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Microbial Ecology at Rhizosphere: Bioengineering and Future Prospective

4

Shyamalina Haldar and Sanghamitra Sengupta

Abstract

Rhizosphere, the interface between soil and plant roots, is a chemically complex environment which supports the development and growth of diverse microbial communities. Studies in rhizosphere science have undoubtedly improved our ability to steer the knowledge into technological applications in agricultural industry, ecological engineering, and nature restoration. In this chapter we provide a holistic perception of rhizosphere functioning with a highlight on the ecological drivers that promote colonization of coherent functional groups of microorganisms influencing plant life through several direct and indirect mechanisms. We also discuss how the activities of the indigenous microbes from rhizosphere may be exploited toward developing profitable techniques or methods in sustainable agriculture, biotechnology, and environmental management. In this context, we emphasize on the need for high degree of innovation and active collaboration between basic research and technology development wings for the best use of the knowledge in order to meet the increasing global demand for food, fiber, and bioenergy.

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4.1   Introduction

Rhizosphere represents one of the most diverse habitats on our planet (Trabelsi and Mhamdi 2013). It is technically defined as the soil adhering to the root which is chemically enriched with the substances released from the plants and stimulate microbial growth and activities. Over the past two decades, a growing body of empirical research has shown that ecological and biochemical processes in the rhizosphere are mediated by intricate arrays of direct and indirect interactions occurring between the plants and residing microorganisms which cumulatively make the microenvironment unique, physically, chemically, and biologically (Fig. 4.1). Rhizosphere processes, at a global scale, utilize approximately half of the total energy fixed by photosynthesis in terrestrial ecosystems, contribute roughly 50 % of the total carbon dioxide emitted from terrestrial ecosystems, and mediate virtually all aspects of biogeochemical transformation, biomass turnover, and nutrient cycling (Hopkins et al. 2013). Plants and the rhizobiome together contribute to a significant extent, for the preservation of biodiversity and ecological sustainability of urban green infrastructures (Weyens et al. 2015). Consequently, there is a worldwide effort to comprehend and model rhizosphere functioning using multiscale information generated through genetics, genomics, metabolomics, and system biological approaches for effective translation of this knowledge for the upliftment of human health and living (Weyens et al. 2015). Fortunately for us, due to recent technological advances, the paradigm of microbiology has shifted toward understanding and
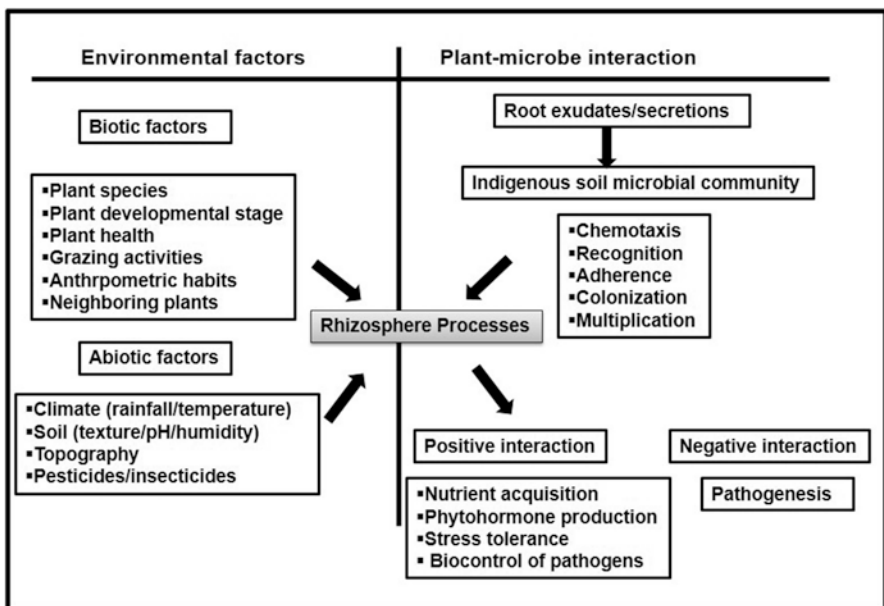

Fig. 4.1 Physical, chemical & biologial interactions affecting plant's rhizosphere

predicting the function of rhizo-consortia instead of a single dominant species. We are beginning to understand how plant systems interact with their environment, monitor biotic or abiotic stresses, and battle diseases in the field by modulating the associated microbial forum (Hill et al. 2013). Efforts have been initiated to engineer the knowledge into practical application such as production of sustainable food, fiber, and energy, maintenance of forest ecology and biodiversity, management of water resources, and alleviation of climate change (Mark et al. 2006; Jones 2008; Dessaux et al. 2016). In this book chapter, we summarize this worldwide endeavor by throwing light on the mechanistic and the ecological knowledge of the rhizosphere accumulated so far with a focus on agro-economy, biotechnology, and environmental management.

4.2   Microbial Ecology in the Rhizosphere

Following the colonization in the terrestrial ecosystem, "plants" as sessile organisms communicate with innumerable microorganisms residing in its ecosystem. The most significant part of this operates belowground, in general, and in the rhizosphere, in particular. Studies on rhizosphere date back to 1904, when Lorenz Hiltner (1904) observed that microbes are more abundant in rhizosphere than they are in distant soil environment. Since then a huge body of literature has accumulated and unequivocally demonstrated that this narrow zone of soil is a highly favorable site for microbial activities. It may contain up to 10^{11} microbial cells per gram root and more than 30,000 prokaryotic species (Egamberdieva et al. 2008; Mendes et al. 2011). Rhizosphere may be imagined as a cloud of microbes, vital for plant growth and survival, surrounding the plant root. Microbial proliferation at the plant roots and root–soil interface is supported by diverse varieties of root exudates (Badri et al. 2009). It is estimated that the collective genome of the rhizosphere microbial community is much larger than that of the plant itself and hence affectionately referred to as the plant's second genome (Berendsen et al. 2012). At present, the entire consortium of plants and associated microorganisms is perceived as a holobiont and is no longer recognized as "individual entities" (Dessaux et al. 2016).

4.2.1   Rhizosphere: A Platform for Microbial Growth

4.2.1.1 Rhizosphere as a Chemical Hotspot
Microbial colonization in rhizosphere is rooted to the phenomenon of "rhizosphere processes" which is collectively composed of various physicochemical and biological turnovers defined by the host plant through the uptake of minerals and water and subsequent release of nutrients and carbon dioxide, exudation, and secretion of an array of chemical compounds (Philippot et al. 2013). Significant advances in our knowledge about plant exudate chemistry and the impact of "rhizodeposition" on microbial growth at the root–soil interface have been made in the last few years (Smalla et al. 2001; Dunfield and Germida 2003; Nunan et al. 2005; Mougel et al.

2006). It may be surmised from these studies that many soil microorganisms remain dormant in the absence of organic input due to general carbon (C) limitation in normal soil (Owen et al. 2007). Growth of plants triggers an increase in the rate of turnover of soil organic matter (SOM) in the order of 20- to 30-folds around areas of exudation, and this pulse of organic input often fosters microbial activity and associated soil organic matter (SOM) turnover (Xiao et al. 2007). In contrast to bulk soil, rhizosphere is thus extremely nutrient rich due to the abundance of low molecular weight (LMW) compounds released during normal root cell metabolism (root exudates): both low and high molecular weight compounds that are synthesized for secretions (root secretions) and compounds released by plant cell lysis (Marschner 1995). Microorganisms thrive on these resources and form a plant-specific assemblage in the rhizosphere.

Mucilage secreted from the growing roots contains hydrated polysaccharides, organic acids, vitamins, and amino acids and can also bind to water molecules. This creates a well-hydrated environment supportive of microbial growth. Developing roots generally support fast-growing microorganisms like bacteria, whereas matured roots support slower-growing organisms such as fungi and actinomycetes; the latter produce less mucilage and fewer cell lysates due to the absence of border cells and emerging lateral roots and also leak less water due to the deposition of a water-impermeable layer around epidermal cells. Outward diffusion of nutrients and inward movement of salts and minerals during transpiration develop complex chemical gradients around the root and create a range of distinct microbial habitats. LMW carbon compounds such as sugar, organic acids, amino acids, and flavonoids are readily assimilated by microorganisms and play a primary role in regulating microbial community dynamics in the rhizosphere (Bais et al. 2006). Flavonoids, a diverse class of polyphenolic compounds, often serve as important chemical cues in mediating plant–microorganism interactions (reviewed by Shaw et al. 2006). Surfactant-active compounds such as carboxylic compounds in the root exudates have been found to increase the solubility of the heavy metals/toxic substances and make them bioavailable to root-colonizing microorganisms (Balseiro-Romero et al. 2014). Root volatiles include sulfur-containing compounds or the terpene (E)-b-caryophyllene which serve as foraging cues for parasitic entomopathogenic nematodes [EPNs] (Hiltpold and Turlings 2012; van Dam and Bouwmeester 2016). Organic phosphorus which is, in general, poorly available is solubilized through grazing by nematodes (Wenke et al. 2010). Phenolic compounds such as salicylic acid and gamma-aminobutyric acid (GABA) in the root exudates are suggested to send specific signals for soil bacteria, namely, *Sphingomonas*, *Methylobacterium*, *Frankineae*, *Variovorax*, *Micromonosporineae*, and *Skermanella* (Badri et al. 2013).

4.2.1.2 Factors Affecting Rhizo-Atmosphere

Much of our current understanding about rhizosphere incidences has emerged from studies on agricultural or horticultural crop plants: model species such as *Arabidopsis thaliana* (Bulgarelli et al. 2012) and *Medicago truncatula* (Kisiel and Kepczynska 2016) and a few noncultivated plant species such as arbuscular mycorrhizal associations (Bennett and Bever 2007). The excerpt from these findings points that plant

genetic makeup unequivocally plays a dominant role in the selection of rhizobacterial community. This is not surprising because the variety and amount of the compounds synthesized and released by roots are mostly under the plant's physiological and genetic control (Costa et al. 2006; Berg and Smalla 2009; Badri et al. 2009). Corroboratively root microbiome of plants grown in the same soil has been found to differ between plant species (Curlango-Rivera et al. 2013; Bonito et al. 2014) and between ecotypes, chemotypes, and genotypes within species (Micallef et al. 2009; Hill et al. 2013; Bulgarelli et al. 2013). To be more specific, plant-specific variation in root exudation is regulated both quantitatively and qualitatively by the root system architecture (RSA) which is determined by the inherent genetic factors and varies across plant species (Badri and Vivanco 2009). Secretion of phytochemicals and proteins from roots is an important way for plants to respond to various environmental factors and stresses (Walker et al. 2004; Bais et al. 2004). Root structure additionally affects oxygen pressure and carbon and nitrogen availability which in turn influences nitrogen transformation by soil microorganisms (Blossfeld et al. 2011). Furthermore, root growth changes the physical and chemical properties of the soil, including the mineral and organic content, the water potential, the pH, and the salinity.

The type and condition of soil also influence the nature of rhizodeposits. Nutrient deficiency is a major factor enhancing the secretion of metabolites by plant roots (Rengel and Marschner 2005). Besides, the presence or absence of particular minerals or toxic metals affects the composition of root exudation. For example, citric, malic, and oxalic acids are secreted to detoxify aluminum (Wang et al. 2006). Secretion of phenolic compounds is increased in phosphorus-deficient soils (Khorassani et al. 2011), while secretion of flavanones and flavones is enhanced in nitrogen-limiting conditions (Schultze and Kondorosi 1998). Mineral deficiency enhances the production of elicitors that influence root exudation. For example, potassium deficiency increases jasmonic acid-mediated defense responses (Schachtman and Shin 2007). Hypoxia due to high soil moisture causes an increased anaerobic respiration rate resulting in accumulation of ethanol, lactic acid, and alanine in the rhizosphere (Rivoal and Hanson 1994). Low temperature and light reduce secretion of root exudates. For example, the exudation of tannins and phenolic compounds in *Vicia faba* was greatly reduced at 4 °C compared to the amounts secreted at 30 °C (Bekkara et al. 1998). The root exudation process follows diurnal rhythms with exudation increasing during light periods (Watt and Evans 1999). In the root exudates from *Alnus glutinosa* (L.), the flavonoid content has been found to be increased under light conditions (Hughes et al. 1999). Root exudation is even affected by neighboring plant species. Quantity of glucosinolates in the root exudates is increased when *Arabidopsis* plants are grown at a higher density causing a shift of the rhizobiota toward the glucosinolate-utilizing microorganisms (Wentzell and Kliebenstein 2008). Root-induced pH changes in the rhizosphere influence bioavailability of phosphate and copper by modulating adsorption and precipitation of ions and soil minerals, respectively, and thereby shape the microbial ecology in the root environment (Bravin et al. 2009).

4.2.2 Microbial Community Structure

In general, the microbes take the advantage of the nutrients that the plant provides as discussed above, and in effect, they assist their host plant in making more essential nutrients (reviewed in Mendes et al. 2013). Therefore, microorganisms typically represent the largest fraction of belowground biomass. One gram of soil is thought to constitute tens of thousands of microbial "species" (reviewed in Kent and Triplett 2002). Microbes in rhizosphere can be broadly classified as bacteria, fungi, nematodes, protozoa, and actinomycetes. Of these, bacteria and fungi are most well documented.

4.2.2.1 Bacteria

The ratio of the microbial population in the rhizosphere (R) to that in the bulk soil (S), i.e., R/S value, is >=20 for the bacteria, while that for fungi and actinomycetes are 10 and 2–3, respectively (Bagyaraj and Rangaswami 2005). The overall proportion of aerobic bacteria is relatively less in the rhizosphere because of low level of oxygen due to root respiration. Rhizosphere is programmed to recruit wide range of bacterial genera, beneficial to the plants by using the signals from the host. The beneficial bacteria are collectively termed as plant growth-promoting rhizobacteria (PGPRs). The most common genera of bacteria observed in the rhizosphere include *Acinetobacter, Agrobacterium, Alcaligenes, Arthrobacter, Azospirillum, Azotobacter, Bacillus, Cellulomonas, Flavobacterium, Micrococcus*, *Mycobacterium, Pseudomonas*, and *Rhizobium*. PGPRs may be categorized depending on their modes of beneficial action into biofertilizers, phytostimulators, biopesticides, and elicitors of tolerance to abiotic and biotic stresses (Bhattacharyya and Jha 2012; Bhardwaj et al. 2014; Perez-Montano et al. 2014; Yang et al. 2009). A list of common beneficial bacteria is given in Table 4.1.

Biofertilizers directly promote plant growth by endowing plants with nutrients such as nitrogen, phosphorus, and trace elements (iron) which otherwise would have remained inaccessible to the plants. They are composed of *Rhizobium* sp., *Pseudomonas fluorescens*, *Trichoderma* sp. (e.g., *Trichoderma asperellum* and *Trichoderma hamatum*), and *Allorhizobium* sp. Of these, root nodule symbiosis established by *Rhizobium* sp. with legumes for nitrogen fixation has been vividly investigated (reviewed in Wang et al. 2012). Besides nitrogen, iron is another important element required for the growth of plants. However, it is essentially unavailable in aerobic environments, as it tends to form insoluble hydroxides at biological pH (Guerinot 1994). Rhizobia (*Bradyrhizobium japonicum*, *Sinorhizobium meliloti*, *Rhizobium leguminosarum bv. Viciae*, *Rhizobium ciceri*), fluorescent pseudomonads, *Enterobacter*, *Burkholderia*, and streptomycetes are capable of producing LMW compounds called siderophores that complex with ferric iron and several membrane-bound/periplasmic proteins (Neilands 1995; Crosa and Walsh 2002). This iron sequestration helps these bacteria to establish themselves in the rhizosphere and also to provide plants with soluble iron. *Bradyrhizobium japonicum* and *Sinorhizobium meliloti*, on the other hand, also help the plants to take up the natural siderophores (ferrichromes) present in the soil directly by forming heterologous

Table 4.1 Mechanism of action of plant growth-promoting rhizobacteria (PGPR) and biocontrol agents (BCAs)

Microbial species	Mechanism of action	References
PGPR (biofertilizers and phytostimulators)		
Rhizobia	Nitrogen fixation; inorganic and organic nutrient solubilization; plant growth regulator (IAA, gibberellins, cytokinines) synthesis	Ferguson and Mathesius (2014)
Pseudomonads	IAA production; siderophore production and phosphate solubilization	Ajilogba and Babalola (2013)
Firmicutes		
Burkholderia		Farag et al. (2013) and Ghosh et al. (2016)
Azotobacter sp.	Cytokinine production; nitrogen fixation	Leaungvutiviroj et al. 2010
BCA (biopesticides)		
Rhizobium sp.	Disease suppression (antibiosis, competition for iron, enhancing plant defense mechanism)	Dutta et al. (2014)
Pseudomonads	Systemic resistance induction; antifungal volatile production; induced systemic tolerance to high temperature and salinity; stabilization of soil aggregates; quorum quenching (QQ)	Ajilogba and Babalola (2013) and Farag et al. (2013)
Firmicutes (*Bacillus* sp.)		
	Induced systemic resistance (ISR); antifungal volatile production; quorum quenching (QQ); induced systemic tolerance (IST) to high temperature and salinity	Shrivastava and Kumar (2015)
Burkholderia	Induced systemic tolerance for drought by producing ACC-deaminase	Onofre-Lemus et al. (2009)
Azotobacter sp.	Oxidative stress tolerance through production of abscisic acid (ABA) and degradation of reactive oxygen species (ROS)	Marsalek and Simek (1992)

PGPRs are also endowed with biocontrol properties, while BCA can also stimulate direct plant growth

siderophores (Powell et al. 1983). Likewise, a large proportion of phosphorus exists in insoluble forms in the soil. Phosphate-solubilizing bacteria like *Enterobacter*, *Pantoea*, *Pseudomonas*, *Klebsiella*, *Cedecea*, *Cronobacter*, *Bacillus*, *Rhodococcus*, *Arthrobacter*, *Chryseobacterium*, *Delftia*, *Gordonia*, *Phyllobacterium*, and *Serratia* identified from the rhizosphere of various plants have shown the ability to solubilize inorganic soil phosphates, such as $Ca_3(PO_4)_2$, $FePO_4$, and $AlPO_4$, by synthesizing organic acids (citric, gluconic, lactic, succinic, and propionic acids), siderophores, and hydroxyl ions (Chen et al. 2006; Sharma et al. 2013).

Rhizobium, *Pseudomonas*, *Bacillus*, *Azospirillum*, *Enterobacter*, *Azotobacter, Pantoea*, and *Streptomyces* are grouped as *phytostimulators* by the virtue of their ability to produce phytohormones like indole-3-acetic-acid (IAA), gibberellic acid (GA3), and cytokines which directly enhance plant growth by modulating root

system architecture (Spaepen et al. 2007; Apine and Jadhav 2011; Duca et al. 2014). Coordination among the hormonal pathways is associated with overall development in plants. In addition, this is important for the maintenance of plasticity of plant morphogenesis essential for plants to respond to environmental cues (Hardtke et al. 2007). Gibberellins regulate cell elongation, cytokinins control cell proliferation, and auxin modulates both (Hardtke et al. 2007; Nakaya et al. 2002). Gibberellins act in collaboration with auxins to regulate the transition of root meristem cells from division to elongation (Hardtke et al. 2007). IAA and cytokinins regulate the root development by acting as a "control switch" between cell division and differentiation, thereby controlling the size of the organs (Barrada et al. 2015). Root morphogenesis and growth are basically controlled through a cross talk between these phytohormones where IAA increases the length and cytokinins maintain the length by inhibiting extra growth (De Vos et al. 2014).

Pseudomonas sp. (e.g., *P. fluorescens, P. cepacia, P. aeruginosa, and P. aureofaciens*) and *Bacillus* sp. (e.g., *Bacillus subtilis*) along with *Streptomyces* sp. are termed as *biopesticides* or *biocontrol agents* (BCAs) due to their role in inhibition of plant pathogens by producing hydrogen cyanide, 2,4-diacetylphloroglucinol, pyrrolnitrin, phenazine, oomycetes, and other compounds and thereby conferring protection against diseases (Kwak and Weller 2013; Haas and Keel 2003). BCA also inhibits the growth of pathogenic bacteria directly by quorum quenching. N-Acyl-homoserine lactone (AHL), an important molecule for cell to cell communication and used by several plant pathogens to establish virulence, is degraded by N-acyl-homoserine lactonase (AHL-lactonase), produced by *Bacillus* sp. Fluorescent pseudomonads can suppress the growth of pathogens by efficiently competing with them for the siderophores. Pyoverdines, produced by pseudomonads have a very high affinity toward iron in comparison to other microbes and thereby can limit the availability of iron for the pathogens in the rhizosphere (Cezard et al. 2015).

The other groups of rhizobacteria (*Burkholderia* sp., *Enterobacter* sp., *Rhizobium* sp.) assist plants to tolerate stress due to accumulation of reactive oxygen species and 1-aminocyclopropane-1-carboxylate (ACC). The latter molecule is an intermediate in ethylene biosynthesis. Ethylene is activated under nutrient stress and is harmful for the plants during post-harvest phases (Khan et al. 2015). *Bacillus subtilis* and *Achromobacter piechaudii* enhance salinity tolerance in plants growing in coastal regions, while *Paenibacillus polymyxa* and *Rhizobium tropici* have been reported to provide tolerance to drought stress in *Arabidopsis*, tomato and common bean (Mayak et al. 2004; Zhang et al. 2008; Timmusk and Wagner 1999; Yang et al. 2009).

4.2.2.2 Fungi

Both symbiotic and pathogenic fungi reside in the rhizosphere. One gram of rhizosphere soil harbors 10^5–10^6 organisms. Arbuscular mycorrhizal fungi (AMF), belonging to *Glomerales*, are one of the oldest groups of fungi that have been hypothesized to form the most primitive interaction with plant roots. This multitrophic symbiosis is present ubiquitously in the terrestrial plants, both from natural

and agricultural ecosystems, including gymnosperms, ferns, angiosperms, halophytes, hydrophytes, and xerophytes. Therefore, the beneficial role of AMF in biofertilization and bioremediation has been widely explored (reviewed in Lee et al. 2013). The beneficial outcome of the root–AMF association is mutually determined by the microbial consortia and soil chemistry (Khan 2006). The positive effect of AMF on plant physiology is modulated in the presence of specific microbe–microbe interaction. For example, co-inoculation with mycorrhization helper bacteria (MHB) such as *Bacillus* sp. in nutrient-poor soils has been found to improve the mycorrhizal effects (Vivas et al. 2003). AMF improve the productivity, biomass and diversity of plants by mineral sequestration (phosphorus scavenging and nitrogen acquisition), nutrient acquisition, and increased tolerance of the plants to abiotic stresses [drought/salinity resistance] (Lenoir et al. 2016; Porras-Soriano et al. 2009). In addition, AMF alter the overall microbial activity in the soil by modulating the rhizodeposits and improving the soil quality through immobilization of heavy metals (Yang et al. 2015). The wide surface area of the extra-radical mycelium and the synthesized iron-containing protein, "glomalin," by AMF, cooperatively determine the beneficial activities of AMF. Glomalin also contributes to the sequestration of toxic elements to enhance survival rate of the plants in polluted soils (Khan 2006). Glomalin has a role in the stabilization of soil aggregates leading to an improved penetration of the soil by water and air and also rendering an enhanced resistance to soil toward erosion (Rillig and Mummey 2006). AMF may act as a biocontrol agent by protecting the host plant against biotic stresses such as plant-parasitic nematode (PPN) infection by induced systemic resistance (ISR) and direct competing with the nematodes for space and nutrients (Schouteden et al. 2015). Increased rate of root respiration and respiratory acclimation due to AMF colonization in tropical plants is also reported. This indicates a role of AMF in terrestrial organic carbon influx as well (Fahey et al. 2016).

A common mycorrhizal network (CMN) is sometimes shared among the plants. AMF in this instance contribute to the transfer, distribution, and partitioning of carbon, nitrogen, phosphorus, and water from source (resource-rich plants) to sink (resource-poor plants) (Walder et al. 2016). This net translocation offers multiple benefits to the plants under environmental stresses not only by providing an access to resources from other plants but aiding to a speedy revival from the periods of rigorous water stress and protecting against pathogens (Babikova et al. 2013). AMF can also act as a support system for seedling establishment and can influence plant invasion success (Klironomos 2002). Recent observations have shown that the co-occurrence of complementary diverse AMF species among the plants in a single region helps in increased plant to plant facilitation, an important ecological process practiced by the woody plants to establish themselves in semiarid areas (Montesinos-Navarro et al. 2012). However, species richness and genetic variation among AMF is the major factor influencing plant species diversity and ecosystem functioning (van der Heijden et al. 2006). Conversely, response to AMF inoculation is also dependent on the genotype of plants. But this plant genotype-dependent AMF colonization has been explored inadequately to date (Montes-Borrego et al. 2014). In natural systems, among the AMF, *Glomus* sp. has been most comprehensively

studied for their pertinent role in plant productivity as biofertilizers and BCA (Labidi et al. 2015). Another widely studied AMF species in pot cultures is *Rhizophagus irregularis* (Tisserant et al. 2013). Nevertheless, recent advancements in "omics" techniques have helped to assess a huge number of both active and spore-forming AMF taxa from the soil, indicating that molecular diversity of soil AMF is enormous and thus might be manipulated toward sustainable agriculture and phytoremediation (Davison et al. 2012).

Trichoderma sp. is another important fungal BCA that combats with plant pathogens via multifarious mechanisms including competition, antibiosis, induced resistance, and parasitism and thereby offer an indirect beneficial effect on plant health (Zhang et al. 2015a, 2016). Many species of *Trichoderma* have been reported to exert direct effects on plant growth through solubilization of plant nutrients and/or better uptake of macro- and micronutrients and through production of plant growth factors (Li et al. 2015). However, our knowledge about *Trichoderma* sp.-mediated plant growth promotion is still limited.

4.2.2.3 Others

Although bacteria and fungi form the most significant members of the microbial consortia in rhizosphere, the other micro-/macroorganisms such as nematodes, protozoa, and oomycetes are also present. This latter group of species is mainly marked for their pathogenic invasion with the plants. Nevertheless, they too exert few microbial control properties to inhibit the growth of other pathogens like insects in the rhizosphere (Lacey et al. 2015).

The nematodes are complex eukaryotic invertebrate worms and mostly free-living which parasitize plants as well (reviewed in Kenney and Eleftherianos 2016). Among the nematodes, the genera *Steinernema* and *Heterorhabditis* have been identified as potent microbial control agents (MCA) that resist the growth of a number of pathogenic insects and pests in the rhizosphere. Beneficial EPNs are obligate parasites that destroy the insect very rapidly and hence are considered as one of the potent BCAs in several cropping systems (Ehlers 2003). Considerable progress toward the application of these EPNs in agriculture and pest management has been made in the past decade (Lacey et al. 2015). Secondary metabolites exuded from root tips play a dual role in attracting the nematodes so that the EPNs are selected over the pathogenic nematodes (Hiltpold et al. 2015). Studies have shown that insect herbivory at the roots could induce the secretion of volatile substances that attract EPN like *Heterorhabditis megidis* in many wild and cultivated plants, and thus this was adopted as an important plant defense mechanism against insects (Rasmann et al. 2005; Ali et al. 2010).

Protozoa, the unicellular animals, feed on microorganisms and form a ubiquitous group of rhizo-fauna. Protozoa by virtue of their grazing activities stimulate microbial decomposition and stimulate the release of organic matter and supplies plants with adequate nitrogen which otherwise would have remained limitedly accessible. Increased availability of nitrogen benefits AMF which transport it via the hyphae to the internal roots. The grazing also fosters rapid transportation of photosynthates from aboveground to belowground roots. In this process, the protozoa subsequently

interact with AMF and strengthen the interaction by controlling the nutrient supply (Koller et al. 2013a, b).

Frankia, nitrogen-fixing *Actinobacteria* that form symbiotic association with actinorhizal plants, has a potential role in increasing soil fertility and thereby enhancing the plant productivity in degrading and nitrogen-limiting soils (Diagne et al. 2013). This actinorhizal association is very productive toward maintenance of soil stability and henceforth facilitates the establishment and development of subsequent plant communities in disturbed landforms (Gtari et al. 2012). *Frankia* indirectly influences the plant productivity mitigating the adverse effects of salinity, drought, and contamination of heavy metals in degraded lands. As a whole, this association considerably enhances the plant growth, nitrogen content in roots and shoots, overall biomass, and survival rate of the plants (Diagne et al. 2013).

4.3 Bioengineering: Turning New Knowledge into Useful Societal Benefit

Demand for food, fiber, fuel, and other amenities will continue to grow as a result of population growth and rising incomes. To meet up these mounting demands, the stress on the natural resources and environment is leading to the resource depletion and environment destruction. Sustainable intensification is proclaimed to be only alternative to overcome this problem (Gregory et al. 2013). The goal of sustainable intensification is to maximize agricultural output from existing farmland while minimizing pressure on the environment. To accomplish this, an integrative approach coalescing biological science with community ecology is needed (Reynolds et al. 2014). In this "omics" era of new molecular tools and biotechnological advances, the knowledge accrued from basic research is expected to contribute more meaningfully to the development of more sustainable systems of intensive production (Ryan et al. 2009).

4.3.1 Rhizosphere Engineering

"Rhizosphere engineering" refers to the manipulation of a plant's root and surrounding milieu with a view to create a "biased" environment that will specifically enhance the crop productivity and plant survival (Ryan et al. 2009). In nature, plants themselves can adapt to any unfavorable environment by developing a variety of strategies; one of them being the modulation of rhizosphere chemistry. The knowledge of plant's inherent mechanisms is basically applied for any kind of "rhizosphere engineering/management." The selection of appropriate crop species, soil amendments, introduction of beneficial microorganisms, and genetic modification of plant and microbial activities are the fundamental components of rhizosphere engineering (Ryan et al. 2009). The benefit of managing rhizosphere is multifold. It not only paves the way to increased production of food/fiber/fuel but also results in diminished dependence on agrochemicals through replacement of their functions with

beneficial microbes, biodegradable biostimulants, or transgenic plants. As a consequence, the environmental and ecosystem integrities are preserved. Bioremediation is another aspect of rhizosphere engineering, which uses natural/genetically modified organisms/plants to degrade environmental pollutants and soil contaminants to restore the environmental and the ecological balance (Bisht et al. 2015). Rhizosphere engineering has emerged as an important tool to provide a cost-effective and environmentally sustainable "green technology" to address several global problems due to population growth. Research has confirmed a considerable progress in this field to date but still holds promise for further development (Ryan et al. 2009).

4.3.2   Rhizosphere Engineering and Agriculture

The goal of plant–microbiome engineering is to stimulate the wide spectrum of interaction among the phytomicrobiome toward overall enhanced beneficial outcome for the plant (Quiza et al. 2015). The two major aspects that are primarily taken care of are irrigation and application of fertilizers. The latter usually shifts the soil microbiome in and around the roots by altering soil pH. The acidic fertilizers (ammonium based) decrease the pH of the rhizosphere, while the basic fertilizers (nitrate based) enhance the alkalinity of the soil (Ryan et al. 2009). The practice of organic agriculture through input of organic fertilizers such as animal manure, biosolids, and composts is well established worldwide (Savka et al. 2002; Lim et al. 2015; Mazzola 2007). However, the lack of knowledge about the population of desired microorganisms in composts results in lack of reproducibility of the methods. Besides, this method adversely affects the soil acidity, salinity, and root colonization of certain species such as AMF. Moreover, biohazards due to toxic materials from biowaste and heavy metals used in compost composition cannot be overlooked (Quiza et al. 2015). To facilitate long-lasting modification in the rhizosphere, plant breeding and establishment of genetically modified (GM) organisms are alternative approaches for organic farming (Ryan et al. 2009). Genetic engineering has much to offer to bring about "new green revolution" in agriculture (Araus et al. 2014). Engineering of rhizosphere is mainly established through three potential means such as *plant-based methods*, *microbiome-based approach*, and *meta-organism-based techniques* (Quiza et al. 2015).

4.3.2.1 Plant-Based Methods
Plant-based strategies of rhizosphere engineering are achieved by either plant breeding (cultivar selection) or specific genetic modification of plant species. The basis for plant breeding is to develop and select cultivar lines that have the ability for (1) enhanced root exudation, (2) systemic resistance to disease and environmental stresses, and (3) increased rate of mutual symbiosis (Magalhaes et al. 2007; Campbell et al. 2002; Farrar et al. 2014). Genetically engineered plants are bestowed with a capacity of producing higher quantity of exudates that are highly specific for beneficial microorganisms (1) synthesizing quorum sensing/quorum quenching signal molecules, (2) altering soil organic anion efflux and transportation of the same

through the roots, (3) modifying soil properties (pH, salinity), and (4) promoting disease suppressiveness in soils (Koyama et al. 2000; Gevaudant et al. 2007; Yang et al. 2007; Mazzola 2007; Savka et al. 2002). These are achieved by introduction of genes of interest in selective plants from either the same species [cisgenic] or different species [transgenic] or deleting the genes that might repress different physiological processes [subgenic] (Wang et al. 2014).

The first genetically modified crop plant was an antibiotic-resistant tobacco plant (Fraley et al. 1999). Introduction of foreign germplasm into crops has been achieved by traditional crop breeders by overcoming species barriers. Farmers have widely adopted this technology to produce GM crops (GMC)/biotech (Bt) crops. Breeding lines of GM cultivars have been well established for the food crops including rice, wheat, potato, egg plants, tomatoes, soybeans, apples, beans, melons, papaya, and plums and for fiber and fuel crops such as cotton and grass and commercially important plants like tobacco (GM Approval Databse-ISAAA.org; www.isaaa.org, 2016 accessed). These crops have been modified for the traits including improved shelf life, stress resistance, herbicide resistance, pest resistance, disease suppression, production of useful goods such as biofuel or drugs, and ability to absorb toxins and for use in bioremediation of pollution. The recent aim of research is to develop locally important crop breeds for developing countries such as production of rice rich in vitamins and iron that may mitigate chronic malnutrition in Asian countries, virus-resistant sweet potato, insect-resistant cowpea, and brinjal in Africa (Bawa and Anilakumar 2013).

To date, most genetic modifications target the properties of aboveground parts of plants. However, recently root-specific modifications have been attempted in the plants like *Arabidopsis* (30 %), tobacco (14 %), rice (11 %), maize (8 %), *Medicago* (5 %), and potato and tomato (both 4 %) (Kabouw et al. 2012). This is possible due to accumulating knowledge on plant root properties and rhizosphere processes (Perez-Alfocea et al. 2011). Drought-resistant transgenic rice lines have been developed by introducing auxin-transporting genes with a root-specific promoter (Jeong et al. 2010), while in another study salt stress-resistant rice has been developed through introduction of *Arabidopsis* gene (AtHKT1) that is accountable for sequestering Na+ in roots (Plett et al. 2010). A decrease in nematode abundance in rhizosphere was recorded in GM rice and potato that constitutively expressed a proteinase inhibitor for nematode control (Kohli et al. 1998; Cowgill et al. 2002). Transgenic lines of potato and tobacco have been established with the property of "quorum quenching" by transforming with quorum sensing signal (NAHL) degrading/synthesizing genes from *Bacillus* sp. and *Yersinia enterocolitica* (Dong et al. 2001; Fray et al. 1999). The transgenic variety of potato could directly inactivate quorum sensing molecules and is tolerant to the pathogen *Pectobacterium*. The transgenic tobacco could synthesize bacterial quorum sensing signal molecules and complemented biocontrol ability of *Pseudomonas aureofaciens*, defective in NAHL synthesis. The genetic transformation of crops to produce insecticidal proteins from the soilborne beneficial bacterium, *Bacillus thuringiensis* (Bt), is now one of the most important elements of pest control management system. Insect-resistant Bt rice (*Oryza sativa*) lines, maize (sweet corn), and cotton have been developed leading to increase in the production of these crops with reduced pesticide application

worldwide (Yang et al. 2011; Abbas et al. 2013; Blanco 2012). Transgenic lines of *Arabidopsis* (AVP1) and *Nicotiana tabacum* (PMA4) with modified H+−ATPase coding gene have been established with enhanced H+ efflux capabilities from roots, salinity resistance, phosphate mineralization, drought resistance, and auxin uptake (Yang et al. 2007; Gevaudant et al. 2007). Transgenic lines of *Medicago sativa, Brassica napus, Hordeum vulgare* (barley), sorghum, carrot, rice, tomato, and tobacco plants have also been established by transformation with genes encoding proteins for synthesis of citrate (citrate synthetase), extrusion of multidrug and toxic compound (MATE), and transport of malate (i.e., Al^{3}+-activated malate transporter gene or ALMT). The latter enhances the efflux of these anions from the roots and subsequently confers aluminum resistance and efficient phosphorus uptake (Koyama et al. 2000; Tesfaye et al. 2001; Delhaize et al. 2007). In recent times, the manipulation of regulatory genes (transcription factors or TFs) to establish stress-tolerant stable crops has emerged as an effective strategy. Transgenic rice, wheat, potato, apple, tobacco, sugarcane, alfalfa, and *Arabidopsis* with enhanced tolerance for drought, salinity, and cold have been developed with the capability of overexpressing TFs involved in regulating stress-responsive genes for abscisic acid (ABA)-dependent pathway or ABA-independent pathway (Wang et al. 2016a, b).

4.3.2.2 Microbiome-Based Approach

Microbiome-based approach involves either direct inoculation of individual microorganism or co-inoculation of mixed cultures of PGPR, AMF, ectomycorrhizal fungi (EMF), and endophytes to modulate crop productivity (Ping and Boland 2004; Ryan et al. 2009). PGPR with BCA promotes plant growth collaboratively through their abilities of biofertilization and phytostimulation through phosphate solubilization, siderophore production, nutrient and mineral uptake, and symbiosis for nitrogen assimilation: plant hormone production on one hand and disease suppression by inducing ISR in plants or through production of antifungal compounds (phenazines, pyoluteorin, and phloroglucinols), antibiotics (hydrogen cyanide, oligomycin, phenazine), and bacteriocins, on the other (Ping and Boland 2004; Paulin et al. 2009). Microbiome can also alter the plant metabolic profile toward producing better yield. However, this method of application of microbial inoculants into the soil requires the availability of cultured isolates and maintenance of their cultivability in soil (Quiza et al. 2015). An alternative strategy is to enhance plant performance through inoculation of recombinant microbial strains into the soil. The GM microorganisms (GMO) not only have an enhanced capability to specifically stimulate plant growth and kill pathogens, but they also stimulate the growth of members from indigenous soil community through transmission of genetic information by horizontal gene transfer [HGT] (Quiza et al. 2015). PGPR/BCA activities are also enhanced in GMO. The first report for GMO was *chiA*-introduced heterologous bacteria. This engineered species degrade chitin from fungal cell membrane to impart suppression of fungal infection. Engineered strains of *Escherichia coli* and *P. fluorescens* containing *chiA* could effectively control the infections caused by *Sclerotium rolfsii* in bean and *Fusarium oxysporum* f. sp. *redolens* and *Gaeumannomyces graminis* (*G. graminis*) var. *tritici* in wheat, respectively (Shapira

et al. 1989). Transformation of ACC-deaminase gene, *acdS*, from *P. putida* into *P. fluorescens* CHA0 strains improved phytostimulation in canola seedlings and disease resistance in cucumber against *Pythium* sp. (Wang et al. 2000). A number of studies have shown that constitutive production or overproduction of antibiotics/antifungal compounds by engineered bacterial strains (*P. fluorescens* Q2–87; *P. fluorescens* BL915) and their subsequent application in field crops reduced the occurrence of diseases in plants (take-all disease and root rot) even more effectively than the wild types (Alsanius et al. 2002). The first study on the effect of inoculated microbes to inhibit pathogenesis in soil was performed by introducing diacetylphloroglucinol (DAPG) producing *P. fluorescens* strains to suppress the growth of *G. graminis* var. *tritici* (Ggt), the causative agent of take-all disease in wheat (Kwak and Weller 2013). Even pretreatment of soil with recombinant strains effectively decontaminated it, reducing the rate of disease outbreak (Timms-Wilson et al. 2000). In addition to application of wild-type and/or recombinant strains, disruption of indigenous microbial population through imposition of mechanical (tillage) or chemical (fungicides, antibiotics) disturbances and thereby introducing beneficial microorganisms in the rhizosphere are another method to establish exogenous communities and modulate the rhizosphere milieu (Bulluck and Ristaino 2002).

4.3.2.3 Meta-Organism-Based Techniques

Interdependence of plants and the microbes in the rhizosphere redefines plant and the rhizobiome collectively as a metabiome or holobiont (Lakshmanan et al. 2014). Therefore, a school of thought in rhizosphere engineering is in the favor of addressing both the partners together, instead of accounting on them separately. This approach is addressed in two ways: (1) crop rotation and (2) inoculation of GMC with GMO.

Crop rotation is a decade-old method that has been applied extensively worldwide. This approach basically involves culturing of plants in turns, so that the residual microorganisms and phytochemicals in the soil from one plant might be beneficial to the next, and thereby an associative rhizo-microbiome can be established (Quiza et al. 2015). Various reports have been documented for utilities of crop rotation. A study from North America showed the association of higher diversity of AMF and the antagonist species *Penicillium canescens* with two cultivars of chickpea (CDC Anna and CDC Amit, respectively). This in turn influenced the productivity of the soil that subsequently helped in the establishment of durum wheat in that same soil (Ellouze et al. 2013). Similarly, the alternate cropping of potato with alfalfa, white lupin, and oats promoted potato yield (Honeycutt 1998). This approach induces the formation of disease-suppressive soils. In addition, this improves organic carbon content, nutrient cycling, and physicochemical characteristics of soil, thereby promoting a diverse microbial community (Honeycutt 1998; Mazzola 2002, 2007).

Inoculation of genetically engineered plants with genetically engineered organisms basically stimulates the plant to exudate specific chemicals which can be degraded by the selected GMO, thereby causing a proliferation of a specific group of organisms. An example is "opine concept" where it has been observed that the transgenic plants (*Lotus corniculatus*) modified to produce opine which is a

xenotopic compound produced from the *Agrobacterium tumefaciens*-induced tumor. Opine, in turn, selects opine-degrading bacteria over others that could maintain themselves at high concentrations, even after removal of the transgenic plants (Oger et al. 1997; Savka et al. 2002). A similar approach was adopted to study the interaction between rhizopine-synthesizing transgenic *Arabidopsis* and rhizopine-degrading transgenic bacteria, and rhizopine-degrading strains were favored in a rhizopine-rich environment (Gordon et al. 1996).

4.3.3 Rhizosphere Engineering in Bioremediation

The hindsight of urbanization, advancement, and development of technologies is increased accumulation of chemical/industrial/agricultural remnants which are often biohazardous. Therefore, there is also a need for "environment cleaning" to save our earth. Most of these pollutants are accumulated in soil and cannot be removed easily until the soil is excavated and treated at a particular site. However, this is arduous and expensive. Therefore, "bioremediation," i.e., the use of plants and their associated microbes to assimilate and degrade/stabilize/volatilize the pollutants, has become an attractive substitute (Eapen and D'Souza 2005; Pilon-Smits 2005). A huge body of literature suggests that bioremediation has been globally accepted as a cost-effective and environment-friendly alternative or complementary technology for conventional remediation (Clemens et al. 2002; Gisbert et al. 2003; Eapen and D'Souza 2005).

Microbial activity and plant intervention are both required for biodegradation of pollutants (Yergeau et al. 2014). Plants can directly take up the pollutants from the soil and degrade them to less bioavailable forms via precipitation in the rhizosphere or via phytase activity, a process known as phytodegradation (Newman and Reynolds 2004). In some cases, a part of the pollutants are lost into the atmosphere during transpiration through leaves. This is termed as phytovolatilization (Zhu and Rosen 2009). However, hydrophobic organic compounds which cannot be taken up by the plants are degraded by the rhizosphere microorganisms. Herbicides, trinitrotoluene (TNT), methyl tertiary butyl ether (MTBE), and trichloroethylene (TCE), which are mobile within plant tissues, are usually degraded by the plants directly, while polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAHs), and other petroleum hydrocarbons are degraded by rhizosphere microorganisms (Harvey et al. 2002).

The process in which the plants stimulate soil microbes to degrade the pollutants is called phytostimulation or rhizodegradation. Besides participating in biodegradation, the microbes also stimulate the plants to take up contaminants from soil and to combat stresses developed due to accumulation of pollutants (Taghavi et al. 2005; Bell et al. 2015). It has been demonstrated that wild-type/genetically engineered microbial strains/microbial consortia accelerate the degradation of pollutants more effectively in the presence of plants (rhizoremediation) to bioaugmentation, the latter indicating the application of microbes in the soil without the plants. This is presumably because rhizosphere processes mediated cooperatively by plants and rhizobiota supplement the activity required for remediation, which cannot take place in bulk soil (Zhuang et al. 2007). Furthermore, plant roots provide greater

surface area, transport the microbes to that proper depth of the soil where the contaminants are present, and induce soil aeration, which enhance oxidative degradation of recalcitrant compounds (Chaudhry et al. 2005). Rhizoremediation is thus better over bioaugmentation (Zhuang et al. 2007).

The process of rhizoremediation which occurs naturally may be manipulated by engineering suitable plant–microbe pairs, such as plant–PGPR or plant-contaminant degrading microbes (Bisht et al. 2015). Beneficial plant–microbe symbioses have been exploited for rhizoremediation of hazardous and xenobiotic compounds like PAHs, PCBs, and TCE by choosing the right type of plant cultivar with appropriate rhizobacteria or by mechanically injecting efficient rhizobacterial strains on plant seeds/roots (Narasimhan et al. 2003; Walton and Anderson 1990). A wide variety of plants including alfalfa, barley, grass, lupin, oat, pepper, pine, poplar, radish, rape, sugarbeat, wheat, willow, and corresponding rhizobacterial strains such as *Pseudomonas fluorescens*, *Burkholderia cepacia*, *Pseudomonas putida*, *Bacillus* sp., *Deinococcus* sp., *Kurthia* sp., *Micrococcus* sp., *Arthrobacter* sp., and *Actinomycetes* have been identified (Kuiper et al. 2001; Bisht et al. 2014).

However, it is to be remembered that rhizoremediation is the outcome of activities of an entire microbial consortium, rather than a particular species (Kuiper et al. 2004). Although there is no dearth of studies involving isolation and characterization of pollutant-degrading rhizobacterial strains, studies on specific plant–microbe pair selection for rhizoremediation system are still limited (Bisht et al. 2015). Nevertheless, attempts of rhizoengineering by modifying plants to increase their size/number and augmenting their competence for biodegradation have been widely undertaken (Kabouw et al. 2012; Zhang et al. 2015b). The process relies on the following elements: (i) enhancement of root biomass to foster accumulation of high quantity of contaminants so that stress tolerance toward accumulated substances develops, (ii) stimulation of secretion of enzymes that will mobilize and degrade the noxious waste, and (iii) modulation of root exudation to attract microbes which are capable of degrading specific pollutants (Bhargava et al. 2012; Abhilash et al. 2009; Lojkova et al. 2014).

For competent biodegradation, plants require the presence of membrane transporter proteins (MTPs) that will export inorganic metal ions from the soil to the root xylem. Transgenic *Arabidopsis* and tobacco plants with overexpressing genes encoding membrane transport proteins result in increased uptake and accumulation of inorganic pollutants and heavy metals like cadmium, calcium, nickel, lead, manganese, and zinc in the plant tissues (Arazi et al. 1999; Hirschi et al. 2000; Van der Zaal et al. 1999). Recombinant DNA technology has mainly been applied to existing hyperaccumulator plant species (*Thlaspi caerulescens*, a natural zinc–cadmium hyperaccumulator) and high biomass species (Pence et al. 2000). Protein engineering has been applied to model plant, *Arabidopsis*, to increase specificity of transport proteins for heavy metals (Rogers et al. 2000). Transformation of *Arabidopsi*s with pea metallothionein-like gene *PsMTA* enhanced their capacity to chelate metal ions (Evans et al. 1992). Overexpression of glutathione synthetase and γ-glutamylcysteine synthetase in *Brassica juncea* (Indian mustard) enhanced cadmium tolerance and accumulation (Zhu et al. 1999). Iron fortification of rice seed by the soybean ferritin gene was also established (Goto et al. 1999). In another study, transfer of the yeast metallothionein

gene (CUP1) caused remarkable improvement of heavy metal tolerance in GM plants (Thomas et al. 2003). Transgenic plants with bacterial pentaerythritol tetranitrate reductase and nitroreductase genes were reported to be more efficient in reductive transformation of TNT (French et al. 1999; Hannink et al. 2007). Even enhanced metabolism of halogenated hydrocarbons in transgenic plants containing mammalian cytochrome P450 2E1 was reported (Doty et al. 2000). Volatilization of heavy metals like mercury and arsenic in wild plants occurs in a very limited manner. However, introduction of a modified bacterial *merA* gene enhanced resistance and rate of reduction for mercury ions in *Arabidopsis* plants (Rugh et al. 1996).

Following AMF inoculation (either single or in combination with PGPR), stress tolerance for heavy metals like cadmium, cesium, iron, lead, trace elements (arsenic), PAHs, PCBs (petroleum), and their accumulation was enhanced in various plants including medicinal plants (*Cassia italica Mill*), food crops (sorghum, barley, oats, legumes, rice), flowering plants (sunflower), switch grass, rye grass, *Miscanthus* sp. via a variety of mechanisms including increasing chlorophyll content, endogenous hormone level, and protein content in the host plant and subsequently decreasing lipid oxidation, accumulation of ROS, and synthesis of ABA, peroxidase (PO), and superoxide dismutase (SOD) (Hashem et al. 2016; Huang et al. 2015; Arora et al. 2015; Mishra et al. 2015; de Melo et al. 2014; Xun et al. 2015; Chan et al. 2013; Arias et al. 2015; Cabral et al. 2015; Lu et al. 2014; Firmin et al. 2015).

However, to date, most studies have been performed under laboratory conditions. Due to various confounding factors, field trials appear to be more complex than anticipated. One field trial for selenium-resistant transgenic *Brassica juncea* (Indian mustard) was undertaken that showed enhanced Se accumulation in the field (Pilon-Smits et al. 1999; Zhu et al. 1999). The availability of genomic sequences of *Arabidopsis* and rice has led to the identification and manipulation of novel key genes and regulatory elements (transcription factors/tissue-specific transporters) for establishment of high biomass species for pollutant remediation and accelerated the pace of translational research and development of technology. Transgenic plants with modified hairy roots to enhance their capacity of absorbing inorganic chemicals have emerged as an attractive model system in the field of phytoremediation (Ibanez et al. 2015). Tailored transgenics is also emerging as a tool to study plant-site-specific or environment-specific gene expression and manipulation toward ecosystem management and environmental cleaning. Hyper-accumulation and increased tolerance for arsenic were established in plants by combining arsenate reductase and gamma-glutamylcysteine synthetase expression to combat arsenic toxicity (Dhankher et al. 2002).

4.3.4 Rhizoengineering for Industrial Application

Knowledge on plant–microbe interactions in the rhizosphere has unfolded diverse functionality of soil microorganisms in medicine and chemical industries in addition to agriculture. In this regard, isolation and purification of "enzymes" from various microbial strains suggest the potential use of microbes in biotechnological and/

or industrial processes. Presently, genetic engineering and protein engineering techniques have been applied to improve the production of enzymes both qualitatively and quantitatively (Gurung et al. 2013). Proteases and carbohydrases such as amylase and cellulase are the dominant enzyme groups isolated from the rhizosphere microorganisms because of their extensive use in dairy, detergent, textile, baking, and starch industries (Underkofler et al. 1958). Presently, hydrolases, which catalyze breakdown of molecules in the presence of water, find an extensive application in industries manufacturing food and beverages, cleaning supplies, clothing, paper products, transportation fuels, pharmaceuticals, and monitoring devices (Gurung et al. 2013).

The species under *Bacillus* genera (*Bacillus subtilis, Bacillus licheniformis*, *Bacillus stearothermophilus*, and *Bacillus amyloliquefaciens*) serve as the richest source of industrial amylases (Konsoula and Liakopoulou-Kyriakides 2007; Sokarda Slavić et al. 2016). Thermostable amylases isolated from *Bacillus subtilis*, *Bacillus licheniformis*, *Bacillus stearothermophilus*, and *Bacillus amyloliquefaciens* are widely used for starch degradation and production of crystalline sugar, dextrose syrup, and maltodextrins (Hua et al. 2014; Hwang et al. 1997). Amylases that can particularly function at halophilic environments have been isolated from halophilic bacteria such as *Chromohalobacter* sp., *Halobacillus* sp., *Haloarcula hispanica*, *Halomonas meridiana*, and *Bacillus dipsosauri* (Gupta et al. 2016; Kumar et al. 2012). Lipase derived from *Bacillus*, *Burkholderia* (*Achromobacter* sp.), *Pseudomonas*, *Enterococcus*, and *Arthrobacter* species are used in food, textile, detergent, cosmetic, biosensor, and medicine industries (Gurung et al. 2013). These enzymes have also found their use in therapeutics at a limited scale. Notable examples include streptokinase from *Streptomycetes*, urokinase from *Bacillus subtilis*, and glutaminase from *E. coli*, and these are used to treat thrombosis and leukemia, respectively (Banerjee et al. 2004; Zaitsev et al. 2010; Spiers and Wade 1976).

In addition, the microbes are genetically modified using genes/transcription factors from metabolic pathways or stress regulatory network to produce high quantities of metabolites like ethanol, N-butanol, glycerol, and mannitol which have wide applications as solvent, extractants, antifreeze, dye base, lubricants, detergents, pesticides, resins, explosives, plasticizers, synthetic fibers, brake fluids, and petroleum derivatives and also in medicine and food industry (reviewed in Jia et al. 2014).

The production of "biofuels" using plants forms another important application of rhizosphere biology. One of the important sources of biofuel is "biomass," i.e., deposition of free energy from photosynthesis. Usually, nonfood crops or residues are used as feedstock for biofuel production. Vegetative parts from sugarcane (*Saccharum* sp.), poplar, switch grass (*Panicum virgatum*), *Miscanthus* species (*Miscanthus x giganteus*), and *Erianthus* species (*Erianthus arundinaceus* Retz.) are utilized for this purpose (Furtado et al. 2014). Thus, any engineering event in plants that accelerate vegetative meristematic activity is advantageous for biofuel production. Genetic diversity among *Saccharum* sp., *Erianthus* sp., and *Miscanthus* sp. has been exploited in breeding programs targeting different genetic markers, growth factors (GFs), enzymes, and transcription factors to introduce disease resistance, adaptability feature, and biofuel traits (Zhu et al. 2014; De Souza et al. 2015).

Genetically modified sugarcane with high biomass and cellulose-degrading microbes has been used for biofuel production (reviewed in Arruda 2012). In another study, tobacco plants transformed with NAC family genes from *Lepidium latifolium* gave rise to increased production of a number of transcription factors that resulted in marked improvement of plant biomass indicating the future potential of NAC gene transgenesis in biofuel production (Singh et al. 2016). Attempts to manipulate cellulase and laccase production in *Arabidopsis*, maize, and rice have also been successful in providing a new direction toward production of lignocellulose-based biofuel (reviewed in Wang et al. 2015). Syngas, produced from lignocellulose, can be fermented to biofuels using acetogenic bacteria such as *Eubacterium limosum*, *Clostridium autoethanogenum*, or *Acetobacterium woodii* (Bertsch and Muller 2015). GM microorganisms with abilities to use hemicellulose-derived C5 sugars (pentoses) may also aid production of biofuel as pentose constitutes one-third of the lignocellulose component of biomass (Silva et al. 2010). In this respect, genetically engineered *Cyanobacteria* are worthy of mentioning as they are being largely used to convert CO_2 into various chemicals directly (Lai and Lan 2015).

4.4 Conclusion and Future Perspectives

Of the countless problems and challenges our globe is facing today, perhaps the most overwhelming is how to shape the "Fourth Industrial Revolution" that has been initiated in this century. New concept, information, and technologies from physical, digital, and biological worlds are propelling toward bringing about an altruistic societal change. Perhaps "biological science" has to offer the most important contribution in today's industrial revolution. Armed with genetic and protein engineering, the new era of synthetic biology integrates engineering to biological principles toward establishment of more systematic, efficient, robust, predictable, and scalable biological systems. The time is just ripe to harness the knowledge of rhizosphere biology with technology to yield fascinating results with beneficial impacts on mankind. Although there is monumental progress in understanding the existing plant–microbe coordination, in-depth knowledge is still missing in many parts. This lacuna needs to be bridged for maintenance of progress rate. Advances have been made utilizing "system approaches" to identify key molecular players (such as genes, RNAs, proteins, etc.) in plant–microbe cross talk associated with plant health and productivity. However, exigent issues still exist and need to be tackled with urgent priority. Last, but not the least, the plant performance needs to be investigated at a population scale. Therefore, multiscale mechanistic models that will link plant, microbes, and field ought to be developed taking care of influential environmental factors (Hill et al. 2013). Developing mixed genetic-ecophysiological models to amend the gap between genetic and environmental parameters is an important goal that may help in overcoming the constraints still prevailing while manipulating genes in recombinant species (Roose and Schnepf 2008). For example, implementation of "synthetic biology" for successful biotransformation has often proven cumbersome due to vulnerability of host organisms to intermittent and

unpredictable environmental parameters (Jia et al. 2014). A robust knowledge of metabolic network and the mechanisms of systemic resistance operating in microorganisms at both cellular and community levels will provide solution to this problem. Besides, there is also a necessity of increasing public awareness and acceptance of genetically modified products (Adenle 2011; Kikulwe et al. 2011). This of course calls for coordinated participation of scientists and other professionals to spread the true information to the community.

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