6 Rhizospheric Plant-Microbe Interactions: Key Factors to Soil Fertility and Plant Nutrition

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Abstract

Plant roots radiate a wide range of potentially valuable small molecular weight compounds into the rhizosphere which play a key role in the chemical, physical, and biological interaction between roots of the plants and the rhizosphere. The microorganisms present in the rhizosphere react with the numerous metabolites released by plant roots by positive, negative, and neutral ways, and these interactions may influence the plant growth and development, change nutrient dynamics, and also alter the plants susceptibility towards diseases and abiotic stresses. The root produces chemical signals that attract the bacteria and other microbes towards it. Beside this, positive interactions also include growth regulator mimics that support the plant growth and the cross-species signaling with other rhizospheric microorganisms. Plant-microbe interactions can influence the plant growth by providing nutrients and increased biotic and abiotic stress tolerance. Most of the agricultural soils have large amounts of inorganic and organic phosphorus (P), but it is present in immobilized form so is usually unavailable to plants. One of the major reasons why P is not readily available to plants is because of the high reactivity of P with some metal complexes. In this regard, the soil inoculants such as fungi, plant growth-promoting rhizobacteria (PGPR), and mycorrhizal fungi play a significant role in the solubilization of inorganic phosphate and mineralization of organic phosphates into easily available form to plants. Similarly, nitrogen (N) fixers provide available N to the plants. N is a key limiting factor in any ecosystem. For treating heavy metal-contaminated tailings and soils, bioremediation is one

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of the cost-effective methods and is emerging as the potential tool for removal of these contaminants from the soil or water. Bioremediation is a versatile process that could be applied in situ or ex situ manner. A wide variety of microorganisms such as bacteria, fungi, yeasts, and algae are being used in bioremediation processes, and some of these have already been employed as biosorbents of heavy metals. Various technologies such as phytoremediation, bioventing, bioleaching, land farming, bioreactor, composting, bioaugmentation, rhizofiltration, and biostimulation are nowadays used for the bioremediation of contaminants from the soil. The aim of this chapter is to focus on the plant-microbe interactions responsible for the maintenance of soil fertility, plant nutrition, and also the remediation of contaminated soil for sustainable agricultural system.

Introduction

Plants and their associated microorganisms play an important role in the formation or modification of soil (Pate and Verboom 2009). The soil formation takes place from the weathering of rocks and minerals and has distinct properties based on their origin, climate, and vegetation. Soil carbon is predominantly derived from plants, directly or indirectly, and while weathering may be due to physical and chemical influences. Most of the weathering processes involve primarily the plant roots, and the microbial activity may depend on the root-derived carbon (Beerling and Berner 2005). Next to water and temperature, nutrients are most crucial environmental factors desired for the development of the terrestrial plants. Rhizosphere is a zone of intense microbial activity, and the microorganisms present in the rhizosphere react with the various metabolites released by plant roots (Akhtar and Siddiqui 2010). Thus, the microorganisms and their products interact with plant roots in a variety of ways such as positive, negative, and neutral (Kuzyakov and Xu 2013). These interactions can influence the plant growth, change nutrient dynamics, and also alter the plants susceptibility towards the disease, abiotic stress, and resistance to heavy metals (Morgan et al. 2005).

The root systems support the aboveground part of the plant. In addition, the soil needs to maintain an appropriate pH, provide the protection from toxic substances and pathogens, and also contain suitable water levels. Besides this, all the essential mineral elements desired by plants are obtained from the soil. Marschner (1995) has recognized about 17 essential elements required for plant growth and reproduction. Amongst all the required essential elements, 14 elements are primarily acquired from the soil solution including the six macronutrients (N, P, K, Ca, Mg, and S) and 8 micronutrients (Fe, Cu, Zn, Mn, Mo, B, Cl, and Ni). Additionally, the plants also accumulate nonessential or toxic elements such as Cd, Pb, and Na from the soil solution.

Most of the essential elements are taken up in the ionic form from the soil solution by plants (White 2003). It is a well-known fact that the plant growth may be limited by the availability of essential elements or by the presence of toxic elements (Morgan et al. 2005). The interactions between microorganisms and the plant roots in rhizosphere assist the plants to acquire essential mineral nutrients and thwart the accumulation of toxic elements. Thus, it would be obvious that the structures of rhizospheric microbial communities are distinct from the bulk soil (Marilley and Aragno 1999), but vary in between plant species and over geographical time scale (Smalla et al. 2001). The different root zones in the same plant can hold distinct microbial communities reflecting qualitative and quantitative differences in root exudation (Yang and Crowley 2000). Moreover, the structure of rhizospheric microbial communities could also be influenced by root infection by pathogenic microorganisms, which promote greater microbial community variability compared to healthy roots (Yang et al. 2001).

The Rhizosphere

Hiltner (1904) recognized rhizosphere as the volume of soil within immediate vicinity of the roots, which is predominantly affected by the activity of plants. The rhizosphere differs from the surrounding soils in most of the physicochemical and biological factors and with extensive microbial population both in numbers and diversity (Phillips et al. 2003). The number of microorganisms present in per gram of soil is much larger in the rhizosphere as compared to bulk soil. This increased microbial activity in the vicinity of the roots could be attributed to root exudates, sloughed senescent root cells, and mucigel described as rhizodeposition (Mukerji et al. 1998). Thus, the rhizosphere is the region in which the materials released from the root and root metabolic activities directly affect microbial density (Table 6.1). The roots continuously release volatile, soluble, and particulate materials through the process of rhizodeposition, and the growth of rhizospheric microorganisms on these materials turn over all the cellular activities and also release the nutrients in the form which could be utilized by plants.

The rhizosphere encompasses not only the region of nutrient uptake by the plant roots but also extends into the soil by the action of their byproducts (Van der Putten et al. 2001). This infusion of organic substrates into the rhizosphere by plants explains very clearly that the biomass and microbial activity are always greater in rhizosphere compared to bulk soil (Bardgett et al. 1998). Root tip is the site of root growth, usually characterized by rapidly dividing cells having the root exudates. The root exudates and sloughed root cells provide carbon to rhizospheric microorganisms, which in turn mobilize N and P in soil for the plants.

Table 6.1 Various root zones in the soil

Root zones	Functions
Rhizosphere	Region around the plant root where materials released from the root modify microbial populations and their activities
Endorhizosphere	Regions of the various cell layers of the root itself where microorganisms also colonize
Ectorhizosphere	An area surrounding the root and containing root hairs, plant, and bacterial mucilage
Rhizoplane	Root surface that can be colonized by microorganisms
Mycorrhizosphere	The ectorhizosphere extends a substantial distance from the root with the development of mycorrhizal fungal associations. Materials released from the fungus increase the microbial populations and their activities around the fungal hyphae
Spermosphere	The region around the germinating seed
Rhizodeposition	Release of materials from the roots

Chemical Compounds Produced by Plant Roots in the Rhizosphere

The general concept about the plant is that an aerial part such as stem and leaves contains greater biomass than roots, but this is actually a misleading impression. For many plants the biomass ratio of root and shoot is greater than the shoot and root biomass ratio. The materials released by plants include a wide variety of organic compounds (Table 6.2). The nature of these compounds depends upon various environment factors like temperature, moisture content, fertilizer dosages, herb, and plant age. The fine hairs of the roots are critical parts of the root system. They release various root exudate products into the environment due to their metabolic activity, and additionally a variety of gaseous metabolites also flow from the roots in the process of rhizodeposition.

Table 6.2 Different compounds released by plant roots in the process of rhizodeposition

Compounds	Exudates components
Amino compounds	Asparagine, α- alanine, glutamine, aspartic acid, leucine/isoleucine, serine, glycine, cystine/cysteine, methionine, phenylalanine, tyrosine, threonine, lysine, proline, tryptophan, β- alanine, arginine, homoserine, cystathionine
Fatty acids and sterols	Palmitic, stearic, oleic, linoleic, linolenic acids, cholesterol, campesterol, stigmasterol, sitosterol
Growth factors	Biotin, thiamine, niacin, pantothenate, choline, inositol, pyridoxine, N-methyl nicotinic acid
Nucleotides, flavonines, and enzymes	Flavonine, adenine, guanine, uridine/cytidine, phosphatase, invertase, amylase, protease, polygalacturonase
Organic acids	Tartaric, oxalic, citric, malic, propanoic, butyric, succinic, fumaric, glycolic, valeric, malonic
Sugars	Glucose, fructose, sucrose, maltose, galactose, rhamnose, ribose, xylose, arabinose, raffinose, oligosaccharide
Miscellaneous compounds	Auxins, scopoletin, fluorescent substances, hydrocyanic acid, glycosides, saponin (glucosides), organic phosphorus compounds, nematode-cyst or egg-hatching factors, nematodes attractants, fungal mycelium growth stimulants and inhibitors, zoospore attractants

Microbial Miscellanies in the Rhizosphere

The rhizosphere is the "cloud" of microbes surrounding the plant roots and is vital for the plant growth and survival. Plant roots construct novel environments for microbes due to change in increased levels of nutrients and intense microbial population (Giri et al. 2005). The microbial density is always high along the root away from the plant tip because respiration of the root is responsible for the change in the environment of the rhizosphere microbes. However, the microbial community developed in the changed environment will also face additional challenges like the availability of nutrients and edaphic and other biotic and abiotic factors which might be limiting for both the plant and their associated rhizospheric microbes.

The plant has an increasing demand for inorganic unavailable nutrients not present in a sufficient rate in the soil. In this regard, the rhizospheric microorganisms make a major contribution to overcome this demand (Table 6.3). The filamentous fungi also play a unique role in the nutrient uptake available to the plant due to their extensive hyphal network. They can derive the carbon from the plant and other limiting nutrients such as N and P from outside the root zone. Some free-living N_2-fixing bacteria like *Azotobacter*, *Azospirillum*, and *Azoarcus* present in the nitrogen-free or low nitrogen input environment play a significant role in the nitrogen fixation and also make the availability of nutrients to plant. Besides this, the rhizospheric community is not only enriched in bacterial and fungal populations but also has protozoans and nematodes. These patrons feed on the nutrient-rich bacteria and fungi and lead to more rapid turnover of the microbe populations in the rhizosphere which could be responsible for the acceleration in the release of nutrients for plant.

Plant-Microbe Interaction and Nutrient Availability

Continuous application of chemical fertilizers for enhancing soil fertility and crop productivity resulted in unforeseen harmful environmental effects such as leaching of nitrate into ground water, surface runoff of N and P, and eutrophication of aquatic ecosystems (Tilman 1998; Gyaneshwar et al. 2002). Besides this, it also negatively impacted the complex system of the biogeochemical cycles (Perrott et al. 1992; Steinshamn et al. 2004). All these events suggested that long-term application of chemical fertilizers not only reduced the soil fertility but also reduced the microbial population in the various agroclimatic conditions.

Despite the various negative effects on the environment, the use of total amount of fertilizers has increased globally to fulfill the food demand

Table 6.3 Microbial density of major groups of microorganisms present in the rhizospheric and non-rhizospheric soils

Microorganisms	Rhizosphere (microbes/g dry soil)	Non-rhizosphere (microbes/g dry soil)	R:S ratio
Algae	5×10^3	27×10^3	0.2
Actinomycetes	46×10^6	7×10^6	7.0
Bacteria	1200×10^6	53×10^6	23.0
Fungi	12×10^5	1×10^5	12.0

of the growing world population through intensive agriculture (Vitousek et al. 1997; Frink et al. 1999). In the last five decades, the rate of NPK fertilizer application has increased tremendously. Thus, there is a challenge to increase the agricultural productivity by minimizing the use of harmful chemical fertilizers. In this regard, the use of microbial inoculants such as PGPR and mycorrhizal fungi play a crucial role to minimize the demand of chemical fertilizers. Thus, the microbial inoculants are considered as promising components of agro-environmental integrated system because these inoculants possess the capacity to promote plant growth, enhance nutrient availability and uptake, and support plants' health (Barea et al. 1998; Dobbelaere et al. 2001; Hodge et al. 2001; Bonfante 2003; Vessey 2003; Kloepper et al. 2004; Han and Lee 2005; Adesemoye et al. 2008; Akhtar et al. 2011).

The arbuscular mycorrhizal (AM) fungi increase the plant growth by water and nutrient uptake (Ames et al. 1983; Akhtar and Siddiqui 2008a; Akhtar and Panwar 2011). The AM fungi have a high affinity towards P-uptake mechanism that enhances P nutrition in plants. The AM fungi could also scavenge the available P through their extraradical hyphae (Bianciotto and Bonfante 2002; Akhtar and Siddiqui 2008b; Akhtar et al. 2011). Apart from this beneficial association between the AM fungi and plant roots, there are few demerits as well. The AM fungi could not be cultured in vitro, due to their obligate nature, limiting the knowledge about the genetic basis of P solubilization and rhizosphere competence (Amijee et al. 1989; Koide 1991). Moreover, a high concentration of soil phosphate, above 100 ppm, could lead to the reduction in hyphal growth and chlamydospore production (Koide 1991). These limitations directly affect the P uptake and also cause the reduction of the benefits to plants (Stewart et al. 2005).

Similarly, the use of PGPR increases seed germination rate, root growth, yield, leaf area, chlorophyll content, nutrient uptake, protein content, hydraulic activity, tolerance to abiotic stress, and shoot and root weight, biocontrol and also delay the senescence (Raaijmakers et al. 1997; Bashan et al. 2004; Mantelin and Touraine 2004; Siddiqui et al. 2007; Bakker et al. 2007; Yang et al. 2009; Akhtar and Siddiqui, 2010). Other beneficial effects of PGPR include enhancing P availability (Rodriguez and Fraga 1999; Akhtar and Siddiqui 2008a; Akhtar and Panwar 2011; Yadav et al. 2012); fixing atmospheric nitrogen (Bashan et al. 2004; Gupta et al. 2012); sequestering iron for plants by production of siderophores (Raaijmakers et al. 1997; Bakker et al. 2007; Akhtar and Siddiqui, 2009), producing plant hormones such as gibberellins, cytokinins, and auxins (Gutierrez-Manero et al. 2001); and synthesizing 1-amino cyclopropane-1-carboxylate (ACC) deaminase (Glick et al. 2007a, b).

Availability of Nitrogen

Nitrogen is an essential element for plant growth and development, and the complex nitrogen cycle has a great impact on soil fertility (Jetten 2008). This cycle is conquered by four major steps, nitrogen fixation, nitrification, denitrification, and nitrogen mineralization (Ogunseitan 2005). It has been reported by earlier researchers that the microbial inoculants have significant roles in nitrogen cycling and utilization of nitrogenous fertilizers in the plant-soil system (Briones et al. 2003; Adesemoye et al. 2009) (Fig. 6.1). The uptake of nitrogen by leguminous (Elsheikh and Elzidany 1997; Akhtar and Siddiqui, 2006; Gupta et al. 2012) and nonlegume plants have been reviewed by many researchers (Kennedy et al. 1997; Dobbelaere et al. 2001;

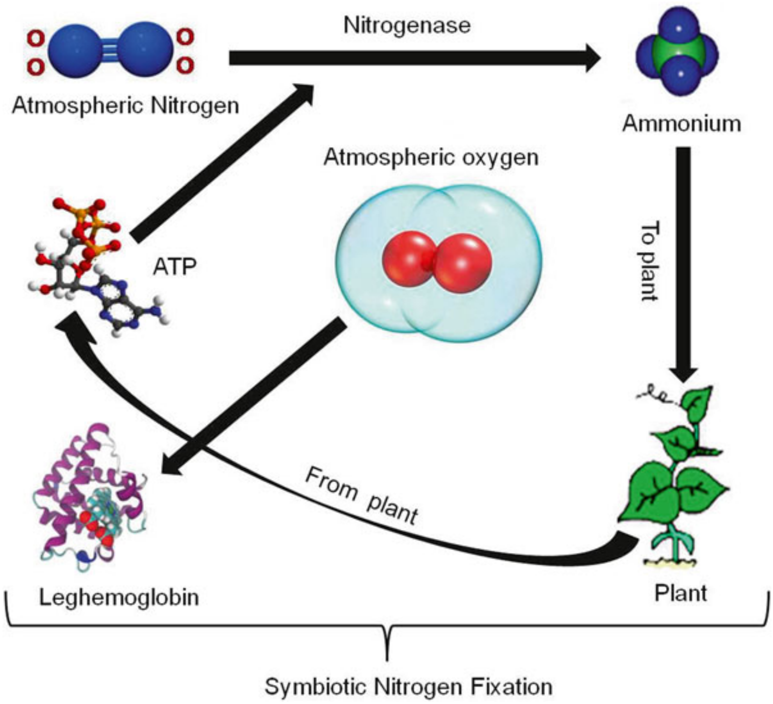

Fig. 6.1 Schematic representation of symbiotic nitrogen fixation in the leguminous plants

Vessey 2003; Egamberdiyeva and Hoflich 2004; Hernandez and Chailloux 2004; Wu et al. 2005; Shaharoona et al. 2008).

Wu et al. (2005) conducted greenhouse experiments on maize utilizing *Glomus mosseae* and *Glomus intraradices* with or without free-living nitrogen fixer, *Azotobacter chroococcum* and found that the co-inoculant increased the plant growth and NPK uptake and improved the soil properties in a much better way. Shaharoona et al. (2008) reported that inoculation of *Pseudomonas fluorescens* (strain ACC50) and *P. fluorescens* biotype F (strain ACC73) increased efficiency at all tested NPK fertilizer levels in wheat under pot and field trials. Amir et al. (2005) found that the inoculation of PGPR enhanced uptake of N and P in oil palm seedlings in nursery. Similarly, Aseri et al. (2008) conducted a field experiment to assess the effectiveness of PGPR (*A. chroococcum*) and AM fungi (*G. mosseae*) on the growth, nutrient uptake, and biomass production of pomegranate in individual or combined inoculations. The results showed that dual inoculation of PGPR and AM fungi led to higher biomass accumulation and uptake of N, P, K, Ca, and Mg. The result of the study thus confirmed that inoculation with mixed strains was more consistent than inoculation of single strain. It is well reported that the uptake of NPK and micronutrients are significantly enhanced in *Azospirillum* spp. inoculated plants under the greenhouse and field conditions. Thus, it would be very crucial to find out the factors behind the successful plant root colonization in *Azospirillum* and other PGPR which is responsible for the increase nutrient uptake.

Nitrogenase is the enzyme responsible for N_2-fixation. It has two components: I (a α2β2 tetramer encoded by *nifD* and *nifK* genes) and II (a homodimer encoded by *nifH* gene). These two components are conserved in structure, function, and amino acid sequence throughout the diazotrophs. These genes are commonly reported to regulate lateral root development and long-distance movement of nitrogen (de Zamaroczy et al. 1989; Ueda et al. 1995; Minerdi et al. 2001). The nitrogenase enzyme complex has been credited for the capacity of PGPR to convert nitrogen into ammonia in a free state. Egener et al. (1999)

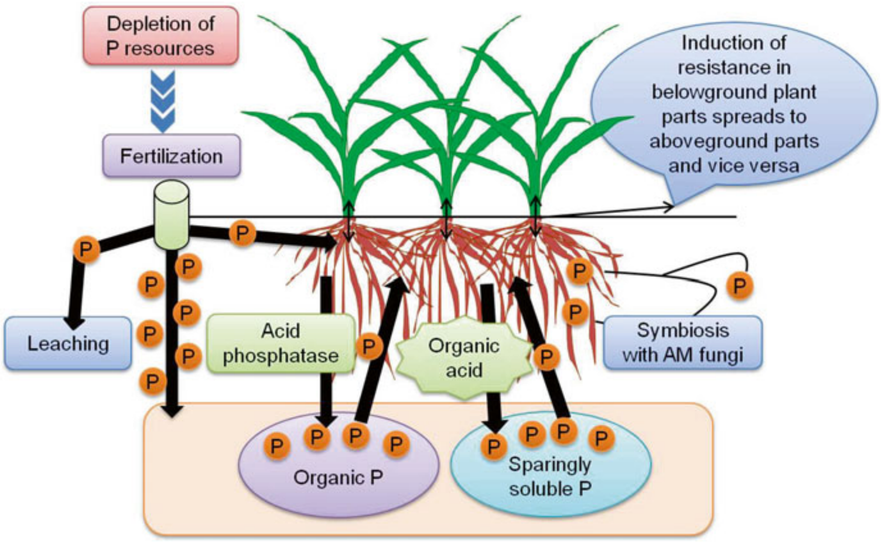

Fig. 6.2 Mechanism of soil P solubilization/mineralization and immobilization

studied root-associated GUS and *nifH* expression to monitor the establishment of N_2-fixing bacteria (*Azoarcus* sp.) on rice roots and successfully localized the expression of bacterial genes of interest in the host plant. They have found that the presence of combined nitrogen such as ammonia has a strong impact on the expression of *nif* gene in most diazotrophs. Similarly, Vande Broek et al. (1993) estimated the qualitative and quantitative associativeness in *nifH* expression in *A. brasilense* on wheat roots through *gusA* fusion plasmid system.

Availability of Phosphorus

Phosphorus is another growth-limiting nutrient generally present in the immobilized organic and inorganic form in the soil. Phosphorus is not readily available to plant due to its high reactivity with some metal complexes such as Fe, Al, and Ca leading to precipitation in the soil or may be present in very low concentration (usually in micromolar amount) (Igual et al. 2001; Gyaneshwar et al. 2002). It is also an important and well-known fact that when the P fertilizers are added to soils, they may not be absorbed or utilized by plants because of their sparingly soluble nature, and thus less amount of P would be available for the growth of agricultural crops (Gyaneshwar et al. 2002). Thus, the farmer may have to add large amount of fertilizers into the fields which later cause environmental problems (Ohno et al. 2005). The inoculants of PGPR and AM fungi play a significant role in the solubilization of inorganic phosphate and mineralization of organic phosphates (Mahmood et al. 2001; Tarafdar and Marschner 1994a; Tawaraya et al. 2006). Moreover, there are many evidences which are related to inorganic phosphate (Pi) transporter and its expression in the external hyphae of AM fungi, which is important in the uptake of P and transfer from the AM fungi to plants (Tarafdar and Marschner 1994b; Harrison and van Buuren 1995).

The mechanism for the solubilization of P was reported by Gharu and Tarafdar (2004) and Chen et al. (2006) (Fig. 6.2). The organic P usually accounting for 30–65 % of total P in soils must be converted to inorganic or low molecular weight organic acids before they could be assimilated by plants. The different forms of organic P in soils are inositol phosphatases, phosphoesters, phosphodiesters, and phosphotriesters. A large part of the organic P is present in the form of inositol phosphatases (phytate) (Rodriguez and Fraga 1999; Zimmermann 2003). Phosphatases refer to any enzyme that can hydrolyze phosphate esters and anhydrides including phosphoprotein phosphatases, phosphodiesterases, diadenosine tetraphosphatases, exonucleases, 5′-nucleotidases phytases, phosphomonoesterases, alkaline, and acid phosphatases (Zimmermann 2003).

The role of phosphatases in the mobilization of phosphorus, originating from the organic soil sources, by AM fungi and PGPR has been reviewed by several researchers (Tarafdar and Marschner 1994b; Idriss et al. 2002; Rodriguez and Fraga 1999). Moreover, molecular tools have been also used to elucidate plant-microbe interactions in phosphorus metabolism (Rodriguez et al. 2000; Chen et al. 2006). Minder et al. (1998) indicated that the genetic control system of phosphate uptake is based on the phosphate regulatory protein *PhoB*, which is mediated by the transmembrane sensor protein *PhoR*. They have suggested that phosphorylated *PhoB* acts as a transcriptional activator to the *Pho* box in the promoter region of genes belonging to the *Pho* regulon and concluded that the product of the *PhoB* gene regulates the cellular response to environmental phosphate limitation. A study on *Bradyrhizobium japonicum* and soybean concluded that *PhoB* is responsible only for phosphate-limited growth, not for symbiotic nitrogen fixation (Minder et al. 1998). Subsequently, Ruiz-Lozano and Bonfante (1999) have investigated the role of *Burkholderia* sp. and AM fungi in P metabolism and found that through shunting off mechanism, the phosphorus is transferred from fungus to the plant. Ruiz-Lozano and Bonfante (1999) also characterized an operon *Pst*-like system in *Burkholderia* similar to *E. coli* phosphorus uptake by *Gigaspora margarita*. By the possession of a DNA region with nitrogenase-coding genes (*nif* operon), the *Burkholderia* sp. could also affect nitrogen uptake. The approaches are promising to elaborate the role of the interaction of bacteria and AM fungi in the nutrient uptake (Akhtar 2011).

Availability of Other Nutrients

Microbial inoculants have shown their influence towards the uptake of other nutrients besides N and P (Peix et al. 2001; Khan 2005; Wu et al. 2005; Adesemoye et al. 2008). Khan (2005) observed that inoculation of *Pseudomonas* and *Acinetobacter* strains resulted in enhanced uptake of Fe, Zn, Mg, Ca, and K by crop plants. In another study, inoculation of chickpea and barley with strains of *Mesorhizobium mediterraneum* significantly increased the K, Ca, and Mg in addition to P and N in both crop plants (Peix et al. 2001). Kohler et al. (2008) have demonstrated the effects of PGPR (*Pseudomonas mendocina*) and AM fungi (*G. intraradices* and *G. mosseae*) on uptake of N, P, Fe, Ca, and Mn in lettuce under three different levels of water stress. Sheng and He (2006) reported improved uptake of K by the inoculation of *Bacillus edaphicus* and suggested that the production of organic acids (citric, oxalic, tartaric, succinic, and α-ketogluconic) by this strain leads to chelation of metals and mobilization of K from K-containing minerals. Similarly, Giri and Mukerji (2004) reported a significant increase in Mg concentrations in the seedling of *Sesbania aegyptiaca* and *Sesbania grandiflora* by the application of *Glomus macrocarpum*, compared to non-mycorrhizal seedlings in saline soil. Liu et al. (2000) reported an increase in acquisition of Fe, Zn, Cu, and Mn by mycorrhizal fungi in maize. Moreover, sulfur uptake has been achieved through sulfur oxidization (Banerjee et al. 2006) and iron uptake through siderophore-producing bacteria (Bakker et al. 2007). Biswas et al. (2000) reported a significant increase in Fe uptake in lowland rice through inoculation of *Rhizobium leguminosarum* bv. *trifolii* and suggested that the increase in uptake of Fe, P, and K was associated with higher nitrogen rates.

Plant Interactions for Remediation of Contaminated Soils

Soil is an important habitat for thousands of organisms including a variety of fungi, actinobacteria, algae, protozoa, and different types of bacteria. These microorganisms in association with soil particles or soil organic matter in the rhizosphere are essential for the plant. Plant-microbe interactions are now being intensively investigated for decontamination and remediation processes. With the discovery of a number of soil microorganisms that are capable of degrading xenobiotic chemicals including herbicides, pesticides, solvents, and other organic compounds, microbial degradation might provide a reasonable and effective means of disposing toxic chemical wastes. Due to the sensitivity and the sequestration ability of the microbial communities towards the heavy metals, microbes have been used for bioremediation of sites contaminated with them (Hallberg and Johnson 2005; Kao et al. 2006; Umrania 2006). Although microbial communities in metal-polluted bulk soils have been studied, there are a limited number of studies on the composition of microbial community in the plant rhizosphere growing in soils highly polluted with heavy metals (Dell'Amico et al. 2005).

Phytoremediation

Phytoremediation is a kind of bioremediation technique that uses plants to manage or remediate polluted soils. It is an emerging and cost-effective technology. It could be defined as "the elimination, attenuation, or transformation of polluting or contaminating substances by plants into their less toxic forms" (Vidali 2001; Kavamura and Esposito 2008). It can be used as in situ or ex situ technology. Soils could be contaminated with thousands of contaminants varying in their composition and concentration through inadequate residue disposal, accidental wastes, and inappropriate use (Knaebel et al. 1994). These contaminants include nitrates, phosphates, and perchlorates (Nozawa-Inoue et al. 2005); explosives such as hexahydro-1,3,5-trinitro-1,3,5-triazine and octahydro-1,3,5,7-tetranitro-1,3,5,7-tetrazocine (Kitts et al. 1994); monoaromatic hydrocarbons like benzene, toluene, ethylbenzene, and xylene (Rooney-Varga et al. 1999); polycyclic aromatic hydrocarbons (Wang et al. 1990); herbicides such as diuron, linuron, and chlorotoluron (Fantroussi et al. 1999); and heavy metals (Glick 2003).

In case of soil remediation, several factors such as soil characteristics, type, and concentration of contaminants should be considered (Boopathy 2000; Sheoran et al. 2008). The remediation of the harmful contaminants from the soil by plants is an emerging alternative to restore the contaminated sites (Singh et al. 2003; Paquin et al. 2004; Vassilev et al. 2004; Shah and Nongkynrih 2007; Padmavathiamma and Li 2007; Rajkumar and Freitas 2008; Lone et al. 2008; Akhtar et al. 2013). Phytoremediation can be classified according to the method and the nature of contaminants (Lasat 2002; Eapen et al. 2003; Newman and Reynolds 2004; January et al. 2008). The various methods used for the phytoremediation are discussed below (Fig. 6.3).

Phytoextraction

Plants can absorb the concentrated metals in their aboveground parts which can then be harvested. Brennan and Shelley (1999) found that plants have the capability to extract large concentrations of heavy metals into their roots, translocate them to the stem, and produce a large quantity of plant biomass.

Phytodegradation

It is also known as phytotransformation. In this process, plants degrade organic pollutants directly via their enzymatic activities. Some enzymes break down and convert ammunition wastes, others degrade chlorinated solvents such as trichloroethylene, and others degrade herbicides.

Phytovolatilization

Phytovolatilization refers to the uptake and transpiration of contaminants, primarily organic compounds, by plants. The contaminant, present in the soil solution, is taken up and modified by the plant and is released to the atmosphere through the plant leaves by evaporation or vaporization processes.

Phytostimulation

It refers to stimulation of rhizospheric microorganisms capable of degrading the contaminants by the growing roots releasing exudates/nutrients such as carbon sources. This method is useful in removing organic contaminants, such as pesticides, aromatics, and polynuclear aromatic hydrocarbons from soil and sediments (Ukiwe et al. 2013).

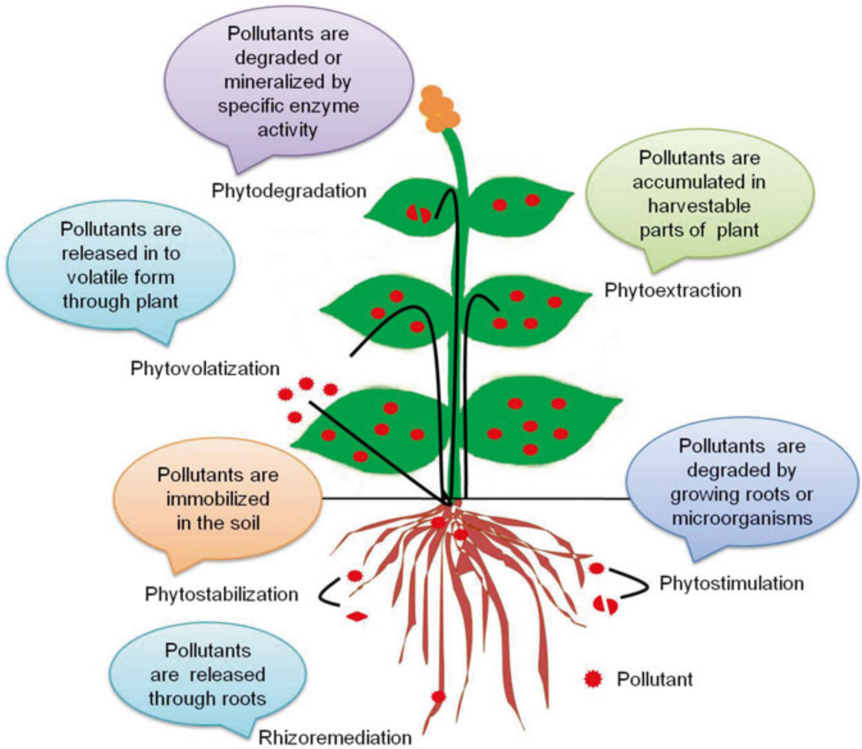

Fig. 6.3 Schematic diagram of different approaches of phytoremediation

Phytostabilization

In this method, the use of plant roots may limit the contaminant by reducing its mobility or leaching in the soil. Plants decrease the amount of water percolating through the soil matrix, which may act as a barrier and reduce the leaching of the contaminant. Phytostabilization can occur through sorption, precipitation, complexation, or metal valence reduction. It is helpful in the treatment of contaminated land areas affected by mining activities (Raskin and Ensley 2000). Phytostabilization is commonly used to treat the metal (arsenic, cadmium, chromium, copper, and zinc) contaminants (Kunito et al. 2001).

Rhizofiltration

It could be used for metals such as Pb, Cd, Cu, Ni, Zn, and Cr which are retained within the roots. It is useful for both terrestrial and aquatic plants for in situ or ex situ purposes. In this method, the contaminants do not translocate to the shoots. The terrestrial plants are more favored for rhizofiltration due to their fibrous and elongated root systems. The main limitation of this method is to adjust to the pH at regular intervals.

Rhizoremediation

In this method, microorganisms are utilized in combination with the plants (Jing et al. 2007). Generally organic pollutants with high hydrophobicity (hence, unable to be absorbed by the plant) are remediated by this method. Microbes play major role in this method. Plants mainly provide the microbes with nutrients and growth factors to proliferate (Siciliano and Germida 1998; Chaudhry et al. 2005).

Rhizoremediation of Organic Contaminants by PGPR

Initially, the PGPR were used for plant growth promotion and biocontrol of plant diseases, but now they are also being used for rhizoremediation of organic contaminants (Narasimhan et al. 2003; Huang et al. 2004, 2005). In contrast to inorganic compounds, microorganisms can degrade and mineralize organic compounds in association with plants (Saleh et al. 2004). Brazil et al. (1995) reported that the bacteria are capable of degrading a certain kind of organic pollutants such as polychlorinated biphenyls isolated from various locations and studied the encoding genes involved in this pathway. Rhizoremediation of various organic pollutants is known when a particular crop plant in combination with their known or unknown microbes are used as reviewed in detail by Kuiper et al. (2004).

Rhizoremediation of Metals by PGPR

A wide range of plants have been tested for their ability to take up high levels of metals by roots form soil and translocate these metals into the leaves and shoots. The use of PGPR as adjuncts in metal phytoremediation can significantly facilitate the growth of plants in the presence of high levels of metals (Zhuang et al. 2007; Glick 2010).

Rhizoremediation by Endophytic Microorganisms

Endophytic bacteria could be defined as bacteria colonizing the internal tissues of plants without causing infection or negative effects on their host (Lodewyckx et al. 2002). With the exception of seed endophytes, the primary site where endophytes gain entry into plants is via the roots (Pan et al. 1997; Germaine et al. 2004). The endophytes either reside inside the plants in specific plant tissues like root cortex and xylem or colonize the plant systematically by transport through the vascular system or apoplast (Mahaffee et al. 1997; Quadt-Hallmann et al. 1997). Endophytic bacteria have been isolated from a variety of healthy plant species ranging from herbaceous crop plants (Lodewyckx et al. 2002; Malinowski et al. 2004; Mastretta et al. 2009), different grass species (Zinniel et al. 2002; Dalton et al. 2004), to woody tree species (Cankar et al. 2005; Moore et al. 2006; Taghavi et al. 2009).

Pseudomonas, *Burkholderia*, and *Enterobacter* are amongst the most common genera of cultivable endophytes (Mastretta et al. 2006). In addition to their beneficial effects on plant growth, endophytes have also been used in phytoremediation (Weyens et al. 2009). Idris et al. (2004) investigated the endophytes from *Thlaspi goesingense*, a hyperaccumulator of Ni in both cultivation-dependent and cultivation-independent techniques. They concluded that the endophytes used in the cultivation-independent techniques have the potential to tolerate higher concentration of Ni than rhizospheric bacteria. This kind of technique is very promising in the phytoremediation of heavy metals, but the actual mechanisms is not well understood, and its application in the phytoremediation of heavy metal is expensive and very complicated (Weyens et al. 2009).

Mycorrhizoremediation

In this advanced approach, symbiotic AM fungi could be used for phytoremediation (Huang et al. 2004; Khan 2006). AM fungi have the potential to efficiently explore the soil volume (Meharg and Cairney 2000). Mycorrhizal association exhibits substantial resistance against the toxic metals (Leyval et al. 1997; Meharg and Cairney 2000) and organic compounds such as m-toluate and petroleum polycyclic aromatic hydrocarbons (Sarand et al. 1998, 1999; Leyval and Binet 1998).

In addition to their protective behavior, mycorrhizae may contribute to resistance of plant-microbial associations through enhanced degradation of organic pollutants in the mycorrhizosphere and lowering the bioavailable concentration of heavy metals in soil (Meharg and Cairney 2000). It is evident from the reports of the earlier researchers that the AM fungi have the potential to increase the uptake of various heavy metals in plants (Liao et al. 2003; Whitfield et al. 2004; Liu et al. 2005; Leung et al. 2006). However, some other studies showed there is no effect of AM fungi or even decreased concentrations in plant tissues (Trotta et al. 2006; Wu et al. 2007). On the basis of contrasting results, it is very difficult to evaluate the potential of mycorrhizal fungi in the uptake of heavy metals in field experiments (Liu et al. 2005; Leung et al. 2006; Wu et al. 2007; Wenzel 2009).

Bioremediation by Microbes

In this process, microorganisms are used for degradation or removal of contaminants from the soil. This method of degradation or removal of environmental contaminant through microbial activity is cost-effective and environmentally safe compared to other physicochemical methodologies used for bioremediation (Akhtar et al. 2013). It could be used both as in situ and ex situ methods. However, there are many loopholes and black holes in this technology such as the use of inappropriate microbial system for removal of metal toxicity, low or inactive microbial populations, or presence of complex pollutant mixtures. The rate and extent of biodegradation depend upon many factors which have been summarized in tabular form (Table 6.4).

For endurance under metal-stressed environment, PGPR have evolved several mechanisms by which they can immobilize, mobilize, or transform metals rendering them inactive so as to tolerate the heavy metal ions. These mechanisms include: (1) exclusion, the metal ions are kept away from the target sites; (2) extrusion, the metals are pushed out of the cell through chromosomal/plasmid mediated events; (3) accommodation, metals form complex with the metal binding proteins or other cell components; (4) bio-transformation, toxic metal is reduced to less toxic forms; and (5) methylation and demethylation. Thus, in general, the immobilization and mobilization are the two main techniques used for the bioremediation of metals by microbes.

Table 6.4 Some major factors affecting the bioremediation process

Factors	Affect
Microbial	Growth until critical biomass is reached, mutation and horizontal gene transfer, enzyme induction, enrichment of the capable microbial populations, and production of toxic metabolites
Environmental	Depletion of preferential substrates, lack of nutrients, and inhibitory environmental conditions
Substrate	Too low concentration of contaminants, chemical structure of contaminants, toxicity of contaminants, and solubility of contaminants
Biological aerobic vs. anaerobic process	Oxidation/reduction potential, availability of electron acceptors, and microbial population present in the site
Growth substrate vs. co-metabolism	Type of contaminants, concentration, alternate carbon source present, and microbial interaction such as competition, succession, and predation
Physicochemical bioavailability of pollutants	Equilibrium sorption, irreversible sorption, and incorporation into humic matters
Mass transfer limitations	Oxygen diffusion and solubility, diffusion of nutrients, and solubility and miscibility in water

Immobilization Techniques

Immobilization is a technique used to reduce the mobility of contaminants by altering the physical or chemical characteristics of the contaminant. This remediation approach can utilize microorganisms to immobilize metal contaminants. It is usually accomplished by physically restricting contact between the contaminant or by chemically altering the contaminant (Evanko and Dzombak 1997, Mulligan et al. 2001; Akhtar et al. 2013). Chemical reagents and bacterial reagents assist with the immobilization of metal contaminants. Most sites contaminated with metals use the solidification and stabilization approach to immobilize metals. Solidification treatment involves mixing or injecting chemical agents to the contaminated soil. The prominent mechanism by which metals are immobilized is by precipitation of hydroxides. The chemical composition of the site, the amount of water present, and the temperatures are all factors important to the successful use of the solidification/stabilization mechanisms (Evanko and Dzombak 1997; Wuana and Okieimen 2011). The stabilization and solidification technique is achieved by mixing the contaminated material with appropriate amounts of stabilizer material and water. The mixture forms a solidified matrix with the waste. The stabilization and solidification techniques can occur both in situ and ex situ. In situ is preferred for volatile or semi-volatile organics. The in situ process is useful for treating surface or shallow contamination.

Mobilization

Microorganisms can mobilize metals through autotrophic and heterotrophic leaching, chelation by microbial metabolites and siderophores, methylation, and redox transformations. Heterotrophic leaching is when microorganisms can acidify their environment by proton efflux thus leading to the acidification resulting in the release of free metal cations. Autotrophic leaching is when acidophilic bacteria retrieve CO_2 and obtain energy from the oxidation of the ferrous iron or reduced sulfate compounds, which causes solubilization of metals (Agrawal 2005). Siderophores are specific iron-chelating ligands and are able to bind to other metals, such as magnesium, manganese, chromium, and gallium, and radionuclide, such as plutonium (Akhtar et al. 2013). Methylation involves methyl groups that are enzymatically transferred to a metal, forming a number of different metalloids. Redox transformations can allow microorganisms to mobilize metals, metalloids, and organometallic compounds by reduction and oxidation processes. There are various metal-mobilization techniques that can also occur in nature (Gadd 2004).

Conclusion

The rhizospheric microorganisms can influence plant growth, nutrition availability, disease susceptibility, resistance towards heavy metals, and various abiotic stresses. Plant growth attributes could be limited by the unavailability of essential elements or the presence of toxic elements. The interactions between plant roots and microorganisms present in the rhizosphere assist them to acquire essential mineral nutrients from the soil and prevent the accumulation of toxic elements. Amongst various rhizospheric microorganisms, free-living and symbiotic nitrogen-fixing bacteria contribute a lot to meet this demand. In the presence of N-free or low nitrogen content, the rhizospheric bacteria accomplish associative nitrogen fixation and thus provide essential nutrients to plants. Moreover, the phosphate-solubilizing bacteria have the capacity to convert inorganic unavailable P form to soluble forms available to plants.

Of the various microorganisms present in the soil, the rhizospheric bacterial community has the potential to increase the plant growth and minimize the disease severity and also is useful in the degradation or removal of toxic elements from water, soil, sludge, and process-waste stream through bioremediation. These technologies could be broadly classified as ex situ and in situ. The ex situ technologies are applied for the physical removal of the contaminated materials for treatment process, while in situ techniques for the treatment of contaminated materials in place. Plant-microbe interactions can thus be applied for diverse aspects by the development of sustainable technologies for enhancement of crop yield, suppression of phytopathogens, degradation of pollutants, and remediation of contaminated sites.

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