Chapter 9

Plant–Microbe Interactions in Phytoremediation

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DEFINITION OF PHYTOREMEDIATION

There are various descriptions of phytoremediation. However, when we look at the terminology, we can see that 'φυτο' (phyto) means plant in Ancient Greek, and 'remedium' means restoring balance from Latin. The term was first used in the 1980s to express the usage of plants to recover degraded or polluted areas (Neil, 2007). Today, there are different definitions of phytoremediation, which relate to its cleaning mechanism, pollutant type, used plant species and even the researcher's study area. However, the most accepted ones are:

- the use of plants for environmental remediation, which involves removing organics and metals from soils and water (Raskin et al., 1994);
- the use of plants, including trees and grasses, to remove, destroy or sequester hazardous contaminants from media such as air, water and soil (Prasad and Freitas, 2003);
- an important tool for decontaminating soil, water and air by detoxifying, extracting, hyperaccumulating, and/or sequestering contaminants, especially at low levels where, using current methods, costs exceed the effectiveness (Heinekamp and Willey, 2007);
- the use of plants and their associated soil microorganisms, soil amendments, and agronomic techniques to remove or render harmless environmental contaminants (Wang et al., 2012).

As is clear from the different definitions, some aromatic hydrocarbons (Joner et al., 2006), alkanes (Lin and Mendelssohn, 2009), phenols (Ibanez et al., 2012), polychlorinated solvents (Kassel et al., 2002), pesticides (Knuteson et al., 2002; Merini et al., 2009), chloroacetamides (Hoagland et al., 1997) and some explosives (Medina et al., 2002) could be remediated by using phytoremediation

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technology (Kvesitadze et al., 2006). Additionally, some trace elements and toxic heavy metals/metalloids such as Ag (Xu et al., 2010), As (Favas et al., 2012), Au (Sasmaz and Obek, 2012), Bi (Wei et al., 2011), Cd (Turgut et al., 2004), Ce (Peili et al., 2011), Co (Saleh, 2012), Cr (Mohanty and Patra, 2012), Cu (Tulod et al., 2012), Fe (Chaturvedi et al., 2012), Hg (Chattopadhyay et al., 2012), Mn (Hua et al., 2012), Ni (Jadia and Fulekar, 2008), Pb (de Souza et al., 2012), Sb (Littera, et al., 2012), Sn (Joseph, 2005), Te (Nolan et al., 1991), Tl (Poscic et al., 2013), U (Pratas et al., 2012), V (Marcano et al., 2006) and Zn (Caraiman et al., 2012) could be accumulated by some plant species and could be removed from any area by using phytoremediation processes.

Nowadays, phytoremediation is becoming an important tool for decontaminating soil, water and air by detoxifying, extracting, hyperaccumulating and/or sequestering contaminants with different types of applications (Heinekamp and Willey, 2007).

Accumulator/Hyperaccumulator Plants

The idea of using plants to remediate metal-polluted soils came from the discovery of hyperaccumulators (Alkorta et al., 2004). These plant species are able to concentrate metals in their above-ground tissues to levels far exceeding those present in the soil or in the non-accumulating species growing nearby (Memon and Schroder, 2009; Ali et al., 2013).

Baker and Brooks (1989) accepted plant species as hyperaccumulators, which accumulate greater than 100 mg kg^{-1} dw Cd, or greater than 1000 mg kg^{-1} dw Cu, Ni and Pb or greater than 10,000 mg kg^{-1} Mn and Zn in their shoots when they grow on metal rich soils.

Recently, van der Ent et al. (2013) recommended a concentration criterion which is given in table form for the different metals/metalloids in dried foliage with plants growing in their natural habitats (Table 9.1). Finally, hyperaccumulator

TABLE 9.1 Relation between Minimum Amount and Metals/Metalloids in Hyperaccumulator Plant Species

Minimun amount	Metals/metalloids
100 mg kg^{-1} dry weight	Cd, Se, Tl
300 mg kg^{-1} dry weight	Co, Cr, Cu
1000 mg kg^{-1} dry weight	As, Ni, Pb
3000 mg kg^{-1} dry weight	Zn
10,000 mg kg^{-1} dry weight	Mn

Source: van der Ent et al. (2013).

plants are accepted as capable of accumulating more than a 100 times more potentially phytotoxic elements than non-accumulators species (Chaney et al., 1997; Raskin and Ensley, 2000; Pulford and Watson, 2003).

Currently, 420 species belonging to 45 plant families are recorded as heavy metal hyperaccumulators and this number is likely to change in the future (Cobbett 2003; Rajakaruna et al., 2006; Mudgal et al., 2010).

Ni is one of the most accumulated metals by many different hyperaccumulator plants (more than 300). Some well known hyperaccumulator plant species, their families and accumulated heavy metal/metalloids are: *Azolla pinnata* for Cd in Azollaceae (Rai, 2008), *Bidens pilosa* for Cd (Sun et al., 2009), *Sonchus asper* for Pb and Zn (Yanqun et al., 2005) and *Helianthus annuus* for Cd, Cr and Ni (Turgut et al., 2004) in Asteraceae, *Alyssum bertolonii* and *Alyssum murale* for Ni (Li et al., 2003; Bani et al., 2010), *Arabidopsis thaliana* for Cu, Mn, Pb and Zn (Lasat, 2002), *Arabidopsis halleri* for Cd and Zn (Reeves and Baker, 2000; Cosio et al., 2004), *Brassica junceae* for Ni and Cr (Saraswat and Rai, 2009) and *Brassica oleracea* for Cd (Salt et al., 1995a), *Cardaminopsis halleri* for Cd and Zn (Sun et al., 2007), *Rorippa globosa* for Cd (Wei et al., 2008), *Thlaspi caerulescens* for Cd, Ni and Zn (Lombi et al., 2001; Cluis 2004) in Brassicaceae, *Sedum alfredii* for Cd, Pb and Zn (Li et al., 2005; Sun et al., 2007) in Crassulaceae, *Euphorbia cheiradenia* for Pb (Chehregani and Malayeri, 2007) in Euphorbiaceae, *Clerodendrum infortunatum* and *Haumaniastrum katangense* for Cu (Rajakaruna and Bohm, 2002; Chipeng et al., 2010) in Lamiaceae, *Astragalus racemosus* and *Astragalus bisulcatus* for Se (Vallini et al., 2005), *Pteris vittata* for As, Cr and Se (Baldwin and Butcher, 2007; Kalve et al., 2011) in Pteridaceae, *Solanum nigrum* and *S. photeinocarpum* for Cd (Sun et al., 2008; Zhang et al., 2011) in Solanaceae and *Viola baoshanensis* for Cd (Wu et al., 2010) in Violaceae.

PHYTOREMEDIATION APPLICATIONS

Phytoremediation can be divided into phytoextraction, rhizofiltration, phytostabilization, phytodegradation, rhizodegradation, phytovolatilization and phytorestauration; and various physiological mechanisms are involved in each of these processes (Figure 9.1).

Phytoextraction deals with the absorption of toxic metals and metalloids by roots and their transportation to and accumulation in above-ground (harvestable) parts of plants resulting in reduced soil metal concentrations (Pulford and Watson, 2003; Kvesitadze et al., 2006; Zhao and McGrath, 2009; Zhang et al., 2010; Ali et al., 2013).

The following are well-known plants used for phytoextraction processes: Indian mustard (*Brassica juncea*) for As, B, Cd, Cr(VI), Cu, Ni, Pb, Se, Sr and Zn (Raskin et al., 1994; Salt et al., 1995a; Salido et al., 2003); Alpine pennycress (*Thlaspi caerulescens*) for Cd and Zn (Zhao et al., 2003; Cosio et al., 2004); alyssum (*Alyssum wulfenianum*) for Ni (Reeves and Brooks, 1983); canola (*Brassica napus*), kenaf (*Hibiscus cannabinus* L. cv. Indian) and tall fescue (*Festuca

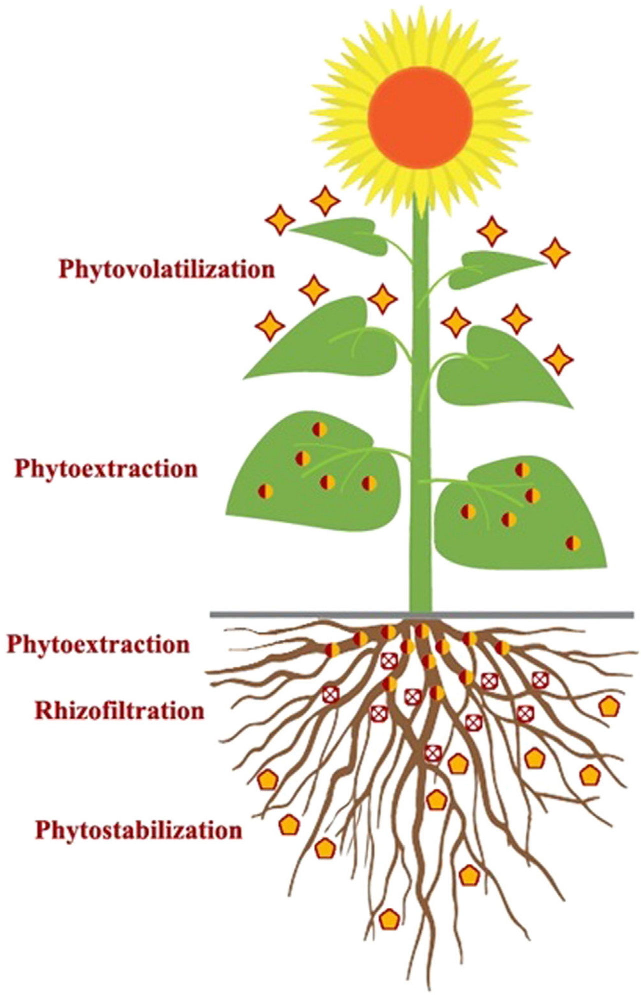

FIGURE 9.1 Schematic model of the various phytoremediation methods.

arundinacea Schreb cv. Alta) for Se (Bañuelos et al., 1997); poplar (*Populus* sp.) for As and Cd (Pierzynski et al., 1994); sunflower (*Helianthus annuus*) for Cs and Sr (Adler, 1996); Sudangrass (*Sorghum vulgare* L.), alfalfa (*Medicago sativa*) and maize (*Zea mays*) for Pb, Zn, Hg and Ni (EPA, 2000).

Rhizofiltration is used for the removal of pollutants, mainly metals from aquatic environments such as damp soil and ground and/or surface waters by adsorption or precipitation onto roots or other submerged organs of metal-tolerant aquatic plants related to their physiological and biochemical characteristics (Young, 1996; Salt et al., 1998; Kvesitadze et al., 2006; Jadia and Fulekar, 2009).

For this aim, the mainly used plants and elements are: *Azolla caroliniana* for As (Favas et al., 2012); *Eichhornia crassipes* for As, Cs, Co, Hg and Mn (Karkhanis et al., 2005; Nateewattana et al., 2010; Chattopadhyay et al., 2012; Saleh, 2012); *Lemna minor* and *Lemna gibba* for Ag, Au and Ni (Khellaf and Zerdaoui, 2010; Sasmaz and Obek, 2012; Favas et al., 2012; Pratas et al., 2012); *Typha angustifolia* for As, Cd, Cr, Cu, Fe, Mn, Ni, Pb and Zn (Chandra and Yadav, 2010); Indian mustard for Cu, Cd, Cr, Ni, Pb and Zn; sunflower for Cu, Cd, Cr, ^{137}Cs, Ni, Pb, ^{90}Sr, U and Zn; *Brassica juncea* for Cd and Pb (Dushenkov et al., 1995; Salt et al., 1995a); and *Medicago sativa* for Cr, Cu, Ni, Pb and Zn (Gardea-Torresdey et al., 1998).

Phytostabilization (phytoimmobilization) is based on plants' ability to immobilize contaminant metals in soils or sediments by sorption, precipitation and complexation. By decreasing metal mobility, these processes prevent leaching and groundwater pollution and minimize soil erosion and migration of sediments (Barceló and Poschenrieder, 2003; Kvesitadze et al., 2006; Ali et al., 2013). This process does not remove the contaminant from the soil, but it reduces the hazard of the contaminant (Arthur et al., 2005).

Sorghum sp. for Cd, Cu Ni, Pb and Zn (Jadia and Fulekar, 2008); *Solanum nigrum* for Ni (Ferraz et al., 2012); *Eucalyptus urophylla* and *Eucalyptus saligna* for Zn (Magalhães et al., 2011); *Vigna unguiculata* for Pb and Zn (Kshirsagar and Aery, 2007) have been used for this process.

Phytodegradation is the elimination of organic pollutants, which are easily entered into plant tissues or the rhizosphere by decomposition through internal or secreted plant enzymes or products (Barceló and Poschenrieder, 2003; Prasad and Freitas, 2003; Peer et al., 2005; Pilon-Smits, 2005).

Hybrid poplars (*Populus trichocarpa* × *Populus deltoides*) (Newman et al., 1997; Gordon et al., 1998), tropical leguminous tree *Leucaena leucocephala* (Doty et al., 2003), hairy root cultures of *Catharanthus roseus* (Bhadra et al., 2001) were studied materials used for phytodegradation processes. *Datura innoxia* and *Lycopersicon peruvianum* containing peroxidase, laccase and nitrilase have been shown to degrade soil pollutants (Schnoor et al., 1995; Lucero et al., 1999). Recently, *Blumea malcolmii* for Malachite Green dye (Kagalkar et al., 2011), *Erythrina crista-galli* for petroleum (de Farias et al., 2009) and *Chlorella pyrenoidosa* for pentachlorophenol (Headley et al., 2008) were used for phytodegradation processes.

Rhizodegradation defines the decomposition of organic pollutants such as xenobiotics in the soil by microorganisms in the rhizosphere (Mukhopadhyay and Maiti, 2010; Ali et al., 2013). Decomposition describes breakdown of a compound into its smaller constituents or its transformation to a metabolite and thus, rhizodegredation is one of the most important phases in the process of remediation of organic pollutants (Arthur et al., 2005).

Some trees, such as orange (*Citrus* sp.), apple (*Pyrus* sp.) and mulberry (*Morus* sp.) are able to excrete flavonoids and coumaric acid into the soil, stimulating the degradation of polychlorinated biphenyls (Donnelly et al., 1994;

Gilbert and Crowley, 1997; Kvesitadze et al., 2006) Additionally, *Salix nigra* was used for rhizodegredation of perchlorate (Yifru and Nzengung, 2008); orchardgrass (*Dactylis glomerata*), smooth bromegrass (*Bromus inermis*), tall fescue (*Festuca arundinacea*), Illinois bundle flower (*Desmanthus illinoensis*), perennial rye-grass (*Lolium perenne*), switchgrass (*Panicum virgatum*) and eastern gamagrass (*Tripsacum dactyloides*) were used for atrazine (Lin et al., 2011); *Kandelia candel* was used for phenanthrene and pyrene (Lu et al., 2011); and *Sesbania cannabina* for petroleum hydrocarbons (Maqbool et al., 2012).

Phytovolatilization is the uptake of pollutants (organics such as tetrachloroethane, trichloromethane, tetrachloromethane, etc. and/or certain metals such as As, Hg and Se) and their subsequent release into the atmosphere by transpiration, either in their original form or after metabolic modification (Susarla et al., 2002; Ali et al., 2013). Rice, rabbit foot grass, *Azolla* and pickle weed are known as the best Se volatilizers (Hansen et al., 1998; Pilon-Smits et al., 1999; Lin et al., 2000; Zayed et al., 2000; Hooda, 2007). Parrot's feather (*Myriophyllum brasiliense*), iris-leaved rush (*Juncus xiphioides*), cattail (*Typha latifolia*) and club-rush (*Scirpus robustus*) are also potential Se phytoremediator species in wetlands (Pilon-Smits et al., 1999; Arthur et al., 2005). *Brassica juncea* and several species of the genus *Astragalus* were also identified as valuable plants for removing Se from soils (Raskin et al., 1997; Bañuelos et al., 1998).

The hydraulic control technique uses plants that absorb large amounts of water through the plant body by transpiration and prevents the spread of contaminated wastewater into uncontaminated areas (Quinn et al., 2001; Barceló and Poschenrieder 2003; Kvesitadze et al., 2006). The most convenient plants for this application are poplar, birch, willow, eucalyptus, etc. (Gatliff 1994; Pivetz 2001; Kvesitadze et al., 2006).

Phytorestoration involves the complete remediation of contaminated soils which stabilizes wastes and prevents exposure pathways via wind and water erosion (Bradshaw 1997; Prasad and Freitas, 2003).

INTERACTIONS BETWEEN PLANTS AND MICROBES IN PHYTOREMEDIATION

Soil is unique in having a life-supporting system and provides ecosystem services essential for planetary functions, including primary production, the regulation of biogenic gases and the earth's climate, biogeochemical and water cycling, and the maintenance of biodiversity (Magdoff and van Es, 2000; Welbaum et al., 2004). A considerable amount of total land is contaminated due to various human activities and a gradual increase of this level is predicted in coming years.

Soils continuously exposed to metals such as As, Cd, Cu, Hg, Ni, Pb and Zn have high levels of accumulation leading to toxicity through various agricultural activities including agrochemical utilizations and long-term application of urban sewage sludge in agricultural soils, industrial activities and vehicle exhausts, as well as from anthropogenic sources (Modaihsh et al., 2004; Sabiha-Javied et al., 2009; Akguc et al., 2010). In turn, elevated levels of accumulations could pose potential threats to food safety issues and potential health risks due to transfers of metals from soils to plants (Ahmadpour et al., 2012; Ali et al., 2013). These metals are known to be potentially toxic to plants and animals and are of concern as their abilities to cause DNA damage and their carcinogenic capacity in animals and humans are probably related to their mutagenic abilities (Knasmuller et al., 1998; Baudouin et al., 2002). The potential threat from heavy metals is related to their non-degradable structures and therefore, without disturbance they persist in soils for a very long time (Neil, 2007). In order to minimize the access of heavy metals to the food chain and recover areas contaminated with heavy metals, the employment of cleanup strategies including soil excavation, soil washing or burning or pump and treat systems is obligatory and they are already being used for cleaning soil up. However, the applications of these non-biological remediation technologies for cleaning-up the sites contaminated with heavy metals causes destruction of biotic components of soils and implementation of these technologies are difficult and too expensive (Raskin et al., 1994).

A new practical and cost effective plant-based technology known as phytoremediation that uses plants and their associated microbial flora for environmental cleanup has gained acceptance (Salt et al., 1995a; Salt et al., 1998). Efficient degradation of organic compounds can be accomplished by employing a plant-based remediation technology which acts as a transformation system to metabolize organic compounds while taking advantage of plants' nutrient utilization processes (Kassel et al., 2002; Kvesitadze et al., 2006). Alternatively, toxic elements including heavy metals can be removed from the environment by using this plant-based technology through absorption and bioaccumulation (Zhao and McGrath, 2009; Zhang et al., 2010; Ali et al., 2013).

Phytoremediation efficiency is determined by key factors: the establishment of vital plants with biomass production, active root proliferation and/or root activities with the root symbiosis formation, assisting phytoremediation in the rhizosphere. In turn, assembly of microbial consortia can benefit the plant. Apart from many beneficial interactions, there is resource competition between plants and microbes (Kaye and Hart, 1997). Due to the constraints of limiting resources and resource competition, which commonly occur at polluted sites, microbial growth and biodegradation may become limited (Moorehead et al., 1998; Joner et al., 2006; Unterbrunner et al., 2007). Although excessive supply of nutrients could provide suitable conditions for stimulation of heterotrophic and pollutant adapted bacteria, this may not necessarily lead to achieving enhanced rates of phytoremediation. This was shown for hydrocarbon degradation in a crude-oil-contaminated soil. Pollutant degradation was not affected or even inhibited by the addition of nutrients (Chaineau et al., 2005).

The second aspect to be highlighted relates to rhizospheric control over pollutant toxicity. Plants and microorganisms can become adapted to toxic pollutant concentrations. Phyto-/rhizoremediation are being successfully exploited not only for removing pollutants but also for contributing to alleviation of toxicity by decreasing pollutant concentration in the rhizosphere. Resistance in plants and beneficial rhizospheric soil-borne microbes against (multiple) pollutants is one of the most important features and a prerequisite for their use of any phytoremediation technology (Burd et al., 2000; Belimov et al., 2005).

Soil-borne microbial communities showing different capabilities of genetic and functional activities can vary extensively in soils and have influences on soil functions, due to the fact that they are involved in fundamental metabolic processes (Nannipieri et al., 2003). Interactions between microbes are controlled by specific molecules (Pace 1997) and are shown to be responsible for key environmental processes including the biogeochemical cycling of nutrients and matter and the maintenance of plant health and soil quality (Barea et al., 2004). For an eminence bioremediation, formation of large numbers of metabolically active populations of beneficial soil-borne microbes are a necessity (Metting, 1992). In these soil-borne microbes, the driving factors are high adaptability in a wide variety of environments, fast growth rate, and biochemical versatility to metabolize a variety of natural and xenobiotic chemicals for a well-established ecosystem (Narasimhan et al., 2003).

The mutualistic relationship between plants and their associated rhizospheric microbial communities is complicated. Uptake efficiency of trace elements by plants can be augmented by soil-borne microbes such as rhizospheric bacteria (De Souza et al., 1999; Weyens et al., 2009a, b). In general, for successful rhizoremediation, a plant species must have a dense and highly branched root system to harbor large numbers of bacteria, primary and secondary metabolism, and establishment, survival, and ecological interactions with other organisms (Salt et al., 1998; Kuiper et al., 2004).

The primary contact point between plant tissues and pollutants in the soil or water is roots and therefore, they provide a key point for assessment of the phytoremediation potential of a particular plant species. There is a large volume of traffic between soil-borne microbes, roots and soil constituents at the root–soil interface (Lynch, 1990; Linderman, 1992; Glick, 1995; Kennedy, 1998; Bowen and Rovira, 1999). The high volume of interactions between roots, microbes and microbial communities creates a dynamic environment known as the rhizosphere. The physical, chemical and biological state of the root-associated soil differs from that of the root-free bulk soil, and physical, chemical and biological conditions are shown to influence diversity, numbers and activity of microorganisms in the rhizosphere microenvironment (Kennedy, 1998). Rhizospheric processes resulting from the activities of diverse groups of rhizospheric communities can be expected to affect uptake of heavy metals by plants. It has been shown that plants grown in non-sterile conditions exhibited no iron-deficiency symptoms and had a higher iron level in roots in comparison to plants grown in sterile conditions. This seems to be the result of rhizospheric microbial activity, which facilitates iron acquisition (Masalha et al., 2000).

Some rhizospherial strains have ability to release different substrates such as antibiotics (including antifungals), hydrocyanic acid, indoleacetic acid (IAA), siderophores, 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase which lead to increase in bioavailability and root absorption of heavy metals, including both essential (e.g. Fe and Mn) and non-essential (e.g. Cd) (Barber and Lee, 1974; Crowley et al., 1991; Salt et al., 1995). An investigation was performed to show the correlation between metal resistance and metal mobilization abilities of rhizobacteria under heavy metal stress. The highest degree of the biochemical activity of isolates and metal resistance was recorded for phosphate solubilizers; then, for siderophore producers, and finally for acid producers. The data imply that phosphate solubilization and siderophore-mediated solubilization and acid production are adopted by rhizobacteria and provide mobilizing metals in soil (Abou-Shanab et al., 2005). Uptake and translocation of trace elements may vary considerably and often depend on the species and type of trace elements. To varying degrees, different metals exhibit different mobility rates and the mobilization rate could be higher than others for a particular metal within a plant.

The complex feedback mechanisms allow plant roots and rhizosphere microorganisms to adapt to changing soil conditions as they grow. The vast majority of the soil-borne microbial population found is in contact with the plant roots, and their numbers can reach up to 10^9–$10^{12}\,g^{-1}$ of soil around the roots (Whipps, 1990), leading to a biomass equivalent to 500 kg ha^{-1} (Metting, 1992). This enrichment in vegetated soils is due to the availability of nutrients via plant root exudation (Brimecombe et al., 2001).

As growth facilitators, plant hormones released by some rhizospheric microorganisms stimulate root growth and thereby the secretion of root exudates. Plant exudates including carbohydrates, amino acids, lipophilic compounds and chelating agents (citric, acetic, other organic acids, etc.) released from plant roots exert favourable effects on sustaining a broad range of microbial communities in the rhizosphere (Anderson et al., 1993). Plants subjected to phosphorus deficiency attempt to mobilize phosphorous components present in the soil by increasing citric acid level in root exudates (Hooda, 2007). Mucigel, a gelatinous lubricant for root penetration secreted by the root cells contributes to increasing root mass apically through the soil during growth. Soil microorganisms use this supply of compounds for proliferation to generate the plant rhizosphere (Anderson et al., 1993). Plant survival is promoted in toxic and nutrient-limited environments through occurring interactions between plants and rhizosphere- and root-associated microbes. Various metallic ions are found to be immobile; therefore, they have limited bioavailability because of their low solubility (in water) and strong binding (of soil particles) characteristics, restricting their uptake by plants. But microorganisms colonizing plant roots can contribute to increasing the bioavailability of various heavy metal ions for uptake (Hooda, 2007).

For accumulation of metals by the plants from the soil, the metals must be mobilized in the soil solution. The bioavalability of metals is increased in soil through several means. Soil-bounded metal uptakes by roots of metal-starved plants are achieved by secreting phytosidophores (the chelating amino acids) into the rhizosphere for mobilization of metals via chelation and solubilization (Kinnersely, 1993). Also, pH seems to be a major element in controlling of mobilization (Gadd, 2004; Wenzel, 2009). The changes in pH can also affect speciation of metals/metalloids in solution (Anjum et al., 2012). Organic exudates released by soil-borne microorganisms increase bioavailability of metal ions including Fe^{2+} (Crowley et al., 1991; Burd et al., 2000), Mn^{2+} (Barber and Lee, 1974) and Cd^{2+} (Salt et al., 1995) for root absorption. Biosurfactants (e.g. rhamnolipids) are produced by some bacteria to make hydrophobic pollutants more water soluble (Volkering et al., 1998). Rhizosphere chemistry can be modified by two mechanisms, acidification and exudation of carboxylates, assisting in the mobilization of metals (Ma et al., 2001).

Some bacterial strains have detoxification abilities for toxic compounds. *Xanthomonas maltophyla* (Blake et al., 1993), *Escherichia coli* and *Pseudomonas putida* (Lasat, 2002) have been shown to catalyze the reduction and precipitation of highly mobile and environmentally less hazardous compounds. Most bacteria seem to posses multiple metal-resistance systems. Research conducted by Abou-Shanab et al. (2005) showed that all the rhizobacterial strains tested in the study were found to be tolerant to multiple metal ions. Similar findings had been previously reported by Sabry et al. (1997). Moreover, many anaerobic microorganisms may independently remove a number of metals from the environment by reducing them to a lower redox state. Biologically mediated reduction and oxidation of metals/metalloids may affect solubilization. Iron (III) can be used as a terminal electron acceptor by specialized anaerobic bacteria. Various metals including Cr (VI), Fe (III), Hg (II), Mn (IV), Se (VI) and U (VI) can be utilized by specialist dissimilatory metal-reducing bacteria. Microbial reduction is exploited not only for mobilization of Fe and Mn, but also for immobilizing of metals including Cr, U (Gadd, 2004), and Se (Di Gregorio et al., 2006).

Metals can be immobilized by microorganisms in various other ways including accumulation of them in their biomass or on cell walls via intracellular sequestration (Gadd, 2004) or precipitation, or adsorbtion (Leyval and Joner, 2000; Fein et al., 2001). It was shown that *Bacillus subtilis* strain SJ-101 protected *Brassica juncea* against Ni toxicity when inoculated together because of its high capacity for Ni (Zaidi and Musarrat, 2004). Mineralization of dissolved metal–organic complexes may be considered to be another cause of microbially mediated immobilization. The release of oxygen through wetland plants such as cattail (*Typha latifolia*) and common reed (*Phragmites australis*) in anaerobic soils increases the redox potential in the rhizosphere (Flessa and Fischer, 1992; Brix et al., 1996). This leads to induction of the formation of ferric Fe plaque and subsequently causes sorption and immobilization of metals (Doyle and Otte, 1997) and metalloids (Blute et al., 2004).

A number of endophytic and rhizobacteria in plant–bacteria combinations are involved in the degradation of toxic compounds in the rhizosphere. Endophytic bacteria can be defined as bacteria colonizing the internal tissues of plants without causing symptoms of infection or negative effects on their host (Schulz and Boyle, 2006). With the exception of seed endophytes, the root is the primary site for endophytes to gain access into plants. Several microscopic studies confirm this route of colonization (Pan et al., 1997; Germaine et al., 2004). After entry, endophytes either remain localized in specific plant tissues such as the root cortex or the xylem or colonize inner host tissues by transport through the vascular system or the apoplast (Mahaffee et al., 1997; Quadt-Hallmann et al., 1997). Endophyte-bearing plant samples comprise of herbaceous crop plants (Lodewyckx et al., 2002; Malinowski et al., 2004), different grass species (Zinniel et al., 2002; Dalton et al., 2004) and woody tree species (Cankar et al., 2005; Pandey et al., 2005). In general, the most common genera of cultivable endophytic species are Pseudomonaceae, Burkholderiaceae and Enterobacteriaceae (Mastretta et al., 2006).

Plant–endophyte associations rely on beneficial interactions. While plants provide nutrients and a harbour for endophytes, plant growth and health can be improved directly or indirectly via production of metabolites by endophytes (Bacon and White, 2000; Garbeva et al., 2001; Tan and Zou, 2001). Growth promotion effects of endophytic bacteria are related to preventing the growth or activity of plant pathogens through competition for space and nutrients, production of hydrolytic enzymes, antibiosis, and induction of plant defense mechanisms and through inhibition of pathogen-produced enzymes or toxins. Production of plant growth regulators including auxins, cytokinins and gibberellins, suppression of stress ethylene production by ACC-deaminase activity, nitrogen fixation and the mobilization of unavailable nutrients such as phosphorus and other mineral nutrients may be involved in the direct growth promoting mechanisms (Weyens et al., 2009b).

Transpiration rate and concentrations are considered to be critical factors in the phytoremediation of some organic contaminants. Removing trichloroethene (TCE) from soils the plants use a phytovolatilization mechanism (Xingmao and Burken, 2003). Thus, in phytoremediation plants are employed to provide optimum conditions for microbial degradation of pollutants and to accomplish the extraction of pollutants inside the plants (Boominathan et al., 2004; Tamaoki et al., 2008). Therefore, the role of providing optimum conditions for root colonizing bacteria and a simple way of extracting pollutants are two benefits provided by plants in phytoremediation (Suresh and Ravishankar, 2004). Besides symbiotic bacteria, studies concentrated on using fungi in phytoremediation technology. One example is the use of arbuscular mycorrhizae (AM) fungi that is more suitable for establishing symbiotic relationships with 80–90% of land plants (Huang et al., 2004; Khan, 2006). The volume of soil explored by mycorrhizae can be in an efficient manner due to their small diameter. Bioavailablity of pollutants can be modified by mycorrhizae through competition with roots and other microorganisms for water and pollutant uptake, protection of roots from direct interaction with the pollutant via formation of the ectomycorrhizal sheath, and impeded pollutant transport through increased soil hydrophobicity (Meharg and Cairney, 2000). Mycorrhiza associated plants have been reported growing on heavy-metal-contaminated soil (Shetty et al., 1994; Chaudhry et al., 1998, 1999). Root absorption (up to 47-fold) and the acquisition of plant nutrients including metal ions can be increased by the presence of fungal symbiotic associations (Smith and Reed, 1997). However, there are contradictory observations in the results of mycorrhizal effect on metal uptake. There are reports that mycorrhizae may have inhibitory effects on Cu, Zn (Scheupp et al., 1987; Heggo et al., 1990) and Cd accumulation (Weissenhorn and Leyval, 1995; Joner and Leyval, 1997; Schutzendubel et al., 2002). Arbuscular mycorrhizal colonization of *Thlaspi praecox* showed interfering effect on heavy metal (Cd and Pb) uptake (Vogel-Mikus et al., 2005). The inhibition may be related to the mycorrhizal protection of the plants from heavy metal toxicity, although the mechanism of protection is unclear. In addition, mycorrhizae have been reported to both enhance uptake of essential metals in the presence of low levels of metals and decrease uptake of metals in the presence of phytotoxic levels (Frey et al., 2000). The mechanisms in plant–microbe interactions are still broadly unclear; enhanced plant uptake mediated by microbes may be due to a stimulatory effect on root growth, microbial production of metabolites may involve altered plant gene expression of transporter proteins or microbial effect on the bioavailability of the element (DeSouzaet al., 2000).

In addition to effects of microbial associations, a vast number of organic pollutants can be taken up by direct activities of the plants themselves from the soil through their roots. The decomposition of organic residues with the release of plant nutrient elements including C, K, N, S, and phosphate carried out by soil microorganisms is important (Macek et al., 2000).

RHIZOSPHERE MICROBIOME

The microbial inhabitants are an integral natural active part of the biota in soils. Exposure of bacteria to plants in various ecological systems including rhizospere gives rise to stimulation of growth by directly affecting plant metabolism in the absence of a major pathogen. These bacteria belong to diverse genera, including *Acetobacter*, *Achromobacter*, *Anabaena*, *Arthrobacter*, *Azoarcos*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Clostridium*, *Enterobacter*, *Flavobacterium*, *Frankia*, *Hydrogenophaga*, *Kluyvera*, *Microcoleus*, *Phyllobacterium*, *Pseudomonas*, *Serratia*, *Staphylococcus*, *Streptomyces*, *Vibrio* and the well-known legume symbiont *Rhizobium* (Bashan et al., 2008).

Broadly, there are three separate, but interacting, components recognized in the rhizosphere. These are the rhizosphere (soil), the rhizoplane and the root itself. The plants that are colonized by microbial communities have a soil zone termed rhizosphere that is influenced by roots through the release of substrates.

In turn, those substrates stimulate microbial activity in the rhizosphere. The rhizoplane is the root surface, including the strongly adhering soil particles. The root itself is a part of the system. Root tissues are colonized by certain microbes known as the endophytes (Kennedy, 1998; Bowen and Rovira, 1999). Microbial colonization occurs in patches along the root tissues and/or the rhizoplane known as root colonization, whereas the colonization of the adjacent volume of soil exists under the influence of the root known as rhizosphere colonization (Kloepper et al., 1991, 1994). The rhizosphere can comprise up to 10^{11} microbial cells/g of root (Egamberdieva et al., 2008) and more than 30,000 prokaryotic species (Mendes et al., 2011). The rhizospheric microbial diversity is enormously diverse, including tens of thousands of species. This complex plant-associated microbial community is crucial for plant health (Berendsen et al., 2012).

Recent studies showed that the composition of the rhizosphere microbiome can be determined by plants through active secretion of substrates that are known to vary between plant species and be able to shape distinct rhizomacrobial communities. Therefore, different plant species host specific rhizospheric microbial communities when grown on the same soil (Sorensen, 1997; Jaeger et al., 1999). The difference between the chemical conditions of the rhizosphere and the bulk soil is the result of various processes induced by plant roots and/or by the rhizobacteria (Marschner, 1995; Hinsinger, 2001).

Interactions between plants and rhizospheric microbes could stimulate the production of compounds that could alter soil chemical properties in rhziosphere. For example, the increased accumulation of Hg by plants could be the result of decreased pH by rhizobacteria of the plants (De Souza et al., 1999). A study of the influence of hydrogen and aluminum ions on the growth of the associative nitrogen-fixing and growth-promoting bacteria *Azospirillum lipoferum* 137, *Arthrobacter mysorens* 7, *Agrobacterium radiobacter* 10 and *Flavobacterium* sp. L30 showed that the response of plants to the inoculation varied under different values of pH (from positive to negative) (Belimov et al., 1998).

Exudates released by plant roots are used by rhizospheric microbes as nutrients. It is estimated that the proportion of net photosynthetic carbon transferred to the roots is between 30–60% and 10–20% of root needs comes from rhizodeposition (Marschner 1995; Salt et al., 1998). Exudates consist primarily of low molecular weight (LMW) and high molecular weight (HMW) organic acids. The total concentration of organic acids measured in roots usually ranges from 10 to 20 mM, generally comprising of lactate, acetate, oxalate, succinate, fumarate, malate, citrate, isocitrate and aconitate. The remainder of organic solutes in roots consists of sugars (90 mM) and amino acids (10–20 mM) (Jones, 1998). The HMW organic acids are mucilage and ectoenzymes (Knee et al., 2001).

It is essential for bioremediation that using such soils treated with metals and/or acids increases their biological activity (Boon et al., 1998), especially for mineral soils with a low content of organic matter (Priha et al., 1999). The exudates create favourable conditions for rhizospheric microbial populations leading to increase in their mass well beyond those of the bulk soil, attracting motile bacterial and fungal hyphae. Consequently, stimulation of an array of positive, neutral or negative interactions with plants occurs (Gerhardson, 2002).

Microbial cells have the ability to produce and recognize signal molecules. This allows the whole population to form biofilm over large areas of the root surface and a concerted action is taken by the whole population after a critical level is exceeded. This phenomenon is known as quorum sensing. Many microbes control gene expression by employing quorum sensing in response to cell population density. The successful infection and formation of nitrogen fixing nodules by rhizobial bacteria upon legume roots is carried out chemotactically through certain root exudates leading to activation of rhizobial nodulation genes, Nod factors during adhesion and colonization of the legume root surface. Many quorum sensing signal molecules such as N-acyl-homoserine lactones (AHLS) play important roles in the regulation of expression and repression of the symbiotic genes (Daniels et al., 2004).

Plants, as well as their plant-derived chemicals, including those generated from the roots applied to unplanted soil, can nurse degradative microbes when applied to unplanted soil (Shann, 1995). Spoilage of organic matter and many other substrates is found to be two to three times higher in the rhizosphere than in the bulk soil (Jones, 1998). Plants produce a broad range of diverse low molecular mass secondary metabolites. Based on the estimation, the total number of plants exceeds 500,000 (Hadacek, 2002). Secondary metabolites are taken into account as non-essential for the basic metabolic processes of the plant (Dixon, 2001).

The effects of microbial communities in the rhizosphere are apparent in determining plant health and findings also verify the importance of the root microbiome.

STIMULATION OF PLANT GROWTH BY MICROBIAL COMMUNITIES

Many plants are not capable of gaining sufficient biomass for noticeable rates of remediation when elevated levels of pollutants are present (Harvey et al., 2002; Chaudhry et al., 2005). The remediation process of contaminated soils is limited and slowed because of their poor nutrient nature. Soil microbes are thought to exert positive effects on plant health via mutualistic relationships between them. However, microbes are sensitive to pollution, and depletion of microbial populations, both in terms of diversity and biomass, often occur in such contaminated soils (Shi et al., 2002).

Biotic or abiotic stress through a small change in the physico-chemical-biological properties of rhizosphere soils can cause a dramatic effect on plant–microbe interaction. Plant growth promoting microbes as rhizosphere inoculums are receiving attention in profitability of phytoremediation process; this partly depends on the plant's ability to withstand metal toxicity and to yield adequate biomass (Rajkumar and Freitas, 2008; Kuffner et al., 2010; Ma and Wang, 2010; Maria et al., 2011; Aafi et al., 2012). Phytoremediation and bioaugmentation are the terms used in combination to describe rhizoremediation, in conjunction with plant growth promoting rhizobacteria (Kuiper et al., 2004).

The PGPR (plant growth promoting rhizobacteria) are defined by three intrinsic characteristics: the organisms are capable of colonizing the root; the organisms have capability for survival, proliferation and competition in micro-habitats associated with the root surface; and the organisms are able to promote plant growth (Lugtenberg et al., 1999, 2001; Rothballer et al., 2003; Espinosa-Urgel, 2004; Gamalero et al., 2004).

The PGPR have been divided into two groups: those that are found to be involved in nutrient cycling and phytostimulation, including fixing atmospheric nitrogen and supply it to plants, synthesizing siderophores which can sequester iron from the soil and provide it to plant cells, synthesizing phytohormones such as auxins, cytokinins and gibberelins, solubilizing minerals such as phosphorous, making them more readily available for plant growth and synthesizing the enzyme ACC-deaminase, which can lower ethylene levels; and those that are found to be involved in the biocontrol of plant pathogens resulting from any one of a variety of mechanisms including antibiotic production, depletion of Fe from the rhizosphere, induced systemic resistance, production of fungal cell wall lysing enzymes, and competition for binding sites on the root (Bashan and Holguin, 1998; Glick et al., 2007). There are a number of reports stating that some PGPR species are able to be resistant to relatively high concentrations of heavy metals and remain active in moderately acidic soils (Belimov et al., 1998; Ivanov et al., 1999). Such naturally occurring rhizobacteria could assist phytoremediation both indirectly, by increasing the overall fertility of the contaminated soil and enhancing plant growth through nutrient uptake and control of pathogenity, and, also directly, catabolizing certain organics and/or intermediate partly oxidized biodegradation products (Kamnev et al., 1999).

Applied cadmium-resistant, rhizosphere-competent bacterial strains increased root and shoot biomass production of *Brassica napus* grown in cadmium-polluted soil (Sheng and Xia, 2006). Similarly, a PGPR consortium consisting of N_2-fixing *Azotobacter chroococcum* HKN5, P-solubilizing *Bacillus megaterium* HKP-1, and K-solubilizing *Bacillus mucilaginosus* HKK-1 was applied to increase growth and biomass production of *Brassica juncea* grown on Pb–Zn mine tailings and upon inoculation, increased production, in terms of growth and biomass has been observed (Wu et al., 2006).

The growth of *Brassica juncea* on nickel-polluted soil was stimulated by utilization of the PGPR *Bacillus subtilis* strain SJ-101 capable of producing the phytohormone indole acetic acid and solubilizing inorganic phosphates (Zaidi et al., 2006).

The root associated bacteria having ACC-deaminase activity has provided a better root growth and proliferation to the plant in polluted soils (Arshad et al., 2007). Inhibition of root growth and proliferation as a consequence of high concentrations of ethylene produced by plant roots occurs in response to toxicity and other stresses. Bacterial ACC-deaminase can significantly decrease ACC levels by metabolizing its ethylene precursor ACC into a-keto butyric acid and ammonia (Glick, 2005). PGPR with ACC-deaminase activity leading to better metal tolerance were found in the rhizosphere of the Ni tolerant *Thlaspi goesingense* (Idris et al., 2004).

Kluyvera ascorbata SUD165, an interesting example of PGPR was found to be resistant to a range of heavy metals and was reported to protect plants from nickel toxicity without affecting Ni uptake by seedlings or its accumulation in the plant (Burd et al., 1998). The plant growth-promoting effect in the presence of Ni may relate to the ACC-deaminase activity of this bacterium (Shah et al., 1998).

It was shown that *Brassica napus* and *Brassica campestris* were protected against metal toxicity by metal-resistant PGPR containing ACC-deaminase producing bacteria (Burd et al., 1998; Belimov et al., 2001). IAA (auxin) is also produced by many PGPR and is believed to play an important role in plant–bacterial interactions (Lambrecht et al., 2000). Therefore, any direct influence on IAA production by bacteria may in turn affect their phytostimulating efficiency. It has been demonstrated that bacterial excretion of auxins into the soil is beneficial for plants, in conjunction with making the bacterial plant-growth-promoting effect (Steenhoudt and Vanderleyden, 2000; Kamnev, 2003).

It has been found that presence of Cu^{2+} and Cd^{2+} in soils caused significantly reduced level of IAA produced by nonendophytic and facultatively endophytic strains of *Azospirillum brasilense*, leading to alteration of the plant-growth-stimulating efficiency of associative plant–bacterial symbioses in heavy-metal-polluted soils (Kamnev et al., 2005). As a matter of fact, while low levels of bacterial IAA promote root elongation, high levels of bacterial IAA stimulate lateral and adventitious root formation (Glick, 1995) but inhibit root growth (Xie et al., 1996). Hence, plant growth can be improved by altering the hormonal balance within the affected plant via plant growth-promoting bacteria (Glick et al., 1999).

Plants are able to take up microbial Fe complexes with siderophores serving as a Fe source for plants (Reid et al., 1986; Bar-Ness et al., 1991; Wang et al., 1993). Therefore, protection of plants from becoming chlorotic in the presence of high levels of heavy metals can be provided by the utilization of a siderophore-producing bacterium in the rhizosphere of plants. Thus, enhanced plant growth could be accomplished by treating plants with associated plant-growth-promoting bacteria in the presence of heavy metals including Ni, Pb and Zn (Burd et al., 1998, 2000), thereby enabling plants to have longer roots and get better established during the early stages of growth (Glick et al., 1998). Similarly, Cr-resistant *Pseudomonas* were isolated from paint industry effluents and used to stimulate seed germination and growth of *Triticum aestivus* in the presence of potassium bichromate (Hasnain and Sabri, 1996). In this case, the bacterial enhancement of seedling growth was associated with reduced chromium uptake. It was found that axenic saltmarsh bulrush plants inoculated with different rhizospheric bacteria accumulated more Se than plants grown under axenic conditions (De Souza et al., 1999).

Production of organic acids by soil fungi (Gadd, 1999) and bacteria, including rhizobacteria (Goldstein et al., 1999; Nautiyal et al., 2000), may promote solubilization, mobility and bioavailability of metals and accompanying anions by lowering the pH and supplying metal-complexing organic acid ligands (Kamnev and Van der Lelie, 2000). These microbially driven processes are a prerequisite for mineral weathering (Barker et al., 1998; Banfield et al., 1999).

Toxic heavy metal constituents coming from the dissolving minerals increase their bio- and phytoavailability in soils through these microbially driven processes leading to alteration in the fertility of soils. For instance, Hg and Se accumulations are promoted by naturally occurring rhizobacteria in the rhizosphere of wetland plants (De Souza et al., 1999). These plant-growth-promoting rhizobacteria could be deployed to increase efficiency of phytoextraction. Using *Pseudomonas aeruginosa* PAO1 and its three isogenic lipopolysaccharide (LPS) mutants, while the precipitation of essential volumes of Fe and La is controlled on the cell surface, Cu was bound at the cell surface of all the four strains assuming common surface functional groups responsible for Cu binding (Langley and Beveridge, 1999). It was found that the precipitation of Cd compounds was promoted by certain rhizobacteria on the plant root surface leading to a reduction in the bioavailability of Cd uptake by roots and enhancing their growth (Van der Lelie et al., 2001). A novel siderophore, also known as alcaligin E from a metal-tolerant bacterium, *Ralstonia eutropha* CH34 was found to have the capacity for binding Cd resulting in immobilizing and exclusion of Cd from metabolism (Diels et al., 1995; Gilis et al., 1998). The immobilization of heavy metals entrapped within the insoluble crystalline and/or amorphous phases (e.g. phosphate minerals) can be created in natural microbial communities (Douglas and Beveridge, 1998; Lins and Farina, 1999).

The root exudates provide an abundance of energy for the microbial transformation of organic compounds in the resolver zone. Soil microorganisms are also known to produce biosurfactants for facilitating removal of organic pollutants (Volkering et al., 1998). Direct detoxification of metals by utilization of root exudates (through forming chelates with metal ions) can be carried out in such soils contaminated with heavy metals.

The PGPR has important roles in facilitating plant growth on soils contaminated with both heavy metals and organic compounds and detoxification of soils and is exploited for phytoremediation purposes.

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