^{+2} ions in Ca/Mn clusters of the water-splitting complex of PSII (Sigfridsson et al. 2004; Faller et al. 2005). Cd exposure induces striking changes in chloroplast number and ultrastructure, resulting in distortion of shape and size of thylakoids (Najeeb et al. 2011). Cd stress also deforms thylakoid discs and grana, decreases stored starch, and plastoglobuli deposit, as reported in *Picris divarticata*, *Hordeum vulgare*, Oryza *sativa* L.) and *Brassica* (Ying et al. 2010; Wang et al. 2011; Elhiti et al. 2012; Parmar et al. 2013).

3.3 Effect on Plant Growth and Biomass

Cadmium toxicity negatively affects general growth, induces growth deformities in many species of plants (Haider et al. 2021). A substantial decrease in the leaf growth and development was reported in *Capsicum annuum* L. and *Brassica oleracea* L. under Cd exposure (León et al. 2002; Jinadasa et al. 2016). Also, Cd toxicity decreased shoot and root growth of *Solanum tuberosum* L. at 60 mg/kg of Cd in pot trials, shoot dry matter of cucumber at 0.05 mM of Cd concentration, and the development of root, stem, and leaves of pepper at 2 mM and 10 mM of Cd, respectively, in the hydroponic system (Xin et al. 2014; Hassan et al. 2016). The long-term effect of Cd stress exhibits a rapid and significant decline in crop yields, especially in cereal production, due to disruption of nutrient uptake and photosynthesis in plants (Rizwan et al. 2016). Plant growth inhibition under Cd stress is well reported in many species, such as rice (*Oryza sativa)*, rape plant (*Brassica napus* L.), mungbean (*Vigna mungo*), chickpea (*Cicer arietinum* L.), tomato (*Lycopersicon esculentum* L.), sorghum (*Sorghum bicolour)*, lentil (*Lens culinaris* L.), durum wheat (*Triticum turgidum*) and soybean ((*Glycine max* L.) (Rizwan et al. 2012; Mondal et al. 2013; Roy et al. 2016; Dutta et al. 2018; Pramanik et al. 2018; Pal and Sengupta 2019; Zhao et al. 2019; Zhi et al. 2020; Bansal et al. 2021).

3.4 Effect on Seed Germination

Cadmium toxicity to plants diminishes water content in seedlings and delays the breaking of seed dormancy, and ultimately, the seed fails to germinate. The failure of seed germination severely hampers crop productivity. The inhibitory effect of reduced water content for embryos resulting from Cd stress was reported in seedling and seed germination of *Arabidopsis* sp., and cowpea (*Vigna unguiculata* L.) (Li et al. 2005; Vijayaragavan et al. 2011). Water deficiency, endospermic starch immobilization, and a decrease in sugar transport to the embryo resulted in the failure of seed germination (Kuriakose and Prasad 2008). Under Cd exposure, low activity of hydrolyzing enzymes, such as α-amylase, has resulted in slow transport of stored foods (Kalai et al. 2016; Haider et al. 2021). Under Cd stress, seeds were failed to germinate in sunflower (*Helianthus Annuus*) by >50% after being treated with 40 and 50 mg kg^{-1} Cd, wheat by 31% at 0.03–4.8 mM of Cd, soybean by 8.0% at 5 mg/L, lettuce by 19% at 5 mg/L, sugarbeet by 18% at 5 mg/L and rice by 100% at 1.0 mM of Cd (Ahsan et al. 2007; Jadia and Fulekar 2008; Li et al. 2013; de Souza Guilherme et al. 2015). However, a little increase in germination at low Cd concentration was reported due to the limiting effect of metal on free oxygen radicals and nitric oxide, which regulate oxidative stress (Shanying et al. 2017). Moreover, Cd has a strong affinity for the Ca-calmodulin binding sites. The binding of Cd to calmodulin greatly affects metabolic activity and seed germination (Huybrechts et al. 2019).

3.5 Oxidative Stress

Cadmium toxicity in plants is mainly caused due to reactive oxygen species (ROS) generation and change in the antioxidant system, which increases oxidative stress. However, Cd is redox-inactive and cannot transfer single electrons to generate reactive oxygen species (ROS). Cd toxicity may generate ROS indirectly through the alternation of the electron transfer chain by disrupting chloroplasts and also by damaging antioxidant defence (Gallego et al. 2012). ROS examples include superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^-). In plants, Cd-induced oxidative damage results in lipid and protein peroxidation, and consequently, disrupts lipid-rich plasma membrane, as well as DNA (Younis et al. 2016; Shanmugaraj et al. 2019). Plants have evolved an advanced antioxidant system to manage oxidative stress that primarily involves enzymatic, such as glutathione reductase (GR), peroxidase (POX), superoxide dismutase (SOD), glutathione peroxidase (GPX), ascorbate peroxidase (APX), catalase (CAT), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and non-enzymatic antioxidants, such as α-tocopherols, non-protein amino acids, alkaloids, phenolic compounds, carotenoids, ascorbic acid (ASA) and reduced glutathione (GSH). Cd stress alters the activity of antioxidative enzymes and non-enzymatic antioxidants (El Rasafi et al. 2020). Under the exposure to Cd, the activity of GR and APX increases in wheat. GR activity also increases in rapeseed (*Brassica juncea* L.), cotton, and mungbean (*Vigna mungo* L.) (Gill and Tuteja 2010; Tran and Popova 2013). However, the scavenging activities of POX in rapeseed, SOD, and CAT in sunflower, common bean, and pea, decrease under Cd stress (Sandalio et al. 2001; Markovska et al. 2009; Haider et al. 2021).

4 Cadmium Detoxification Mechanisms in Plant

To manage Cd toxicity, plants can employ either or both tolerance and avoidance approaches. To avoid Cd toxicity, plants minimize the uptake of Cd through the roots by immobilization. In the tolerance approach, plants store and accumulate Cd in vacuoles, bind it to cell walls, phytochelatins (PCs), peptides, amino acids and proteins. Stress signaling pathways and signaling molecules, such as jasmonic acid, salicylic acid, ethylene and nitric oxide, take part in key pathways to reduce toxic effects of Cd in plants (Tran and Popova 2013; Haider et al. 2021). Plants have several strategies to minimize Cd stress, such as immobilization, dissemination, expulsion, chelation, vacuolar sequestration and compartmentalization, synthesis of stress-signaling molecules and proteins. Plants can immobilize Cd in the rhizosphere by secreting root exudates which contain several low- and high molecular weight organic compounds, including proteins, polysaccharides and phenolic compounds. In the root cell wall, pectins, having egg-box structures, and hemicelluloses are the primary site for cd binding and retention. The plasma membrane can exclude Cd ions from entering the cytosol and help in efflux from the cell. Under Cd stress, plants activate the synthesis of phytochelatin, small metal-binding peptides linked to sulfur metabolism. Phytochelatins with thiolic (–SH) groups of Cys chelates Cd to form complex structures, and as a result, prevent dissemination of free Cd^{+2} ions inside the cytosol. Synthesis of metallothioneins also helps in the chelation of Cd in the cytosol. Plant vacuoles play a very significant role in Cd detoxification by sequestrating it with the help of different ions and metabolites inside the vacuoles. Vacuolar sequestration checks the distribution of free Cd ions inside the cell. Vacuoles have ATPases, NRAMP family transporters, Ca^{2+} ion transporters, and ATP-binding cassette (ABC) type C transporters in their wall, which controls Cd detoxification in the cell vacuole. In *Arabidopsis*, heavy metal ATPase3 (HMA3) in roots regulates Cd concentration in leaves by accumulating Cd in the roots (Di Toppi and Gabbrielli 1999; Halim et al. 2020). Plant antioxidant defence mechanisms can also minimize oxidative damages caused by Cd toxicity (Wang et al. 2008).

5 Mechanisms of Cadmium Tolerance in Plant Growth-Promoting Rhizobacteria

Plant-associated non-symbiotic rhizospheric bacterial strains that assist in plant growth, directly or indirectly, are regarded as Plant growth promoting rhizobacteria (PGPR) (Glick 1995). PGPR plays a significant part in increasing agricultural yield through plant–microbe interaction even in contaminated soil. They are also utilized for the remediation of heavy metals, including Cd, polluted sites. Cd-tolerant PGPR, which helps in phytoextraction to remove Cd from the soil, improve Cd mobilization and bioavailability, increase root surface area for Cd uptake, and elevate translocation of Cd from root to aerial parts to boost Cd accumulation in plants. However, many PGPR strains help in plant growth promotion without raising Cd levels in edible crops that grow in contaminated soils. Several mechanisms have evolved in Cd-tolerant PGPR to cope with the heavy metal toxicity, and as a result, reduce Cd stress in plants. These include efflux, extracellular complexation, biosorption, precipitation, biotransformation and sequestration (Sharma and Archana 2016).

After entry into the cell, Cd must be rapidly and effectively removed from the cell or transformed into a non-or-less toxic form. The energy-dependent cadA efflux transporter protein, encoded by *cadA* gene of plasmid pI258 in *Staphlococcus aureus*, is involved in the removal of cadmium from the cell (Ganesan 2008). The gene *CadB* located on the same plasmid also confers Cd resistance by changing the binding site (Wheaton et al. 2015). The Cad system was also reported in *Ralstonia* sp. CH34. The *cadA* gene codes for cadmium resistance. The *cadB* gene expression is possible only when there is no *cadA* gene. *Alcaligenes eutrophus* confers Cd resistance due to the presence of the Czc system which effluxes cadmium and other heavy metals (zinc and cobalt) (Nies 2003; Hynninen 2010). The efflux system for Cd resistance, consisting of *czcB* and *smtAB* gene, is also present in the *E. coli* P4 strain (Khan et al. 2015). P-type ATPases, cation diffusion facilitator (CDF) family, CBA (Capsule biogenesis/assembly) family, and chemiosmotic family of transporters help in the efflux of Cd ions and Cd resistance (Nies 2003).

Biosorption plays a significant role in minimizing Cd toxicity to the bacterial cell under Cd exposure. The biosorption of Cd ions depends on metal adsorption, complexation, and bioaccumulation and makes it non-available to other organisms (Coelho et al. 2015). Metallothioneins in bacteria are cysteine-rich low molecular weight cytoplasmic proteins that help in positively charged metal (Cd) binding (Naik and Dubey 2017). Many bacteria with negatively charged cell walls or envelop can bind with dissolved Cd^{+2} cations. Bacterial exopolysaccharides (EPSs) with their anionic groups play a significant part in absorbing Cd ions from their vicinity. Metal biotransformations through oxido-reduction reactions, methylation and demethylation confer resistance against heavy metals in bacteria (Silver and Phung 2005).

6 Cadmium Resistant PGPR in Cadmium Detoxification in Plants

Cd bioavailability in the rhizospheric region has been the major reason for Cd toxicity in plants. The use of PGPR strains for plant growth and minimization of Cd uptake in edible crops provides an efficient, ecologically sustainable alternative strategy for bioremediation and maintaining food safety. However, in non-hyperaccumulator plants, Cd-tolerant PGPR could lower the uptake and distribution of Cd into the above-ground plant parts; whereas in hyperaccumulator plants, it may facilitate the Cd uptake and bioaccumulation in the plant. Cd resistant PGPR, such as *Bacillus* sp., *Pseudomonas* spp., *Burkholderia* sp., *Ochrobactrum*, *Chryseobacterium* sp., *Enterobacter* sp., *Serratia* sp., *Klebsiella* sp., reduce a significant amount of the Cd content in edible crops (Table 1). PGPR can alleviate cadmium toxicity through several mechanisms, ensuring plant growth. PGPR characters, such as the production of plant growth regulators including IAA, 1-aminocyclopropane-1-carboxylate deaminase (ACCD) production, siderophore production, organic acid secretion, and phosphate solubilization (Fig. 2), help in plant growth enhancement and minimization of Cd toxicity in Cd-polluted soil (Table 2) (Pramanik et al. 2018).

6.1 Cadmium Immobilization in Soil

PGPR-induced Cd stabilization in soil has great importance for diminishing Cd bioaccumulation in crops and simultaneously enhancing agricultural productivity and crop quality. PGPR can reduce the mobilization and phytoavailability of Cd by acting directly as biosorbents or as bioaccumulators (Voleskya and Holant 1995). Due to the high area-to-volume ratio of the bacterial cell and many metal attachment sites, PGP bacteria can act as excellent biosorbents (Gadd 1990). Cd binding extracellular polymers, such as exopolysaccharides and proteins, are produced by PGPR strains and could bind a substantial quantity of harmful heavy metals including Cd to immobilize them by precipitating as insoluble sulfides and oxides. Cd ions bind to the polyphosphate bodies, phytochelatins (PCs), metallothioneins (MTs) and other proteins to form various types of metal complexes, as reported in *Pseudomonas putida.* Chelator-Cd complexes are then transported to the vacuole for sequestration (Rayner and Sadler 1989; Dong et al. 2007). The release of organic molecules and slimes outside the bacterial cell wall increase Cd biosorption and sequestration in the root (Madhaiyan et al. 2007).

6.2 Cadmium Precipitation

PGP bacteria have anions, such as sulfides and phosphates on their cell walls. Cd^{2+} ions could bind with these negatively charged surfaces. The binding and subsequent precipitation of Cd^{2+} reduces its phytoavailability (Lamelas et al. 2006). For example, sulfate-reducing bacteria carried out sulfate reduction in presence of organic substances or H_2, and as a by-product, precipitate less soluble Cd sulfides (CdS) (Violante et al. 2010; Menon and Voordouw 2018). Also, PGPR under Cd and other heavy metals exposure produce H_2S that reacts with free Cd^{+2} extracellularly to precipitate, as CdS.

6.3 Plant Growth-Promoting Activities to Counter Cadmium Toxicity

6.3.1 Nitrogen Fixation

Nitrogen (N) is by far the most vital micronutrient for plant growth enhancement and agricultural productivity. It also enhances Cd tolerance in plants, with the production of nitrogen metabolites, such as GSH and phytochelatins, which play a significant part in defence against Cd toxicity. The presence of nitrogen in agricultural soil increases RuBisCo activity and photosynthetic yield, along with Cd tolerance (Jalloh et al. 2009). PGPR can fix free atmospheric nitrogen, act as a biofertilizer and remove N limitation in soil for plants. It was reported in a study that N_2-fixing Cd-tolerant *Klebsiella mobilis* promotes grain production in barley and reduces Cd concentration under Cd stress (Pishchik et al. 2002).

6.3.2 Phosphorus Solubilization

Phosphorus (P) also plays a significant function in overall plant growth and crop productivity. Complexation and biosorption of Cd with the phosphate groups present in the cell wall play significant roles in regulating Cd uptake and distribution in plant parts. P amendment in Cd-polluted soil enhances the quantity of chlorophyll and, as a result, improves photosynthetic yield in *Zea mays* (Jiang et al. 2007). (Many bacteria are capable of organic and inorganic phosphate complexes solubilization in soils, resulting in enhancement of P bioavailability. Application of phosphate solubilizers in Cd-polluted soils stimulates Cd immobilization as a result of the precipitation of Cd-phosphate complexes (Park et al. 2010). Similarly, many zinc solubilizing PGPR increases Zn phytoavailability (Saravanan et al. 2011). It is believed that Zn solubilization in the soil is an efficient strategy to promote crop productivity by limiting Cd bioavailability to plants and diminishing Cd uptake through roots.

Table 1 Cadmium resistant PGPR-plant interaction in alleviating cadmium stress in plants

PGPR strains	Plant	Cd concentration	Effects and mechanisms	References
Pseudomonas sp. K32	*Oryza sativa*	Exhibit resistance to 4000 μg/ml of Cd	Improve rice seedling growth through IAA production, nitrogen-fixation and phosphate solubilization under Cd stress; Cd bioaccumulation by the strain reduces Cd uptake by plant	Pramanik et al. (2021)
Bacillus licheniformis	*Spinacia oleracea* L	25, 75 and 125 ppm of Cadmium chloride (CdCl$_{2)}$	With the exogeneous application of melatonin, enhance antioxidant enzymes (SOD, POX, CAT) activity, inhibits lipid peroxidation and chlorophyll damage	Asif et al. (2020)
P. fluorescens 21, *P. putida* 23	*Hordeum vulgare* L	10 mg Cd kg^{-1} soil	Increase root growth, decrease Cd content in roots and improve mineral nutrition of the plant; Cd immobilization in soil organic matter due to Cd sequestration by bacterial siderophores	Shabayev et al. (2020)
Enterobacter sp. EG16, *Enterobacter ludwigii* DJ3	*Lycopersicon esculentum* L	50 and 100 mg kg^{-1} of CdCl$_2$ concentration	Improve shoot and root dry weight, decrease Cd transport to aerial parts; Cd immobilization due to bacterial adsorption, bioaccumulation and chelation, resulting in a decrease in Cd bioavailability in soil	Li et al. (2020)
Serratia sp. CP-13	*Linum usitatissimum* L	5–10 mg Cd kg^{-1}	Increase plant biomass, antioxidation, photosynthetic pigments, minerals uptake, decrease lipid peroxidation through IAA production, ACC deaminase activity and phosphate solubilization	Shahid et al. (2019)
Bacillus cereus M4	*Oryza sativa* L	Cd exposure of 1.0 mg/kg soil	Reduce Cd uptake and bioaccumulation in rice, reduce oxidative stress by producing Glutathione, enhance IAA production	Wang et al. (2019)
Pseudomonas aeruginosa, *Burkholderia gladioli*	*Lycopersicon esculentum* L	Cd stress of 0.4 mM	Enhances photosynthetic pigment content, fresh weight, root and shoot length through the production of phytohormone, mineral uptake, N$_2$ fixation; Production of Cd chelating thiol compounds reduces Cd bioavailability in soil and bioaccumulation in seedling	Khanna et al. (2019a)
Klebsiella michiganensis	*Oryza sativa* L	Cd concentrationof 200 μg/ml	Promotes plant growth through IAA production, ACC deaminase activity and phosphate solubilization reduces Cd bioavailability due to Cd sequestration	Mitra et al. (2019)
Paenibacillus sp. ISTP10	*Gossypium hirsutum* L	60 mg of Cd kg^{-1} of dry soil	Increase chlorophyll content, plant fresh and dry weight, shoot and root length through N$_2$ fixation, phosphorous solubilization, production of IAA, EPS, ammonia, HCN, and siderophores	Kumari and Thakur (2018)
Enterobacter Aerogenes MCC 3092	*Oryza sativa* L	Show resistance to 4000 mg ml^{-1} Cd	Enhance chlorophyll pigments, increase shoot and root length through IAA production, N$_2$ fixation, phosphate solubilization, and ACC deaminase activity	Pramanik et al. (2018)
Serratia marcescens RSC-14	*Solanum nigrum*	Cd resistance up to 4 mM (minimum inhibitory concentration)	Enhance plant growth, root elongation through bacterial cell wall binding, Cd efflux, production of (IAA), antioxidant enzymes, non-enzyme antioxidants, acetoin, butanediol, and phosphate solubilization, three CzcD proteins provide Cd tolerance and transportation	Khan et al. (2017a)

6.3.3 Secretion of Organic Acid

Excretion of organic acids, such as gluconic acid, succinic acid, salicylic acid, oxalic acid and citric acid by PGPR, are well reported. These organic acids help in Cd detoxification in plants by chelating with free Cd^{+2} ions. The release of organic acids by PGPR is a well-known mechanism that affects the mobility of Cd ions in rhizospheric soil by altering soil pH, organic matter contents and ionic strength (Halim et al. 2020). For instance, gluconic acid production by glucose dehydrogenase enzyme was studied in many PGPR. It was reported that gluconic acid produced by *Enterobacter asburiae* enhances growth in *Vigna radiata* under Cd exposure. Organic acids also upregulate antioxidant defence systems, such as SOD and POX under Cd stress (Goldstein 1995; Kavita et al. 2008), and help in phosphate solubilization in soil.

6.3.4 Siderophore Production

Siderophores play an important role in improving the iron status of the plant. It also binds with heavy metals to restrict metal mobility and increase accumulation (Rajkumar et al. 2010). These are low molecular weight compounds released by rhizospheric bacteria that bind to iron (Fe^{+3}) ions with great affinity. Siderophores, with their iron-binding ability, improve iron bioavailability which would result in plant growth. Also, the increase in iron level, in return, would affect the uptake of Cd, thus imparting Cd resistance. In *Pseudomonas* sp., synthesis of green pigmented siderophore, i.e. pyoverdine, has been reported under Cd stress (Dao et al. 1999). It enhances plant growth and reduces Cd intake in *Vigna mungo* (Tripathi et al. 2005). Siderophore producing *P. aeruginosa* also enhances iron intake in *Brassica* sp. under Cd stress (Sinha and Mukherjee 2008).

6.3.5 ACC Deaminase Production

Ethylene, a stress-signaling molecule, is produced from L-methionine through the intermediate products, *S*-adenosyl-1-methionine (SAM) and 1-aminocyclopropane-1-carboxylic acid (ACC). Ethylene triggers the production of SOD, APX and ROS, which ultimately results in senescence in plants. ACC deaminase (ACCD) cleaves the immediate ethylene precursor, ACC, to produce α-ketoglutarate and ammonia, and resultantly, reduce ethylene formation. The production of ACCD plays a significant role in Cd resistance mechanisms in plants (Glick 2005; Saleem et al. 2007). ACCD activity stimulates seed germination, root formation in tomato and plant growth in mustard and rape plants under Cd stress (Grichko et al. 2000; Belimov et al. 2001).

6.3.6 IAA Production

PGP traits, such as root hair formation and root elongation, shoot elongation, are immensely controlled by the productions of phytohormones, e.g. IAA, gibberellins and cytokinins. IAA production is regarded as one of the widely accepted plant growth-promoting traits for PGPR. IAA produced by PGPR strains enhances root elongation in *Brassica napus* (Sheng and Xia 2006). Plant growth promotion and alleviation of Cd toxicity by IAA producing *Enterobacter aerogenes* MCC 3092 and *Pseudomonas* sp. SNA5 in rice and wheat, respectively, was reported when exposed to Cd (Verma et al. 2015; Pramanik et al. 2018).

7 Conclusions and Future Prospects

PGPR has been enhancing crop productivity and crop quality in stressed soil through different plant growth-promoting mechanisms. With the recent interesting progress, bioremediation of cadmium stress in plants through PGPR has emerged as a promising technique. However, the use of PGPR on a commercial scale will require much deliberation regarding the preservation of the quality and efficacy of the PGPR product and delivery mechanisms. Future studies will also look into the bacterial genes responsible for PGP traits. It might help in developing and designing bacteria with many PGP traits. The use of genetically engineered PGPR will be more effective in reducing Cd toxicity and plant growth promotion with their multifunctional PGP traits (Glick 2012). Rapid improvement and application of modern tools and nanotechnology open the door for the production of PGPR-mediated bionanohybrids, nano-fertilizers and biosensors. These bionanohybrids will play a vital role in Cd immobilization and maintaining macro and micronutrient balance in the rhizospheric soil. Future improvement and advancement of PGPR-based new technology in Cd detoxification in soil and plants will guide and bring in agricultural prosperity in the coming decades.

In recent decades, rapid accretion in anthropogenic activities led to cadmium contamination in the environment. The increase of cadmium pollution in the agricultural soil has led many scientists to focus on developing rapid, low-cost and efficient Cd detoxification technologies for

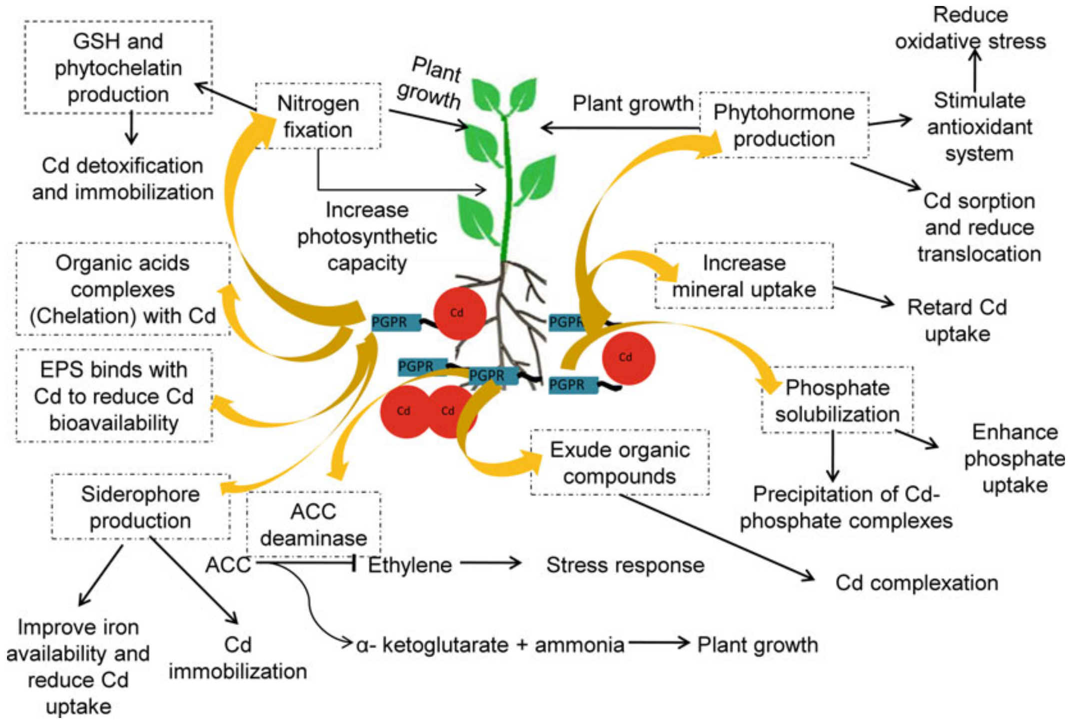

Fig. 2 Mechanisms of PGPR in alleviating cadmium stress in plant

Table 2 Mechanisms of PGPR for cadmium detoxification in plants

Plant growth-promoting traits	Mechanisms of plant growth	Cd detoxification mechanisms	Examples of PGPR strains	References
ACC deaminase (ACCD) production	Alteration of ethylene, which enhances senescence, synthesis by producing α-ketoglutarate and ammonia; NH_4^+ act as N-source	Indirectly decreases Cd-stimulated ROS generation and decreases oxidative damage	*Pseudomonas* sp., *Pseudomonas fluorescens*, *Enterobacter aerogenes* MCC 3092, *Azoarcus* sp. CIB, *Klebsiella michiganensis*	Govindasamy et al. (2015), Pramanik et al. (2018), Mitra et al. (2018b), Fernández-Llamosas et al. (2020), Halim et al. (2020)
IAA production	Act as a plant growth regulator, enhance root hair development and root elongation	Stimulates Cd biosorption and translocation; decrease oxidative damage	*Azospirillum* spp., *Bacillus subtilis*, *Enterobacter* sp. *strain* EG16, *Pseudomonas putida*, *Lysinibacillus varians strain* KUBM17, *Klebsiella michiganensis*, *Bacillus cereus* strain *ALT1*	Bhattacharyya and Jha (2012), Chmielowska-Bąk et al. (2014), Chen et al. (2016), Mitra et al. (2018b), Sahile et al. (2021)
P solubilization	Enhance phosphate bioavailability by converting insoluble phosphorus to a soluble form	Precipitation of cadmium-phosphate compounds	*Burkholderia* sp., *Azotobacter* sp., *Bradyrhizobium* sp., *Klebsiella michiganensis*, *Leifsonia* sp., *Enterobacter* sp., *Enterobacter ludwigii* GAK2	Bhattacharyya and Jha (2012), Guo and Chi (2014), Ahmad et al (2016), Mitra et al. (2018b), Adhikari et al. (2020)
Zn solubilization	Increase Zn bioavailability	Reduce Cd uptake	*Pseudomonas aeruginosa*, *Serratia liquefaciens*, *Pseudomonas moraviensis*, *Enterobacter hormaechei*, *Pseudomonas frederiksbergensis*	Saravanan et al. (2011), Kumar et al. (2019), Fahsi et al. (2021)

(continued)

Table 2 (continued)

Plant growth-promoting traits	Mechanisms of plant growth	Cd detoxification mechanisms	Examples of PGPR strains	References
Siderophore production	Improve iron availability; promote the formation of complexes with Fe_3^+	Lowers Cd availability to plants and its uptake, repress ZIP transporters	*Pseudomonas putida*, *Lysinibacillus varians strain* KUBM17	Rascio and Navari-Izzo, (2011), Pal and Sengupta (2019)
Nitrogen fixation	Improve N_2 content in soil and their bioavailability; increase photosynthetic yield	Production of reduced glutathione (GSH) and phytochelatin (PC) (redox agents)	*Bradyrhizobium* sp., *Enterobacter* sp., *Klebsiella michiganensis*, *Pseudomonas putida strain* KUBM18, *Lysinibacillus varians strain* KUBM17	Guo and Chi (2014), Mitra et al. (2018a, b), Pal and Sengupta (2019)
Organic acid secretion	Solubilization of organic and inorganic phosphates, Zn and other essential nutrients	Cd chelation and precipitation	*Enterobacter asburiae*, *Burkholderia gladioli*, *Pseudomonas aeruginosa*, *Bacillus cereus*	Majewska and Kurek (2011), Kavita et al. (2008), Khanna et al. (2019b), Sahile et al. (2021)

plants. Further research on how plant growth-promoting rhizobacteria interact with Cd ions and plants in response to cadmium stress would allow us to comprehend the knowledge of the phytoavailability of cadmium in rhizospheric soil effectively. The knowledge about these processes provides insight into the strategies employed by bacteria for Cd detoxification in plants. It would also aid in the prediction of the plant response in a stressed environment. This chapter summarizes the current understanding of natural and anthropogenic sources of cadmium contamination, the intricate interaction between rhizospheric growth-promoting bacteria, soil and plant under Cd stress. Here, PGPR acts as a mediator that regulates bioavailable Cd level and their detoxification in plant cells in a sustainable manner. The knowledge about these processes offers valuable insights into the strategies for developing PGPR-based bioremediation technologies to mitigate the growing risk of Cd toxicity for worldwide agricultural yield and productivity.

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