14 Perspectives of Plant Growth-Promoting Actinomycetes in Heavy Metal Phytoremediation

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Abstract

Phytoremediation is an emerging technology that uses plants and their associated microbes to clean up pollutants from the soil, water, and air. In recent years, heavy metal phytoremediation assisted by plant beneficial actinomycetes has been highly used for cleaning up metal-polluted soils since these bacteria play an essential role in plant growth, metal/nutrient acquisition, metal detoxification, and alleviation of biotic/abiotic stress in plants. Direct plant growth promotion by actinomycetes is based on hormonal stimulation and improved nutrient acquisition by plants. Similarly, diverse mechanisms, viz., soil acidification and production of metal mobilizing/immobilizing substances by actinomycetes, are involved in heavy metal uptake by plants, which is often directly connected with the efficiency of phytoremediation process. Based on these beneficial plant-actinomycetes interactions, it is possible to develop microbial inoculants as environmentally friendly bio-tool for use in heavy metal phytoremediation. In this study, we highlight the diversity and plant growth beneficial features of actinomycetes and discuss their potential role on plant growth and phytoremediation process in metal-polluted soils.

Keywords

Plant-associated microorganisms • Actinomycetes • Heavy metals • Rhizosphere • Siderophores • 1-Aminocyclopropane-1-carboxylic acid

14.1 Introduction

The development of numerous technologies and industrialization ends up with the result of release of heavy metals as pollutants into the environment (Doble and Kumar 2005; Rajkumar et al. 2009). Particularly, the contamination of

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soil with heavy metals is a major worldwide problem in the current decade (Kamran et al. 2014). The heavy metal accumulation in soil adversely affects both the ecosystem and human health. Although some metals are essential for life, they are highly toxic to microorganisms (Fig. 14.1), plants, animals, and humans at higher concentrations. They affect various physiological and biochemical process by displacing other metal ions, blocking essential functional groups, disintegrating cell organelles (Vangronsveld and Clijsters 1994), acting as genotoxic substance, and disrupting the physiological process such as photosynthesis, respiration, protein synthesis, and carbohydrate metabolism.

Application of various physical, chemical, and biological strategies for decontaminating the polluted sites is a challenging task because heavy metals cannot be degraded and thus persist in the environment indefinitely. In order to clean up the contaminated sites, heavy metals should be concentrated and extracted from the contaminated sites by conventional methods for proper disposal or reuse. Although various strategies (such as land filling, excavation, fixation, solidification, and leaching) have been applied to remediate the contaminated sites, most of these methods are either extremely costly or simply involve the isolation of the contaminated sites or adversely affect the soil biological activity and fertility (Pulford and Watson 2003; Wu et al. 2010). Currently, the biological-based technique has been extensively used as an alternative method to remove pollutants from air, soil, and water or to render pollutants harmless (Chowdhury et al. 2015). "Phytoremediation" is one of the key processes of bioremediation that involves the use of plants and their associated microbes to relief, transfer,

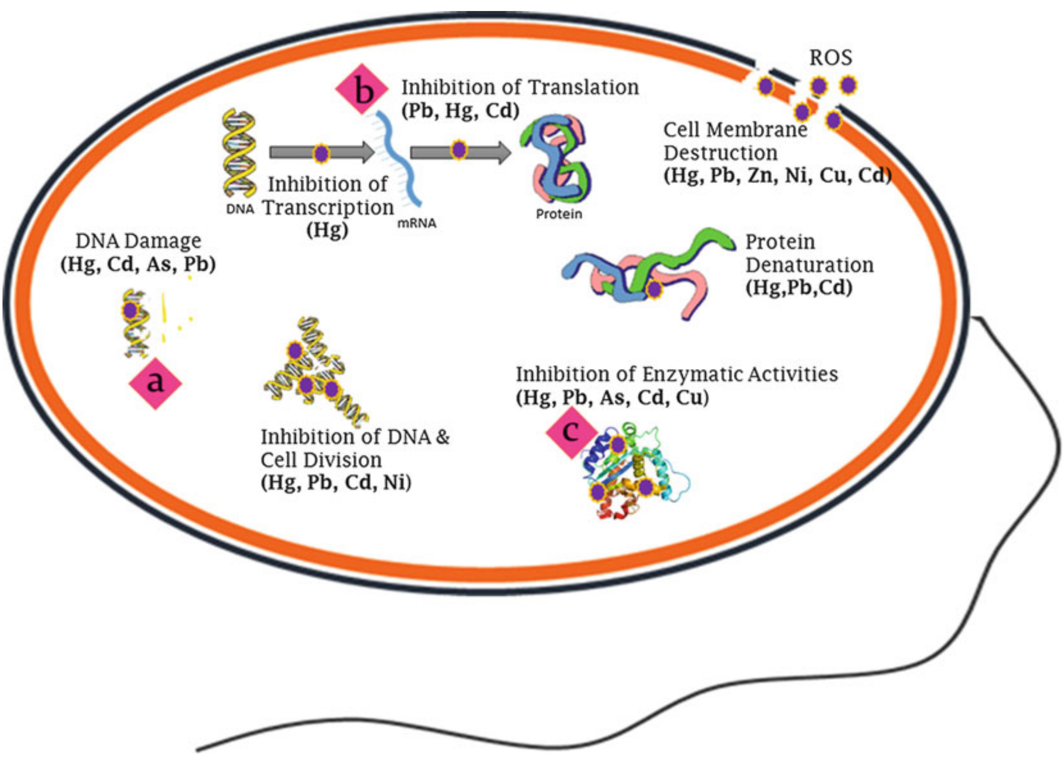

Fig. 14.1 The major molecular mechanism involved in heavy metal toxicity. (*a*) Production of reactive oxygen species by auto-oxidation and Fenton reaction causes DNA damage, cell membrane disruption (e.g., Fe and Cu) (Valls and de Lorenzo 2002), (*b*) blocking of essential mechanisms by damaging biomolecules (e.g., Cd and Hg), (*c*) displacement of essential metal ions (Fe) in biomolecules by heavy metals (Cu and Cd)

stabilize, or degrade the pollutants from soil, sediments, surface waters, and groundwater (Elekes 2014; Paz-Ferreiro et al. 2014; Laghlimi et al. 2015). The concept of phytoremediation was first proposed by Chaney (1983), which paved the way for the development of process of removing environmental contaminants using plants. The success of phytoremediation is dependent on the potential of the plants to tolerate the metal stress and produce high amount of biomass within a relatively short period. In recent years, plant-associated beneficial microbes have been used to enhance heavy metal phytoremediation process (Rajkumar et al. 2012). The plant-associated microbes accelerate phytoremediation process in metal-polluted soils by promoting plant growth and play a significant role in altering heavy metal accumulation in plants through producing various metabolites (e.g., siderophores, organic acids, and plant growth regulators) and various reactions in the rhizosphere (e.g., acidification, chelation, precipitation, and oxidation-reduction reactions). In turn, plant roots release nutrients through exudation which support the growth, survival, and colonization potential of microflora, involved in phytoremediation process.

Actinomycetes are gram positive, aerobic, sporulating, and filamentous bacteria which are ubiquitous in soils. Actinomycetes gain their importance among the researchers due to the production of enormous secondary metabolites and enzymes including antibiotics, degrading enzymes, enzyme inhibitors, immunosuppressants, phytotoxins, phytohormones, pesticides, and insecticides (Erikson 1949; Bèrdy 1995; Park et al. 2002; Hamaki et al. 2005; Imada 2005; Doumbou et al. 2011). They also directly promote plant growth by producing phytohormones (auxin, cytokinins, and gibberellins) and siderophore, solubilizing phosphate, fixing atmospheric nitrogen, and suppressing stress-ethylene production in plant through 1-amino cyclopropane-1-carboxylate (ACC) deaminase activity (Misk and Franco 2011; Sadeghi et al. 2012; Harikrishnan et al. 2014a) (Table 14.1). Moreover, the actinomycetes possess many properties that make them good candidates for application in bioremediation of soils contaminated with inorganic and/or organic pollutants. They produce extracellular enzymes that degrade a wide range of complex organic compounds. They play an important role in the recycling of organic carbon and are able to degrade complex polymers by production of extracellular degrading enzymes and peroxidases (Goodfellow and Williams 1983; Ball et al. 1989; Pasti et al.1990; Mason et al. 2001). Therefore, the utilization of metal-resistant actinomycetes, which are associated with plants, could be of particular importance as they can provide/solubilize nutrients such as Fe and P to plants, which could reduce the toxic effects of heavy metals. In addition, the metabolites produced by actinomycetes (e.g., siderophores and organic acids) bind Fe and other heavy metal ions and thus enhance their bioavailability in the rhizosphere of plants (Braud et al. 2009; Rajkumar et al. 2010). The resulting increase in plant growth and heavy metal accumulation by plants enhance the efficiency of phytoremediation in metal-contaminated soil.

This paper details recent advances in understanding plant and actinomycetes interaction and describes how their beneficial partnerships can be exploited as a strategy to accelerate plant growth and phytoremediation potential in heavy metal-polluted soils.

14.2 Actinomycetes and Heavy Metal Interaction

Microbial mechanisms conferring both plant growth promotion and heavy metal resistance have significant environmental importance because of their potential use in phytoremediation. In order to survive in metal-polluted environment, actinomycetes have evolved a number of mechanisms, by which they tolerate high concentrations of heavy metals (Pavel et al. 2013). Actinomycetes have been shown to alter heavy metal toxicity/bioavailability through various metal-independent mechanisms including (a) reduction of cellular sensitivity, (b) siderophore-heavy metal complexation, (c) intracellular metal sequestration,

Table 14.1 List of plant growth-promoting actinomycetes

Bacterial strains	PGP traits	References
Streptomyces sp.	Siderophore production, IAA, and GA3 production	Goudjal et al. (2015)
Streptomyces sp.	Gibberellic acid, IAA, abscisic acid, kinetin, and benzyladenine	Rashad et al. (2015)
Streptomyces aurantiogriseus	IAA production, antagonistic against *Rhizoctonia solani* in rice sheath blight	Harikrishnan et al. (2014a, b)
Streptomyces sp., *Micromonospora* sp., *Nocardia* sp., *Actinomadura* sp., *Microbispora* sp., and *Actinoplanes* sp.	Antagonistic against soil-borne pathogens of soybean	Dalal and Kulkarni (2014)
Streptomyces sp.	Production of IAA and siderophore	Rafik et al. (2014)
Actinomycetes	Production of HCN, IAA, siderophore, and phosphate solubilization	Damle and Kulkarni (2014)
Streptomyces sp.	ß-1,3-Glucanase, IAA, and HCN production	Gopalakrishnan et al. (2013, 2014)
Streptomyces sp.	Siderophore production	Lee et al. (2012)
S. rochei, *S. carpinensis*, *S. thermolilacinus*	Production of siderophore, IAA, and phosphate solubilization	Jog et al. (2012)
Rhodococcus sp.	IAA production	Costa and Melo (2012)
Rhodococcus erythropolis	Enhancing plant growth under Cr^{6+} toxicity	Patel et al. (2012)
Frankia sp., *Actinoplanes* sp., *Micromonospora* sp., and *Streptomyces* sp.	Production of IAA, gibberellin, and zeatin	Solans et al. (2011)
Streptomyces and non-identified *non-Streptomyces* strains	Control egg hatching of the nematode *Meloidogyne incognita*	Ruanpanum et al. (2010)
Actinomadura glauciflava, *Nonomuraea rubra*, and *Nocardia alba*	Protease activity, ammonia, IAA, and siderophore production	Nimnoi et al. (2010)
Streptomyces sp.	Siderophore production, phosphate solubilization, and N_2 fixation	Franco-Correa et al. (2010)
Leifsonia soli	Plant growth promotion by ACC deaminase production	Madhaiyan et al. (2010)
Microbacterium azadirachtae	IAA production, P solubilization, ACC deaminase activity, and sulfur oxidation	Madhaiyan et al. (2010)
Streptomyces sp.	Production of zeatin, gibberellic acid, and IAA and antagonism against *Pseudomonas savastonii*	Ghodhbane-Gtari et al. (2010)
Actinoplanes campanulatus, *Micromonospora chalcea*, and *Streptomyces spirali*	Reduction of root crown rots induced by *Pythium aphanidermatum* in cucumber	El-Tarabily et al. (2010)
Actinomadura sp.	Production of antifungal compounds, IAA, and siderophores	Khamna et al. (2009)
Micromonospora aurantiaca	Strong antagonistic activity against *Pythium ultimum* and *Fusarium oxysporum* and IAA and P solubilization activity	Hamdali et al. (2008a, b)
Streptomyces kasugaensis	Antagonistic activity against *Pyricularia oryzae*	Schluenzen et al. (2006)
Micromonospora carbonacea	Cell wall degradation of *Sclerotina minor*	El-Tarabily et al. (2000)
Streptomyces cacaoi	Antagonism against fungi	Copping and Duke (2007)
S. olivaceoviridis and *S. rochei*	Auxin, gibberellin and cytokinin production	Aldesuquy et al. (1998)
Micromonospora endolithica	P solubilization activity	El-Tarabily et al. (1997)

and (d) exclusion through permeability barriers. Several actinomycetes can adopt to resist the toxicity of heavy metals by altering the sensitivity of cellular components. Particularly, the mutations and DNA repair mechanisms may contribute to the protection toward plasmid and genomic DNA. Similarly, the metal-resistant components such as metallothioneins produced by actinomycetes can effectively bind heavy metals (Stillman 1995; Garbisu and Alkorta 2003) by which they can mobilize or immobilize and thus reduce their toxicity to tolerate heavy metal. For instance, glutathione offers resistance to the cell by suppressing the free radical formation from Cu(II) and Fe(II) and also to Ag(I), Cd(II), and Hg(II) (Rouch et al. 1995; Bruins et al. 2000). Similarly, the production of siderophores by actinomycetes can also play an important role in complexing toxic metals and in decreasing their toxicity. Siderophores are the iron-chelating secondary metabolites produced by various microorganisms under iron-limiting conditions. Actinomycetes are abundant producer of siderophores which plays a key role in the remediation of heavy metals. Many siderophores (e.g., desferrioxamine B, desferrioxamine E, rhodotorulic acid) are relatively stable biomolecules, protected from environmental peptidases and lytic enzymes by modifying structural composition (Sessitsch et al. 2013). In general, the siderophores produced by rhizosphere microbes form complexes with Fe(III) at the soil interface, desorb Fe from soil matrix, and thus increase Fe solubility and bioavailability in the soil solution. The siderophores also possess affinity to other trace element ion (Hider and Kong 2010) by which the bacteria reduce the harmful effects of metal and help in phytoremediation process. Dimkpa et al. (2009a, b, c) reported that the bacterial culture filtrates containing three hydroxamate siderophores secreted by *Streptomyces tendae* F4 significantly promoted plant growth and enhanced the uptake of Cd and Fe by cowpea relative to the control. Similarly, a recent study by Ji et al. (2012) observed that the production of siderophore desferrioxamine B (DFOB) accounted for the increased uptake of Fe and Pu by bacteria and reported that Pu^{4+}-DFOB and Fe^{3+}-DFOB complexes inhibit uptake of the other ions and compete for shared binding sites or uptake proteins. These results suggest that Pu-siderophore complexes can generally be recognized by Fe-siderophore uptake systems of microbes. Similarly, siderophores also played an important role in biocontrol of plant pathogens and in enhancement of plant growth promotion (Shanmugaiah et al. 2015).

The mechanism of metal tolerance exhibited by the actinomycetes is also due to the ability of its cell wall to bind with metal ions and accumulate in intracellular at higher concentrations (Lin et al. 2011; Singh et al. 2014; El Baz et al. 2015). For instance, a recent study by Lin et al. (2011) demonstrated the intracellular accumulation of Zn^{2+} and Cd^{2+} in a novel species, *Streptomyces zinciresistens*, under in vitro conditions and reported the interaction of heavy metals with amino, carboxyl, hydroxyl, and carbonyl groups accounted for the observed metal biosorption. In addition, certain actinomycetes reduce mobility of heavy metals through oxidation or reduction reactions. Such transformation especially plays a key role in the reduction of the toxicity of certain elements such as Cr and Hg in soils. For example, a *Streptomyces* sp. isolated from riverine sediments was shown to reduce the mobile and toxic CrO_4^{2-} to non toxic Cr^{3+} (Amoroso et al. 2000). In a similar study, Ravel et al. (1998) demonstrated the Hg reducing potential of *Streptomyces* sp. isolated from the Baltimore Inner Harbor, at a site heavily contaminated with metal. They reported that this bacterium significantly reduced Hg(II) to elemental and volatile Hg and thereby reduce their toxicity to tolerate Hg.

Actinomycetes can also reduce the heavy metal bioavailability through producing extracellular polymeric substance (EPS). The EPSs are high-molecular-weight polymers which are composed of sugar residues. Lead, cadmium, and uranium are the most common heavy metals which bind to the EPS which results in the restriction of heavy metal entry in the cell. Albarracin et al. (2008) investigated biosorption potential of a copper-resistant *Actinobacterium*, *Amycolatopsis* sp. ABO, and found that these isolates were able to accumulate 25 mg/g of Cu. Intracellularly copper was distributed in cytosolic fraction (86 %), cell wall (11 %), and ribosome/membrane fraction (3 %).

The cells exposed to excess concentration of heavy metal has to manage with the production of toxic reactive oxygen species including superoxide anions in the Fenton reaction (Stohs and Bagchi 1995). These molecules are detoxified via superoxide dismutases (SODs) which dismutate the superoxide to O_2 and H_2O_2 (Fridovich 1995). Subsequently, the hydrogen peroxide is detoxified in a catalase-mediated reaction. Schmidt et al. (2005) isolated a strain *Streptomyces acidiscabies* which showed tolerance to various metals (Ni, Cu, Cd, Cr, Mn, Zn, and Fe) conferred by Ni-containing SODs. The gene *sodN* code for the Ni-containing SODs is not only activated by Ni but also Cu, Fe, and Zn. Summers (1985) has reported that Hg-resistant *Streptomyces* sp. was able to detoxify the Hg through converting Hg^{2+} to volatile Hg^0 by mercuric reductase enzyme.

The largest mechanism of metal-resistant system in microbes is active transport or efflux system. Some efflux systems involve ATPases, and others are chemiosmotic ion/proton pumps. These mechanisms actively pump back toxic ions that have entered the cell out of the cell via active transport (ATPase pump) or diffusion (chemiosmotic ion/proton pump). As, Cr, and Cd are the three metals most commonly associated with efflux resistance. It has been shown that a particular family of *Actinobacteria* including *Streptomyces* and *Mycobacterium* sp. use efflux-like mechanism for metal removal and antibiotic tolerance. An example is the ABC transport system for antibiotics, which can also be used as efflux pump for many metals (Borges-Walmsley et al. 2003). Albarracin et al. (2005) explained that the Cu resistance mechanisms of actinomycetes could be similar to that encountered in other bacteria such as the PcoABCDRS system of *Escherichia coli* or its homologue CopABCDRS of *Pseudomonas* sp. and *Xanthomonas campestris* (Nies 1999). Thus, the conservation of Cu pumps along evolution may indicate that uptake, reduction, or efflux of copper in actinomycetes could be also due to P-type ATPases. The schematic representation of metal-resistant mechanisms of actinomycetes in metal-polluted soil is presented in Fig. 14.2. Taken together, these reports clearly indicate the potential of actinomycetes to tolerate/reduce heavy metal toxicity and suggest that suitability of these microbes for heavy metal bioremediation.

14.3 Heavy Metal Phytoremediation

The emerging technology of bioremediation which paved the potential way for removal of heavy metals is phytoremediation. The term phytoremediation denotes the broaden area of remediation of polluted environment using plants which includes:

1. *Phytoextraction*: Cultivation of metal hyperaccumulating plants to remove the metals by concentrating them in harvestable parts of the plant
2. *Rhizofiltration*: Adsorption/precipitation of metals onto roots or absorption by roots of aquatic metal-tolerant plants
3. *Phytostabilization*: Immobilization of metals in the soils by adsorption onto roots or precipitation in the rhizosphere
4. *Phytovolatilization*: Conversion of pollutants to volatile form and their subsequent release to the atmosphere
5. *Phytohydraulics*: Absorption of large amount of water by fast-growing plants and prevent expansion of contaminants into adjacent uncontaminated areas
6. *Rhizodegradation*: Decomposition of organic pollutants by rhizosphere microorganisms
7. *Phytoresaturation*: Revegetation of barren area by fast-growing plants that cover soils and thus prevent the spreading of pollutants into environment (Masarovičová and Kráľová 2012)

Although a large number of plants are tolerating/accumulating high concentrations of heavy metals, the adverse environmental conditions

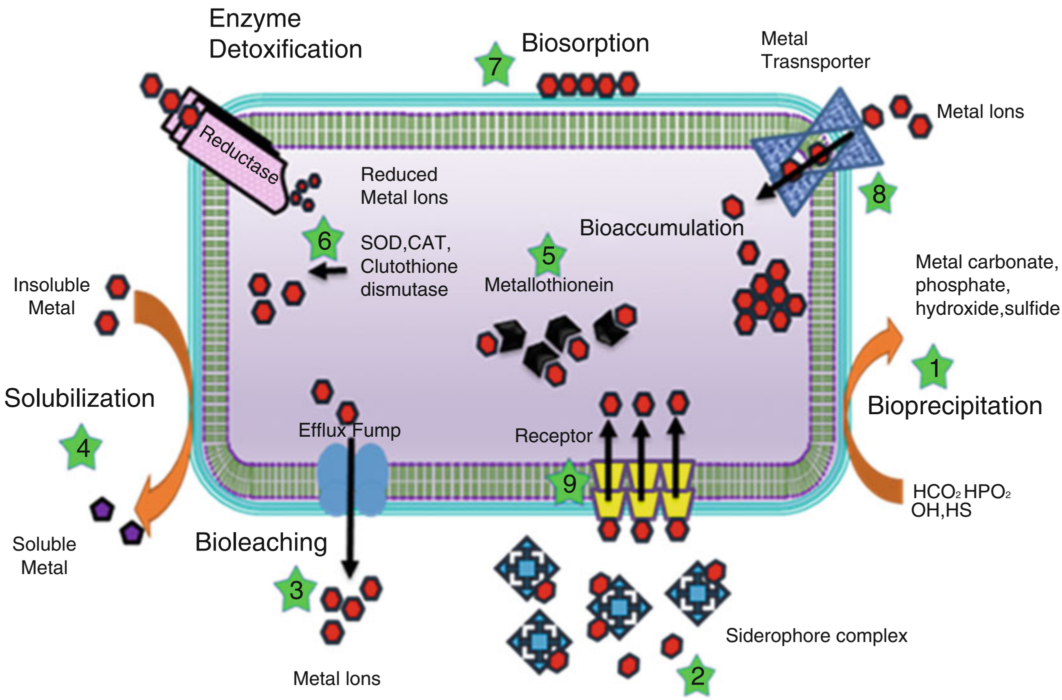

Fig. 14.2 Microbial interactions with heavy metals in polluted soils. (*1*) Precipitation/crystallization of metals occurs due to the production of secondary metabolites; (*2*) secretion of siderophore decreases metal bioavailability by complexation reaction; (*3*) plasmid-DNA-encoded efflux transporters (e.g., ATPase pumps or chemiosmotic ion/proton pumps) expel the accumulated metals outside the cell; (*4*) organic acids secreted by bacteria solubilize the insoluble metal minerals; (*5*) synthesis of metallothioneins and cysteine-rich proteins binds to the metals with greater affinities; (*6*) detoxification of metal by production of enzymes such as reductase and superoxide dismutase; (*7*) metals bind to the cell wall components of anionic functional groups and extracellular polymeric substance secreted by the bacterium; (*8*) metals enter into the cell by metal transporters either through ATP hydrolysis or chemiosmotic gradient across the cytoplasmic membrane

particularly poor soil quality, higher concentrations of metals, multi-metal-contaminated soils, etc., generally impair the plant metabolism and thus reduce growth, survival, and overall phytoremediation potential in polluted soils. To overcome this limitation, the plant-associated bacteria have been extensively used as inoculants that confer plant metal tolerance, improve plant growth and health, mobilize/immobilize heavy metals, and are able to maintain a stable relationship with plants in metal-polluted soils. The following sections summarize the effects of plant-associated actinomycetes on plant growth in metal-polluted soils (Fig. 14.3).

14.4 Plant Growth-Promoting (PGP) Potential of Actinomycetes

Actinomycetes are recognized as a potential group of rhizobacteria which influence the plant growth, yield, and nutrient uptake by an array of mechanisms including the production of auxins, ACC deaminase, nitrogen fixation, siderophore production, and phosphate solubilization. Actinomycetes directly regulate plant physiology by mimicking synthesis of plant hormones, whereas other microorganisms increase mineral and nitrogen availability in the soil as a way to

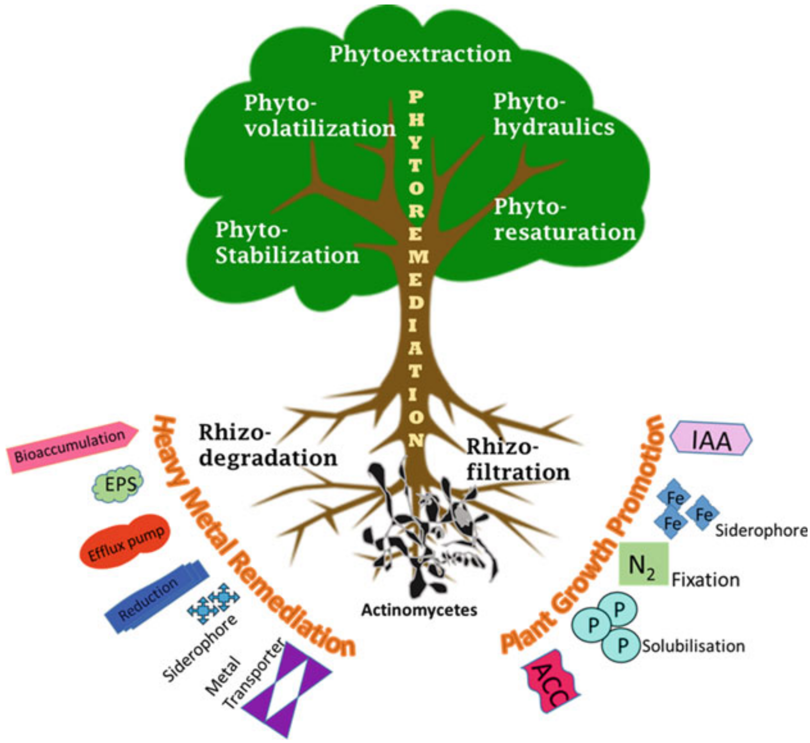

Fig. 14.3 Various types of microbial assisted heavy metal phytoremediation

augment growth. The isolates could exhibit more than two or three PGP traits, which may promote plant growth directly, indirectly, or synergistically (Yasmin et al. 2007).

14.4.1 Indole-Acetic Acid (IAA)

Auxins are classified as the main phytohormone which regulate growth, ontogeny, morphogenesis, and adaptive and repair processes in plants (Shatheesh Kumar 2011). It was shown that auxins play an important role in root formation, elongation, promotion of ethylene production, and fruit ripening (Table 14.2). Among the numerous auxins that can be produced by plants and microorganisms, IAA, have received increasing attention as potential compounds to improve the plant growth and development. Experiments with *Citrus reticulata* revealed that the inoculation with the *Nocardiopsis* of actinomycetes increased the shoot height, shoot fresh weight, and root fresh weight from 20.2 % to 49.1 %, 14.9 % to 53.6 %, and 1.6 % to 102 %, respectively (Shutsrirung et al. 2013). This effect was attributed to the increased level of IAA (222.8 μg/mL) produced by the strain that was able to promote the plant growth. Harikrishnan et al. (2014a) assessed the ability of IAA producing *Streptomyces aurantiogriseus* to promote the growth of rice (*Oryza sativa*) plants and reported that *S. aurantiogriseus*, which produces high levels of IAA, increased the root and shoot length from 3.3 to 9 cm and 3.63 to 10.2 cm, respectively. Likewise, Cruz et al. (2015) also observed that the inoculation with IAA producing actinomycetes increased the growth and yield of rice under greenhouse conditions. The inoculation with *Streptomyces* sp. that had been isolated from wheat field has also been studied in detail (Sadeghi et al. 2012). These bacteria significantly reduced the toxicity of salt stress in wheat plants and promoted the plant growth and nutrient (N, P, Fe, and Mn) uptake under in vivo conditions. Here, it was suggested that IAA production together with other plant growth-promoting mechanisms, such as phosphate solubilization and siderophore

Table 14.2 Phytohormones produced or modulated by *Actinobacteria* (Modified from Hamedi et al. 2015)

Phytohormone	Functions in plant[a]	*Actinobacteria*	References
Indole-3-acetic acid	Stimulates seed and tuber germination, initiates lateral and adventitious root formation, and affects biosynthesis of metabolites	*Micromonospora*, *Streptomyces*, and *Frankia*	Solans et al. (2011), Hirsch and Valdes (2010), Goudjal et al. (2015), and Harikrishnan et al. (2014a)
Brassinolide	Increases content of chlorophyll, stimulates protein synthesis, activates certain enzymes, and regulates cellular differentiation	*Streptomyces*	Merzaeva and Shirokikh (2010)
Salicylic acid	Induces SAR, prolongs life of flowers, inhibits ethylene biosynthesis, and facilitates pollination of certain plants	*Streptomyces*	Lin et al. (2011)
Cytokinins	Key role in plant morphology, leaf senescence, and source-sink relationships, key regulators of the plant growth defense	*Micromonospora*, *Streptomyces* and *Actinoplanes*	Scherlacha and Hertweck (2009), Mohandas et al. (2013)
Jasmonic acid	Induces ISR against necrotrophs, activates phylloptopsis, tuber formation, fruit ripening, and pigment formation	*Streptomyces*	Merzaeva and Shirokikh (2010)
Gibberellins	Stimulate stem elongation by stimulating cell division and elongation. Stimulate bolting/ flowering	*Micromonospora*, *Frankia*, *Actinoplanes*, and *Streptomyces*	Solans et al. (2011), Mohandas et al. (2013), Rashad et al. (2015)
Serotonin (5-hydroxytryptamine)	Structural analog of auxins and plant metabolize serotonin to IAA	*Streptomyces*	Tsavkelova et al. (2005)
Abscisic acid	Phylloptopsis, closure of stomata and aging	*Streptomyces*	Bach and Rohmer (2012), Rashad et al. (2015)

[a]Liu et al. (2009)

production, accounted for the observed increase in growth of the test plants. Several of the plant-associated actinomycetes have also been reported to protect the plants from various soil-borne pathogens (Verma et al. 2011; Harikrishanan et al. 2014a, b). For instance, Verma et al. (2011) reported that the inoculation of spore suspension of *Streptomyces* strain AzR-051 significantly promoted plant growth and antagonized the growth of *Alternaria alternata*, causal agent of early blight disease in tomato plant.

14.4.2 Siderophore Production

Among the various plant growth-promoting traits, the production of siderophores by bacteria is of special significance because of its metal-chelating properties which play pivotal roles in increasing the Fe concentration in the rhizosphere soils and its uptake by plants. Valencia-Cantero et al. (2007) demonstrated the potential of siderophore-producing actinobacterial strain *Arthrobacter maltophilia* to protect *Phaseolus vulgaris* (common bean) form alkaline stress and reported this effect may be due to increased level of siderophores produced by the *A. maltophilia* that were able to increase Fe availability in the rhizosphere of the plants. Rungin et al. (2012) reported that the inoculation of an endophytic *Streptomyces* sp. GMKU 3100 to rice and mung bean plants significantly increased root and shoot biomass and length of test plants compared with non-inoculated and siderophore-deficient mutant treatments. This study indicates that siderophores of *Streptomyces* sp. GMKU played a major role in making sequestered iron available to the plant. Since the siderophores in rhizosphere soil may form complexes with other heavy metal ions and minimize the toxic effects of free metal ions, the heavy metal-siderophore complex is considered as less toxic than the free form of heavy metals. Dimkpa et al. (2008) have pointed out metal-chelating properties of siderophores, accounted for reduced heavy metal toxicity and increased auxin production in plants. They attributed the alleviation of metal toxicity to siderophore and metal complexation, thus protecting auxin from the toxic effects of free form of toxic metals.

14.4.3 ACC Deaminase Activity

Another important way in which the actinomycetes might influence the host plant growth is the utilization of ethylene precursor ACC as the sole source of nitrogen into α-ketobutyrate and ammonia. Actinomycetes containing ACC deaminase metabolize ACC, thereby lowering stress-ethylene level and enhancing plant growth (Glick 2005). *Kibdelosporangium phytohabitans* sp. KLBMP 1111^{T}, a novel endophytic actinomycete isolated from root of the oilseed plant *Jatropha curcas*, has the ability to utilize ACC as a sole source of nitrogen via ACC deaminase enzyme. It also has the ability to produce siderophore and IAA (Xing et al. 2012). Halotolerant non-*Streptomycete Actinobacteria* such as *Micrococcus yunnanensis*, *Corynebacterium variabile*, and *Arthrobacter nicotianae* isolated from saline coastal region of Yellow river were reported to exhibit ACC deaminase activity and were able to significantly promote the growth of canola plants under salt stress condition (Siddikee et al. 2010). Similarly, El-Tarabily (2008) demonstrated that *Streptomyces filipinensis* no. 15 was able to reduce the level of ACC in roots and shoots promotes the growth of the tomato plants. They attributed this effect to the ability of actinomycetes to lower endogenous ACC level and low stress-ethylene accumulation.

14.4.4 Nitrogen Fixation

Nitrogen fixation is a process by which atmospheric nitrogen (N_2) is converted into ammonia (NH_3) (Wagner 2011), which can be assimilated by plants for the synthesis of nitrogenous biomolecules. A few species of *Arthrobacter*, *Agromyces*, *Corynebacterium*, *Mycobacterium*, *Micromonospora*, *Propionibacteria*, and *Streptomyces* have been shown to possess N_2 fixation trait. Similarly free-living or symbiotic *Frankia* can also enhance plant growth and development in different soils and climate regions through nitrogen fixation. Particularly, the actinorhizal nitrogen fixation (symbiotic association between *Frankia* and dicotyledonous plants) plays a major role in establishing the plantations at adverse sites (Diagne et al. 2013). Similarly, some species of *Thermomonosporaceae* and *Micromonosporaceae* family also demonstrated to fix atmospheric nitrogen (Valdés et al. 2005). Similarly, *Streptomyces thermoautotrophicus* has been reported to utilize N_2 as a sole nitrogen source when growing chemolithoautotrophically with CO or H_2 and CO_2 under aerobic conditions at 65 °C (Gadkari et al. 1992).

14.4.5 Phosphate Solubilization

Phosphorus is the second most important nutrient for plants, after nitrogen. It exists in soil as mineral salts or incorporated into organic compounds. Phosphate deficiency is one of the limiting factors in crop production. Microbes are able to solubilize insoluble phosphates in metallic complexes or in hydroxyapatite and release free phosphates (Rodríguez and Fraga 1999). Recent studies investigating the role of actinomycetes in plant growth promotion have demonstrated that the bacterial colonization often results in increased P solubilization and its uptake by plants. For instance, the increased plant growth and P uptake have been reported on the inoculation of *Streptomyces griseus* (Hamdali et al. 2008a, b), *Streptomyces* mhcr0816 and mhce0811 (Jog et al. 2012), *Microbacterium* sp. F10a (Sheng et al. 2009) in wheat plant, *Streptomyces*, and *Thermobifida* in *Trifolium repens* (Franco-Correa et al. 2010).

Although previous studies suggest that the inoculation of plants with beneficial actinomycetes could be a suitable approach for plant growth promotion, several authors have pointed out that single plant growth-promoting trait was not solely responsible for the plant growth. A large number of studies confirm the existence of cumulative effects of microbes such as the production of IAA, ACC deaminase activity, nitrogen fixation, siderophore production, and phosphate solubilization. For instance, Selvakumar et al. (2015) recently reported the potential of osmotolerant *Actinobacterium Citricoccus zhacaiensis* B–4 on the growth of onion plants under PEG-induced drought stress and reported that *Actinobacterium* improved the seedling vigor and germination rate of onion seeds (cv. Arka Kalyan) at osmotic potentials up to −0.8 MPa. They attributed this effect to the ability of the bacterium to exhibit various plant growth-promoting traits including the production of IAA and GA3, solubilization of phosphate and zinc, and ACC deaminase activity. Similarly, Mrinalini and Padmavathy (2014) also demonstrated that endophytic *Streptomyces* sp. Mrinalini7, isolated from neem plant, was able to promote the growth of tomato seedling through several plant growth-promoting traits such as IAA, ACC deaminase, phosphate solubilizing, siderophore, and ammonia production. These examples illustrate mechanisms, by which actinomycetes improve the plant growth and reflect the suitability of these microbes for improving heavy metal phytoremediation process.

14.5 Actinomycetes in Heavy Metal-Polluted Soils

Heavy metal contamination not only affects the plant growth and development but also influences the growth, survival, and activity of plant-associated microbes in polluted sites. However, numerous studies have demonstrated that actinomycetes isolated from metal-polluted soils exhibit multiple-metal tolerance as they have adopted to such environment and play an important role in metal detoxification process in the rhizosphere soil that determines the plant quality and yield (Ahemad and Kibret 2014). For instance, Gremion et al. (2003) characterized the metabolically active bacteria in heavy metal-contaminated rhizosphere soil of *Thlaspi caerulescens* using 16S ribosomal DNA and reverse-transcribed 16S rRNA clone libraries and reported that the dominant part of the metabolically active group of bacteria was *Actinobacteria* in both bulk and rhizosphere soil. Likewise, numerous studies have demonstrated the *Actinobacteria* as a consistently dominant group together with α *Proteobacteria* in metal-contaminated soils (Lazzaro et al. 2008; Karelova et al. 2011; Tipayno et al. 2012), which suggest a potential adaptation of the actinomycetes population to the heavy metal stress condition. The strains *Streptomyces* sp. A160 and S164 and *Streptomyces fradiae* A161 isolated from the soil of the Bay of Bengal showed the resistance to Cu up to 480 mg/L. Further, these strains also exhibited antibacterial and antifungal activity against wide range of pathogenic microbes. Moreover, the filamentous nature of the actinomycetes makes them as a potential heavy metal accumulator (Panday et al. 2004). Recently, Daboor et al. (2014) isolated heavy metal-resistant *Streptomyces chromofuscus* K101 from Nile River and assessed its heavy metal absorption potential. They found that *S. chromofuscus* was able to absorb high concentrations of metals with the order of $Zn^{2+}>Pb^{2+}>Fe^{2+}$ in single or mixture metal reaction. Similarly, Hamedi et al. (2015) assessed cadmium accumulation potential of *Promicromonospora* sp. UTMC 2243 and found that the isolate was able to remove 96.5 % of Cr from aqueous solution. Vinod et al. (2014) reported Cr, Cu, Pb, and Zn accumulation potential of metal-resistant *Streptomyces roseisederoticus* (V5), *Streptomyces flavochromogenes* (V6), *Streptomyces vastus* (V7), and *Streptomyces praguaeneses* (V8) isolated from the rhizosphere soil of *Casuarina equisetifolia*. It was found that the *S. roseisederoticus* (V5) exhibited highest biosorption capacity for Cr, whereas *S. flavochromogenes* (V6) exhibited highest biosorption for Pb.

Several authors have pointed out that actinomycetes and their interactions with heavy metals (e.g., heavy metal biosorption/bioaccumulation, oxidation/reduction, and metal mobilization/immobilization) greatly influence the biomass production and quantity of metal accumulation in plants growing on metal-contaminated field soils. The following sections describe how the metal-resistant actinomycetes influence the plant growth and heavy metal uptake by plants in polluted soils (Table 14.3).

14.6 Role of Actinomycetes in Heavy Metal Phytoremediation

The functioning of plant and microbial interaction can be influenced by properties of rhizosphere soil. Actinomycetes play significant roles in plant growth under adverse environmental conditions by solubilizing plant nutrients, maintenance of soil structure, mobilization/immobilization of toxic chemicals, and controlling of plant pathogens (Giller et al. 1998; Elsgaard et al. 2001; Filip 2002; Jing et al. 2007). Besides, actinomycetes and their host plants can form specific associations in which the plant provides nutrients through root exudation that induces the growth, survival, and colonization potential of rhizosphere microbes. The metal-tolerant actinomycetes, such as *Streptomyces*, *Amycolatopsis*, and *Rhodococcus* (Trivedi et al. 2007; El Baz et al. 2015; Sunil et al. 2015), have been found to have potential to improve the plant growth and heavy metal mobilization or immobilization in metal-polluted soils. The abundant presence of actinomycetes in the metal-contaminated rhizosphere soil and its ability to withstand extreme environment make it suitable as a potential microbe which assisted the plants in remediation of heavy metal (Reinicke et al. 2013). Specifically, the metal-resistant actinomycetes have been reported to possess several traits that can alter heavy metal uptake by plants through acidification or by producing metal mobilizing/immobilizing substances. Experiments with *Sorghum bicolor* (sorghum) revealed that the inoculation of heavy metal-resistant *Streptomyces mirabilis* P16B-1 significantly increased the new tip growth and biomass of the sorghum plants as compared to the controls (Schutze et al. 2013). Similarly, Trivedi et al. (2007) demonstrated the potential of a psychrotrophic actinomycete *Rhodococcus erythropolis* to protect *Pisum sativum* (pea) from the toxicity of Cr in high concentrations and reported that this effect may be due to the reduction of Cr^{6+} to Cr^{3+} and various PGP traits such as the production of IAA, ACC deaminase activity, phosphate solubilization, and siderophore production. Khan et al. (2015) reported the greater potential of the Cr-resistant bacterium, *Microbacterium arborescens* HU33 associated with *Prosopis juliflora*, to protect ryegrass (*Lolium multiflorum*) from the toxicity of high concentrations of heavy metals such as Cr, Cd, Cu, Zn, and Pb grown on the tannery effluent contaminant soil. They attributed this effect to the ability of the bacterium to produce of IAA, siderophore, ACC deaminase, and solubilize P. Further, they reported that the inoculation of bacteria enhanced the heavy metal uptake of ryegrass plants. Javaid and Sultan (2012) reported that *Streptomyces* sp. isolated from the farmlands were shown to reduce toxic form of chromium [Cr(VI)] to less toxic form of Cr (III). This study suggests that by inoculating the plants with Cr-reducing actinomycetes, it should be possible to improve plant growth and Cr (VI) bioremediation.

An experiment with *Arthrobacter creatinolyticus* isolated from the rhizosphere of *Spartina densiflora* also revealed that the inoculation of microbial consortia along with *A. creatinolyticus* significantly increased the seed germination and plant growth under Cu and NaCl stress. In this case, enhanced plant growth could be correlated with various PGP traits such as N_2 fixation and phosphate solubilization (Andrades-Moreno et al. 2014). Likewise,

Table 14.3 Examples of actinomycetes involved in phytoremediation of heavy metals

Actinomycetes	Source of strain	Plants	Metals	Role of actinomycetes in phytoremediation	PGP traits of actinomycetes	References
Microbacterium arborescens HU33	*Prosopis juliflora*	Rye grass	Cr, Cd, Cu, Zn, and Pb	Increased accumulation in root and shoot	ACC deaminase, P solubilization, IAA, and siderophore	Khan et al. (2015)
Streptomyces sp. HM1	Rhizospheric soil	*Zea mays*	Cd	Increased metal tolerance	Increases chlorophyll content, PGP traits	El Sayed et al. (2015)
Streptomyces mirabilis P16B-1	Soil from uranium mining area	*Sorghum bicolor*	U, Cu, Ni, Cd, Co, and Zn	Decreased metal bioavailability	Promote plant growth	Schutze et al. (2013)
Arthrobacter creatinolyticus	Rhizospheric soil	*Spartina densiflora*	Cu	Resistance toward Cu	N_2 fixation and P solubilization	Andrades-Moreno et al. (2014)
Streptomyces sp.	Farm lands	NA	Cr	Converted toxic [Cr(VI)] to less toxic Cr (III)	IAA	Javaid and Sultan (2012)
Arthrobacter sp, *Micrococcus* sp., and *Microbacterium* sp.	Copper mine wasteland	*Brassica napus*	Cu, Zn, Pb, Cd, and Ni	Increased metal uptake and reduced metal stress	ACC deaminase and P solubilization	He et al. (2010)
Cellulosimicrobium cellulans	Rhizospheric soil	Green chilli	Cr	Reduced Cr uptake	IAA and P solubilization	Chatterjee et al. (2009)
Rhodococcus erythropolis	Psychrotrophic metal-contaminated soil	*Pisum sativum*	Cr	Decreased uptake of metals by plants	Promote plant growth – ACC, IAA, siderophore	Trivedi et al. (2007)
Microbacterium arabinogalactanolyticum	Rhizospheric soil	*Alyssum murale*	Ni	Increased Ni accumulation	N_2 fixation	Abou-Shanab et al. (2006)
Arthrobacter spp. UMCV	Rhizosphere soil	Common bean	Fe	Converted Fe^{3+} to soluble Fe	Siderophore	Valencia-Cantero et al. (2007)
Frankia sp.	Rhizospheric soil	*Alnus glutinosa*	Ni	Decreased metal availability	Increased nodulation	Wheeler et al. (2001)
Arthrobacter mysorens	Rhizospheric soil	Barley	Cd and Pb	Decreased toxicity	Increased uptake of nutrients	Belimov and Dietz (2000)

Wheeler et al. 2001 also observed that the inoculation of *Frankia* sp. significantly increased yield of their host *Alnus glutinosa* in the presence of Ni. Although previous studies have demonstrated a significant role of actinomycetes in facilitating the heavy metal uptake by plants, the molecular mechanisms involved in microbe-mediated heavy metal uptake by plants remain unknown. Moreover, there are some opposing viewpoints that the inoculation of actinomycetes reduced heavy metal accumulation in plants. For instance, Chatterjee et al. (2009) reported that the inoculation of Cr-reducing actinomycetes *Cellulosimicrobium cellulans* increased the plant growth and reduced Cr uptake in chilli plants. These contrasting effects may be due to microbial metal mobilization/immobilization potential, rhizosphere soil properties, the differences in the ability of plants to uptake heavy metals, metal toxicity, and its bioavailability.

14.7 Conclusions

The seriousness of heavy metal pollution in the environment dragged the attention of researchers toward sorting out of solutions for the removal of contaminants and a safer life. Though many conventional technologies have been employed, phytoremediation gains much importance because of its safe and eco-friendly method for remediation of these toxic heavy metals. Actinomycetes associated with the plant proved as a potential candidate in assisting phytoremediation. The metal-resistant beneficial actinomycetes not only improve the plant growth in metal-polluted soils but also protect their host plant from metal toxicity and alter heavy metal accumulation in plant tissues. The beneficial effects caused by actinomycetes indicate that inoculation with these microbes might have potential to improve phytoremediation efficiency in metal-contaminated soils. However, almost all the previous research on actinomycete-assisted phytoremediation were carried out in lab or greenhouse conditions; hence, further work including the interactions among actinomycetes, heavy metals, and plant is essential to apply this strategy in metal-polluted field level. Similarly, since the molecular background of mechanisms involved by actinomycetes in plant growth promotion and heavy metal uptake by plants is not yet been fully explored, more research has to be explored in order to make an actinomycete-assisted phytoremediation more effective.

References

Abou-Shanab RAI, Angle JS, Chaney RL (2006) Bacterial inoculants affecting nickel uptake by *Alyssum murale* from low, moderate and high Ni soils. Soil Biol Biochem 38:2882–2889

Ahemad M, Kibret M (2014) Mechanisms and applications of plant growth-promoting rhizobacteria: current perspective. J King Saud Univ Sci 26:1–20

Albarracin VH, Amoroso MJ, Abate CM (2005) Isolation and characterization of indigenous copper resistant actinomycete strains. Chem Erde 65:145–156

Albarracın VH, Winik B, Kothe E, Amoroso MJ, Abate CM (2008) Copper bioaccumulation by the actinobacterium *Amycolatopsis* sp. ABO. J Basic Microbiol 48:323–330

Aldesuquy HS, Mansour FA, Abo-Hamed SA (1998) Effect of the culture filtrates of *Streptomyces* on growth and productivity of wheat plants. Folia Microbiol 43:465–470

Amoroso MA, Schubert D, Mitscherlich P, Schumann P, Kothe E (2000) Evidence for high affinity nickel transporter genes in heavy metal resistant Streptomyces spec. J Basic Microbiol 40:295–301

Andrades-Moreno L, Del Castillo I, Parra R, Doukkali B, Redondo-Gómez S, Pérez-Palacios P (2014) Prospecting metal-resistant plant growth-promoting rhizobacteria for rhizo-remediation of metal contaminated estuaries using *Spartina densiflora*. Environ Sci Pollut Res 21:3713–3721

Bach TJ, Rohmer M (2012) Isoprenoid synthesis in plants and microorganisms. New concepts and experimental approaches. Springer, New York

Ball AS, Betts WB, McCarthy AJ (1989) Degradation of lignin-related compounds by actinomycetes. Appl Environ Microbiol 55:1642–1644

Belimov AA, Dietz KJ (2000) Effect of associative bacteria on element composition of barley seedlings grown in solution culture at toxic cadmium concentrations. Microbiol Res 155:113–121

Bèrdy J (1995) Are actinomycetes exhausted as a source of secondary metabolites? In: Debabov VG, Dudnik YV, Danilenko VN (eds) Proceedings of the 9th international symposium on the biology of actinomycetes. Russia Scientific Research Institute for Genetics and Selection of Industrial Microorganisms, Moscow, pp 13–24

Borges-Walmsley MI, Mckeegan KS, Walmsley AR (2003) Structure and function of efflux pumps that confer resistance to drugs. Biochem J 376:313–338

Braud A, Jezequel K, Bazot S, Lebeau T (2009) Enhanced phytoextraction of an agricultural Cr and Pb-contaminated soil by bioaugmentation with siderophore-producing bacteria. Chemosphere 74:280–286

Bruins MR, Kapil S, Oehme FW (2000) Review: microbial resistance to metals in the environment. Ecotoxicol Environ Saf 45:198–207

Chaney RL (1983) Plant uptake of inorganic waste. In: Parr JE, Marsh PB, Kla JM (eds) Land treatment of hazardous waste. Noyes Data Corp, Park Ridge II, pp 50–76

Chatterjee S, Sau GB, Mukherjee SK (2009) Plant growth-promotion by hexavalent chromium reducing bacterial strain, *Cellulosimicrobium cellulans* KUCr3. World J Microbiol Biotechnol 25:1829–1836

Chowdhury ASMHK, Das P, Sarkar I, Islam R, Aksharin L, Parvin F, Islam Z, Faris M, Shaekh MPE (2015) Phytoremediation of heavy metals (Ar, Cd, Pb) using transgenic rice plants – an overview. Int J Sci Eng Res 6:878

Copping LG, Duke SO (2007) Natural products that have been used commercially as crop protection agents. Pest Manag Sci 63:524–554

Cruz JA, Delfin EF, Paterno ES (2015) Promotion of upland rice growth by actinomycetes under growth room condition. Asian Int J Life Sci 24:87–94

Daboor SM, Haroon AM, Esmael NAE, Hanona SI (2014) Heavy metal adsorption of *Streptomyces chromofuscus* K101. J Coast Life Med 2:431–437

Dalal JM, Kulkarni NS (2014) Antagonistic and plant growth-promoting potentials of indigenous endophytic actinomycetes of soybean (*Glycine max* (l) merril). CIBTech J Microbiol 3:1–12

Damle NR, Kulkarni SW (2014) Screening of rhizomicroflora from the rhizosphere of *Pongamia glabra* for their plant growth-promoting and antimicrobial activities. J Environ Res Develop 9:318

De Carvalho Costa FE, Soares De Melo I (2012) Endophytic and rhizospheric bacteria from *Opuntia ficus – indica* mill and their ability to promote plant growth in cowpea, *Vigna unguiculata* (L.) walp. Afr J Microbiol Res 6:1345–1353

Diagne N, Arumugam K, Ngom M, Nambiar-Veetil M, Franche C, Narayanan KK, Laplaze L (2013) Use of *Frankia* and actinorhizal plants for degraded lands reclamation. BioMed Res 2013:0–9

Dimkpa CO, Svatos A, Dabrowska P, Schmidt A, Boland W, Kothe E (2008) Involvement of siderophores in the reduction of metal-induced inhibition of auxin synthesis in *Streptomyces* spp. Chemosphere 74:19–25

Dimkpa C, Svatos A, Merten D, Bu¨chel G, Kothe E (2009a) Hydroxamate siderophores produced by *Streptomyces acidiscabies* E13 bind nickel and promote growth in cowpea (*Vigna unguiculata* L.) under nickel stress. Can J Microbiol 54:163–172

Dimkpa CO, Merten D, Svatos A, Buchel G, Kothe E (2009b) Siderophores mediate reduced and increased uptake of cadmium by *Streptomyces tendae* F4 and sunflower (*Helianthus annuus*), respectively. J Appl Microbiol 107:1687–1696

Dimkpa CO, Merten D, Svatos A, Buchel G, Kothe E (2009c) Metal-induced oxidative stress impacting plant growth in contaminated soil is alleviated by microbial siderophores. Soil Biol Biochem 41:154–162

Doble M, Kumar A (2005) Biotreatment of industrial effluents. Elsevier, Butterworth-Heinemann, Oxford

Doumbou CL, Hamby Salove MK, Crawford DL, Beaulieu C (2011) Actinomycetes, promising tools to control plant diseases and to promote plant growth. Phytoprotection 82:85–102

El Baz S, Baz M, Barakate M, Hassani L, El Gharmali A, Imziln B (2015) Resistance to and accumulation of heavy metals by actinobacteria isolated from abandoned mining areas. Sci World J 2015:1–14

El Sayed HE, Othaimen HS, Aburas MMA, Jastaniah SD (2015) Efficiency of an Cd-Tolerant actinomycete isolate obtained from wastewater in removal of heavy metals and enhancing plant growth of *Zea mays* L. plant. Int J Curr Microbiol Appl Sci 4:553–565

Elekes CC (2014) Eco-technological solutions for the remediation of polluted soil and heavy metal recovery. In: Hernández-Soriano MC (ed) Environmental risk assessment of soil contamination. In Tech, Rijeka, pp 309–335

Elsgaard L, Petersen SO, Debosz K (2001) Effects and risk assessment of linear alkylbenzene sulfonates in agricultural soil. Short-term effects on soil microbiology. Environ Toxicol Chem 20:1656–1663

El-Tarabily KA (2008) Promotion of tomato (*Lycopersicon esculentum* Mill.) plant growth by rhizosphere competent 1-aminocyclopropane-1-carboxylic acid deaminase–producing *Streptomycete* actinomycetes. Plant Soil 308:161–174

El-Tarabily KA, Hardy GEST, Sivasithamparam K, Hussein AM, Kurtboke DI (1997) The potential for the biological control of cavity-spot disease of carrots, caused by *Pythium chloratum*, by streptomycete and non-streptomycete actinomycetes. New Phytol 137:495–507

El-Tarabily KA, Soliman MH, Nassar AH, Al-Hassani HA, Sivasithamparam K, McKenna F, Hardy GEST (2000) Biological control of *Sclerotinia minor* using a chitinolytic bacterium and actinomycetes. Plant Pathol 49:573–583

El-Tarabily KA, Hardy GEST, Sivasithamparam K (2010) Performance of three endophytic actinomycetes in relation to plant growth-promotion and biological control of *Pythium aphanidermatum*, a pathogen of cucumber under commercial field production conditions in the United Arab Emirates. Eur J Plant Pathol 128:527–539

Erikson D (1949) The morphology, cytology and taxonomy of the actinomycetes. Annu Rev Microbiol 3:23–54

Filip Z (2002) International approach to assessing soil quality by ecologically-related biological parameters. Agric Ecosyst Environ 88:689–712

Franco-Correa M, Quintana A, Duque C, Suarez C, Rodriguez MX, Barea JM (2010) Evaluation of actinomycete strains for key traits related with plant growth-promotion and mycorrhiza helping activities. Appl Soil Ecol 45:209–217

Fridovich I (1995) Superoxide radical and superoxide dismutases. Annu Rev Biochem 64:97–112

Gadkari D, Morsdorf G, Meyer O (1992) Chemolithoautotrophic assimilation of dinitrogen by *Streptomyces thermoautotrophicus* UBT1: identification of an unusual N2-fixing system. J Bacteriol 174:6840–6843

Garbisu C, Alkorta I (2003) Basic concepts on heavy metal soil bioremediation. Eur J Min Process Environ Prot 3:58–66

Ghodhbane-Gtari F, Essoussi I, Chattaoui M, Chouaia B, Jaouani A, Daffonchio D, Boudabous A, Gtari M (2010) Isolation and characterization of non- *Frankia* actinobacteria from root nodules of *Alnus glutinosa*, *Casuarina glauca* and *Elaeagnus angustifolia*. Symbiosis 50:51–57

Giller KE, Witter E, McGrath SP (1998) Toxicity of heavy metals to microorganisms and microbial processes in agricultural soils. Soil Biol Biochem 30:1389–1414

Glick BR (2005) Modulation of plant ethylene levels by the enzyme ACC deaminase. FEMS Microbiol Lett 251:1–7

Goodfellow M, Williams ST (1983) Ecology of actinomycetes. Annu Rev Microbiol 37:189–216

Gopalakrishnan S, Vadlamudi S, Apparla S, Bandikinda P, Vijayabharathi R, Bhimineni RK, Rupela O (2013) Evaluation of *Streptomyces* spp. for their plant growth-promotion traits in rice. Can J Microbiol 59:534–539

Gopalakrishnan S, Vadlamudi S, Bandikinda P, Sathya A, Vijayabharathi R, Rupela O, Kudapa H, Katta K, Varshney RK (2014) Evaluation of *Streptomyces* strains isolated from herbal vermicompost for their plant growth-promotion traits in rice. Microbiol Res 169:40–48

Goudjal Y, Zamoum M, Meklat A, Sabaou N, Mathieu F, Zitouni A (2015) Plant growth-promoting potential of endosymbiotic actinobacteria isolated from sand truffles (*Terfezia leonis* Tul.) of the Algerian Sahara. Ann Microbiol. doi:10.1007/s13213-015-1085-2

Gremion F, Chatzinotas A, Harms H (2003) Comparative 16S rDNA and 16S rRNA sequence analysis indicates that actinobacteria might be a dominant part of the metabolically active bacteria in heavy metal-contaminated bulk and rhizosphere soil. Environ Microbiol 5:896–907

Hamaki T, Suzuki M, Fudou R, Jojima Y, Kajiura T, Tabuchi A, Sen K, Shibai H (2005) Isolation of novel bacteria and actinomycetes using soil-extract agar medium. J Biosci Bioeng 99:485–492

Hamdali H, Bouizgarne B, Hafidi M, Lebrihi A, Virolle MJ, Ouhdouch Y (2008a) Screening for rock phosphate solubilizing actinomycetes from Moroccan phosphate mines. Appl Soil Ecol 38:12–19

Hamdali H, di Hafi M, Virolle MJ, Ouhdouch Y (2008b) Rock phosphate-solubilizing actinomycetes: screening for plant growth-promoting activities. World J Microbiol Biotechnol 24:2565–2575

Hamedi J, Dehhaghi M, Mohammdipanah F (2015) Isolation of extremely heavy metal resistant strains of rare actinomycetes from high metal content soils in Iran. Int J Environ Res 9:475–480

Harikrishnan H, Shanmugaiah V, Balasubramanian N (2014a) Optimization for production of indole acetic acid (IAA) by plant growth-promoting *Streptomyces* sp VSMGT1014 isolated from rice rhizosphere. Int J Curr Microbiol Appl Sci 3:158–171

Harikrishnan H, Shanmugaiah V, Balasubramanian N, Sharma MP, Kotchoni SO (2014b) Antagonistic potential of native strain *Streptomyces aurantiogriseus* VSMGT1014 against Sheath Blight of rice disease. World J Microbiol Biotechnol 30:3149–3161

He LY, Zhang YF, Ma HY, Su LN, Chen ZJ, Wang QY, Qian M, Sheng XF (2010) Characterization of copper-resistant bacteria and assessment of bacterial communities in rhizosphere soils of copper-tolerant plants. Appl Soil Ecol 44:49–55

Hider RC, Kong X (2010) Chemistry and biology of siderophores. Nat Prod Rep 27:637–657

Hirsch AM, Valdes M (2010) *Micromonospora* – an important microbe for biomedicine and potentially for biocontrol and bio-fuels. Soil Biol Biochem 42:536–542

Imada C (2005) Enzyme inhibitors and other bioactive compounds from marine actinomycetes. Antonie Van Leeuwenhoek 87:59–63

Javaid M, Sultan S (2012) Plant growth-promotion traits and Cr (VI) reduction potentials of Cr (VI) resistant *Streptomyces* strains. J Basic Microbiol 53:420–428

Ji C, Juarez-Hernandez RE, Miller MJ (2012) Exploiting bacterial iron acquisition: siderophore conjugates. Future Med Chem 4:297–313

Jing Y, He Z, Yang X (2007) Role of soil rhizobacteria in phytoremediation of heavy metal contaminated soils. J Zhejiang Univ Sci B 8:192–207

Jog R, Nareshkumar G, Rajkumar S (2012) Plant growth-promoting potential and soil enzyme production of the most abundant *Streptomyces* spp. from wheat rhizosphere. J Appl Microbiol 113:1154–1164

Kamran MA, Mufti R, Mubariz N, Syed JH, Bano A, Javed MT, Chaudhary HJ (2014) The potential of the flora from different regions of Pakistan in phytoremediation: a review. Environ Sci Pollut Res 21:801–812

Karelova E, Harichova J, Stojnev T, Pangallo D, Ferianc P (2011) The isolation of heavy-metal resistant culturable bacteria and resistance determinants from a heavy-metal contaminated site. Biologia 1:18–26

Khamna S, Yokota A, Lumyong S (2009) Actinomycetes isolated from medicinal plant rhizosphere soils: diversity and screening of antifungal compounds, indole-3-acetic acid and siderophore production. World J Microbiol Biotechnol 25:649–655

Khan MU, Sessitsch A, Harris M, Fatima K, Imran A, Arslan M, Shabir G, Khan QM, Afzal M (2015) Cr-resistant rhizo- and endophytic bacteria associated with Prosopis juliflora and their potential as phytoremediation enhancing agents in metal-degraded soils. Front Plant Sci 5:755–760

Laghlimi M, Baghdad B, El Hadi H, Bouabdli A (2015) Phytoremediation mechanisms of heavy metal contaminated soils: a review. O J Ecol 5:375–388

Lazzaro A, Widmer F, Sperisen C, Frey B (2008) Identification of dominant bacterial phylotypes in a cadmium-treated forest soil. FEMS Microbiol Ecol 63:143–155

Lee J, Postmaster A, Peng Soon H, Keast D, Carson KC (2012) Siderophore production by actinomycetes isolated from two soil sites in Western Australia. Biometals 25:285–296

Lin YB, Wang XY, Li HF, Wang NN, Wang HX, Tang M, Wei GH (2011) *Streptomyces zinciresistens* sp. nov., a zinc-resistant actinomycete isolated from soil from a copper and zinc mine. Int J Syst Evol Microbiol 61:616–620

Liu N, Wang HB, Liu M (2009) *Streptomyces alni* sp. Nov., a daidzein-producing endophyte isolated from a root of *Alnus nepalensis* D. Don. Int J Syst Evol Microbiol 59:254–258

Madhaiyan M, Poonguzhali S, Lee JS, Senthilkumar M, Lee KC, Sundaram S (2010) Leifsonia soli sp. nov., a yellow-pigmented actinobacterium isolated from teak rhizosphere soil. Int J Syst Evol Microbiol 60:1322–1327

Masarovičová E, Kráľová K (2012) Plant-heavy metal interaction: phytoremediation, biofortification and nanoparticles. In: Advances in selected plant physiology aspects. In Tech, Rijeka, p. 75─102

Mason MG, Ball AS, Reeder BJ, Silkstone G, Nicholls P, Wilson MT (2001) Extracellular heme peroxidases in actinomycetes: a case of mistaken identity. Appl Environ Microbiol 67:4512–4519

Merzaeva OV, Shirokikh IG (2010) The production of auxins by the endophytic bacteria of winter rye. Appl Biochem Microbiol 46:44–50

Misk A, Franco C (2011) Biocontrol of chickpea root rot using endophytic actinobacteria. BioControl 56:811–822

Mohandas S, Poovarasan S, Panneerselvam P, Saritha B, Upreti KK, Kamal R, Sita T (2013) Guava (*Psidium guajava* L.) rhizosphere *Glomus mosseae* spores harbour actinomycetes with growth-promoting and antifungal attributes. Sci Hortic 150:371–376

Mrinalini JS, Padmavathy S (2014) Isolation, screening and characterization of uranium microremediable actinomycetes from fallen leaves of *Azadirachta indica* in Western Ghats. J Radioanal Nucl Chem 302:1303–1307

Nies DH (1999) Microbial heavy-metal resistance. Appl Microbiol Biotechnol 51:730–750

Nimnoi P, Pongsilp N, Lumyong S (2010) Endophytic actinomycetes isolated from *Aquilaria crassna Pierre* ex Lec and screening of plant growth-promoters production. World J Microbiol Biotechnol 26:193–203

Panday B, Ghimire P, Agrawal VP (2004) Studies on the antibacterial activities of the actinomycetes isolated from the Khumbu region of Nepal. J Biol Sci 23:44–53

Park JO, El-Tarabily KA, Ghisalberti EL, Sivasithamparam K (2002) Pathogenesis of *Streptoverticillium albireticuli* on *Caenorhabditis elegans* and its antagonism to soil-borne fungal pathogens. Lett Appl Microbiol 35:361–365

Pasti MB, Pometto AL, Nuti MP, Crawford DL (1990) Lignin-solubilizing ability of actinomycetes isolated from termite (Termitidae) gut. Appl Environ Microbiol 56:2213–2218

Patel HA, Patel RK, Khristi SM, Parikh K, Rajendran G (2012) Isolation and characterization of bacterial endophytes from *Lycopersicon esculentum* plant and their plant growth-promoting characteristics. Nepal J Biotechnol 2:37–52

Pavel VL, Sobariu DL, Tudorache Fertu ID, Statescu F, Gaverilescu M (2013) Symbiosis in the environment biomanagement of soils contaminated with heavy metals. Eur J Sci Theol 9:211–224

Paz-Ferreiro J, Lu H, Fu S, Mendez A, Gasco G (2014) Use of phytoremediation and Biochar to remediate heavy metal polluted soils: a review. Solid Earth 5:65–75

Pulford ID, Watson C (2003) Phytoremediation of heavy metal contaminated land by trees – a review. Environ Int 29:529–540

Rafik E, Rahal E, Ahmed L (2014) Isolation and screening of actinomycetes strains producing substances plant growth-promoting. Indo-Am J Agric Vet Sci 2:1–12

Rajkumar M, Ae N, Freitas H (2009) Endophytic bacteria and their potential to enhance heavy metal phytoextraction. Chemosphere 77:153–160

Rajkumar M, Ae N, Prasad MNV, Freitas H (2010) Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. Trends Biotechnol 28:142–149

Rajkumar M, Sandhya S, Prasad MN, Freitas H (2012) Perspectives of plant-associated microbes in heavy metal phytoremediation. Biotechnol Adv 30:1562–1574

Rashad FM, Fathya HM, El-Zayata AS, Elghonaimy AM (2015) Isolation and characterization of multifunctional *Streptomyces* species with antimicrobial, nematicidal and phytohormone activities from marine environments in Egypt. Microbiol Res 175:34–47

Ravel J, Schrempf H, Hill RT (1998) Mercury resistance is encoded by transferable giant linear plasmids in two

Chesapeake bay *Streptomyces* strains. Appl Environ Microbiol 64:3383–3388
Reinicke M, Schindler F, Roth M, Kothe E (2013) Multi-metal bioremediation by microbial assisted phytoremediation. In: Amoroso MJ, Benimeli CS, Cuozzo SA (eds) Actinobacteria: application in bioremediation and production of industrial enzymes. CRC Press, Boca Raton, pp 87–105
Rodríguez H, Fraga R (1999) Phosphate solubilizing bacteria and their role in plant growth-promotion. Biotechnol Adv 17:319–339
Rouch DA, Lee BTD, Morby AP (1995) Understanding cellular responses to toxic agents: a model for mechanism choice in bacterial metal resistance. J Ind Microbiol 14:132–141
Ruanpanum P, Tangchitsomkid N, Hyde KD, Lumyong S (2010) Actinomycetes and fungi isolated from plant-parasitic nematode infested soils: screening of the effective biocontrol potential, indole-3-acetic acid and siderophore production. World J Microbiol Biotechnol 26:1569–1578
Rungin S, Indananda C, Suttiviriya P, Kruasuwan W, Jaemsaeng R, Thamchaipenet A (2012) Antonie Van Leeuwenhoek 102:463–472
Sadeghi A, Karimi E, Dahaji PA, Javid MG, Dalvand Y (2012) Plant growth-promoting activity of an auxin and siderophore producing isolate of *Streptomyces* under saline soil conditions. World J Microbiol Biotechnol 28:1503–1509
Scherlach K, Hertweck C (2009) Triggering cryptic natural product biosynthesis in microorganisms. Org Biomol Chem 7(9):1753–1760
Schluenzen F, Takemoto C, Wilson DN, Kaminishi T, Harms JM, Hanawa-Suetsugu K, Szaflarski W, Kawazoe M, Shirouzo M, Nierhaus KH, Yokoyama S, Fucini P (2006) The antibiotic kasugamycin mimics mRNA nucleotides to destabilize tRNA binding and inhibit canonical translation initiation. Nat Struct Mol Biol 13:871–886
Schmidt A, Haferburg G, Sineriz M, Merten D, Buchel G, Kothe E (2005) Heavy metal resistance mechanisms in actinobacteria for survival in AMD contaminated soils. Chem Erde 65:131–144
Schutze E, Weist A, Klose M, Wach T, Schumann M, Nietzsche S, Merten D, Baumert J, Majzlan J, Kothe E (2013) Taking nature into lab: biomineralization by heavy metal resistant Streptomycetes in soil. Biogeosciences 10:2345–2375
Selvakumar G, Bhatt RM, Upreti KK, Bindu GH, Shweta K (2015) *Citricoccus zhacaiensis* B-4 (MTCC 12119) a novel osmotolerant plant growth-promoting actinobacterium enhances onion (*Allium cepa* L.) seed germination under osmotic stress condition. World J Microbiol Biotechnol 31:833–839
Sessitsch A, Kuffner M, Kidd P, Vangronsveld J, Wenzel WW, Fallmann K, Puschenreiter M (2013) The role of plant-associated bacteria in the mobilization and phytoextraction of trace elements in contaminated soils. Soil Biol Biochem 60:182–194
Shanmugaiah V, Nithya K, Harikrishnan H, Jayaprakashvel M, Balasubramanian N (2015) Biocontrol mechanisms of siderophores against bacterial plant pathogens. In: Kannan VR, Bastas KK (eds) Sustainable approaches to controlling plant pathogenic bacteria. CRC Press, Boca Raton, pp 167–190
Shatheesh Kumar M (2011) Biotechnological potentials of indigenous cyanobacteria in crop improvement and bioremediation. Ph.D thesis, Bharathidasan University, Tamil Nadu
Sheng XF, He LY, Zhou L, Shen YY (2009) Characterization of *Microbacterium* sp. F10a and its role in polycyclic aromatic hydrocarbon removal in low-temperature soil. Can J Microbiol 55:529–535
Shutsrirung A, Chromkaew Y, Pathom-Aree W, Choonluchanon S, Boonkerd N (2013) Diversity of endophytic actinomycetes in mandarin grown in northern Thailand, their phytohormone production potential and plant growth-promoting activity. Soil Sci Plant Nutr 59:322–330
Siddikee MA, Chauhan PS, Anandham R, Han GH, Sa T (2010) Isolation, characterization, and use for plant growth-promotion under salt stress, of ACC deaminase-producing halotolerant bacteria derived from coastal soil. J Microbiol Biotechnol 20:1577–1584
Singh S, Pandey S, Chaudhary HS (2014) Actinomycetes: tolerance against heavy metals and antibiotics. Int J Bioassays 3:3376–3383
Solans M, Vobis G, Cassan F, Luna V, Wall LG (2011) Production of phytohormones by root- associated saprophytic actinomycetes isolated from the actinorhizal plant *Ochetophila trinervis*. World J Microbiol Biotechnol 27:2195–2202
Stillman MJ (1995) Metallothioneins. Coord Chem Rev 144:461–571
Stohs SJ, Bagchi D (1995) Oxidative mechanisms in the toxicity of metal-ions. Free Rad Biol Med 18:321–336
Summers AO (1985) Bacterial resistance to toxic elements. Trends Biotechnol 3:122–125
Sunil KCR, Swati K, Bhavya G, Nandhini M, Veedashree M, Prakash HS, Kini KR, Geetha N (2015) *Streptomyces flavomacrosporus*, a multi-metal tolerant potential bioremediation candidate isolated from paddy field irrigated with industrial effluents. Int J Life Sci 3:9–15
Tipayno S, Chang-Gi K, Sa T (2012) T-RFLP analysis of structural changes in soil bacterial communities in response to metal and metalloid contamination and initial phytoremediation. Appl Soil Ecol 61:137–146
Trivedi P, Pandey A, Sa T (2007) Chromate reducing and plant growth-promoting activities of psychrotrophic *Rhodococcus erythropolis* MTCC 7905. J Basic Microbiol 47:513–517
Tsavkelova EA, Cherdyntseva TA, Netrusov AI (2005) Auxin production by bacteria associated with orchid roots. Microbiology 74:55–62
Valdés M, Perez NO, Santos PEL, Caballero-Mellado J, Pena- Cabriales JJ, Normand P, Hirsch AM (2005)

Non-*Frankia* actinomycetes isolated from surface-sterilized roots of *Casuarina equisetifolia* fix nitrogen. Appl Environ Microbiol 71:460–466

Valencia-Cantero E, Hernandez-Calderón E, Velázquez-Becerra C, López-Meza JE, Alfaro-Cuevas R, López-Bucio J (2007) Role of dissimilatory fermentative iron-reducing bacteria in Fe uptake by common bean (*Phaseolus vulgaris* L.) plants grown in alkaline soil. Plant Soil 291:263–273

Valls M, de Lorenzo V (2002) Exploiting the genetic and biochemical capacities of bacteria for the remediation of heavy metal pollution. FEMS Microbiol Rev 26:327–338

Vangronsveld J, Clijsters H (1994) Toxic effects of metals in plants and the chemical elements. In: Farago ME (ed) Biochemistry, uptake, tolerance and toxicity. Verlagsgesellschaft, Weinheim, pp 150–177

Verma VC, Singh SK, Prakash S (2011) Bio-control and plant growth-promotion potential of siderophore producing endophytic *Streptomyces* from *Azadirachta indica* A. Juss. J Basic Microbiol 51:550–556

Vinod K, Jaiprakash C, Thamizhmani R, Vimal Raj R, Lall C, Muruganandam N, Arun Govind G, Anwesh M, Reesu R, Chander MP (2014) High metal resistance and metal removal properties of antibiotics producing Actinobacteria isolated from rhizosphere region of *Casuarina equisetifolia*. Int J Curr Microbiol Appl Sci 3:803–811

Wagner SC (2011) Biological nitrogen fixation. Nat Educ Knowl 2:11–14

Wheeler CT, Hughes LT, Oldroyd J, Pulford ID (2001) Effect of nickel on *Frankia* and its symbiosis with *Alnus glutinosa* (L.) Gaertn. Plant Soil 231:81–90

Xing K, Bian GK, Qin S, Klenk HP, Yuan B, Zhang YJ, Li WJ, Jiang JH (2012) *Kibdelosporangium phytohabitans* sp. nov., a novel endophytic actinomycete isolated from oil-seed plant *Jatropha curcas* L. containing 1-aminocyclopropane- 1-carboxylic acid deaminase. Antonie Van Leeuwenhoek 101:433–441

Wu G, Kang H, Zhang X, Shao H, Chu L, Ruan C (2010) A critical review on the bio-removal of hazardous heavy metals from contaminated soils: issues, progress, eco-environmental concerns and opportunities. J Hazard Mater 174:1–8

Yasmin F, Othman R, Saad MS, Sijam K (2007) Screening for beneficial properties of rhizobacteria isolated from sweet potato rhizosphere. J Biotechnol 6:49–52