Rhizosphere Biology: A Key to Agricultural Sustainability

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Abstract

The interactions of plant–microbe enable various types of transformations in the rhizosphere, which might be harmful, neutral, or beneficial. These interactions are proved helpful to plants for enhancing the biological, chemical, and physical properties of soil by facilitating the nutrients balance of the soil. Mutualistic plant–microbe interaction in the rhizosphere can enhance the nutrient uptake from roots, improve the biomass productivity and potentially, the ability to tolerate environmental stress. The microbial communities present in the rhizosphere influences the development of phytopathogens, the fitness of the ecological plants,

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and resistance of heavy metals and acquisition of nutrients. For improving the yields, varieties, and sustainability of the crops, the plant–microbe interaction is now getting considered as a valuable asset. Bioprospecting, the rhizospheric microorganisms with the ability to confer tolerance towards stress to host plant and using their symbiotic interaction with plants to improve the overall plant growth and crop productivity, could significantly aid in decreasing the adverse effects of stress on plants. The emerging field of engineering of ecosystems and rhizosphere marks a promising opportunity to fill critical research gaps and to develop sustainable solutions. Exploration of plant–microbe interactions is the key to understand the mechanism of rhizosphere priming, management of the carbon cycle in soil, and improve the crop productivity under current and future climatic conditions.

Keywords

Agricultural sustainability · Environment · Nutrient uptake · Roots exudates · Soil microbiomes

7.1 Introduction

In the year 1904, Hiltner coined the term “rhizosphere”. It is referred to the soil zone present around the legume roots, which supports the bacterial activity. The rhizosphere is divided into three different types of regions (Lynch and de Leij 2012). These include the ecto-rhizosphere, rhizoplane, and endo-rhizosphere zone. The root tissue, which includes the layers of cortical and endodermis, is known as endo-rhizosphere. The rhizoplane includes the root surface area with the polysaccharide layer of mucilaginous and along with epidermis layer, whereas ecto-rhizosphere is defined as the region soil, which is adjacent to the root (Linderman 1991). Since various organic compounds get accumulated and released by roots exudation in the rhizosphere, this region is enriched with the nutrients (Ligaba et al. 2004). These nutrients are utilized by the microorganisms occurring in these regions as the sources of energy and carbon to increase their microbial activity and growth (Lugtenberg and Kamilova 2009). The microbial communities present in the rhizosphere influences the development of phytopathogens (Nehl et al. 1997), the fitness of the ecological plants (Barriuso et al. 2008), resistance of heavy metals (Kuffner et al. 2008), and acquisition of nutrients (Lynch 1990; Kour et al. 2020c).

The different types of organisms are found in the rhizosphere, namely archaea, nematodes, bacteria, protozoa, algae, fungi, arthropods, and oomycetes (Raaijmakers et al. 2009; Kour et al. 2019b; Yadav et al. 2018). The released nutrients from the plants are utilized by the different groups of the rhizospheric microbiome. It has been observed that in the regulation of plant roots activity and microbial diversity, the rhizodeposits (i.e. exudates) provides the major driving force to them. The pathogenic fungi, nematodes, oomycetes, bacteria, and fungi are the deleterious rhizosphere organisms (Van Baarlen et al. 2007; Tyler and Triplett 2008; Thakur et al. 2020). The defence of the frontline for the roots of plants against the pathogens of soil-borne attack is provided by the rhizosphere (Cook et al. 1995). This book chapter covers different aspects of plant–microbe interactions; new, improved engineering methods for bio-formulations. Efforts have also made to summarize the use of recombinant DNA technology to modify rhizosphere populations and their possible role of rhizospheric microbes in agricultural sustainability.

7.2 Plant–Microbe Interaction

The bacteria which are associated with the plant and capable of colonizing the roots are known as “rhizobacteria”. They are classified into three groups, namely: (1) neutral, (2) beneficial, and (3) deleterious depending on their effects on plant growth. The bacteria stimulating the growth of plant referred to as beneficial rhizobacteria or also known as plant growth-promoting rhizobacteria (PGPR) (Kour et al. 2020b; Singh et al. 2020a). PGPR enhances crops growth indicating their potential in the agriculture field as biofertilizers (Timmusk et al. 1999; Kour et al. 2020f). The rhizospheric microorganisms are capable of forming the NH_4^+ by decomposing the proteins into amino acids via the ammonification process. The nitrification (NO_3^- formation) occurs after the ammonification at a rapid rate in most soils; hence, both NH_4^+ and NO_3^- are available for the plants but majorly NO_3^- is the main nitrogen source for the plants (Sylvia et al. 1999; Marschner 2011).

According to the root exudates quantity and quality, microbes associated with the rhizosphere are often transient (Biswas et al. 2018; Rana et al. 2020a). The rhizosphere-associated microbe’s variation depends on the parameters influencing the chemical and biological aspects of the root (Yang and Crowley 2000; Morgan et al. 2005). The interactions of plant–microbe enable various types of transformations in the rhizosphere; for example, nutrient cycling mainly the sequestration of carbon and nitrogen (Philippot et al. 2013). The interaction between the plant and microbe might be harmful, neutral, or beneficial. The plant–microbe interaction is considered as a valuable asset due to their capabilities to improve the yields, varieties, and sustainability of the crop (Gopal and Gupta 2016). The primary factors which are involved in the inhibition or attraction of microbe’s proliferation in the rhizosphere are the root exudates (Moore et al. 2014). Positive and beneficial interactions among rhizospheric microorganisms are favourable for good practices of agriculture. These interactions are not only important for the plant growth and development but also enhances the biological, chemical, and physical properties of soil by facilitating the nutrient balance of soil via biogeochemical cycles (Velmourougane et al. 2017). There are many ecological benefits due to this interaction, such as the availability of nutrients to the plants and promoting the plant growth (Boddey and Dobereiner 1995; Yadav et al. 2020c). The rhizospheric microbiome is able to protect the plant against the abiotic and biotic stress (Verma et al. 2017; Yadav et al. 2019).

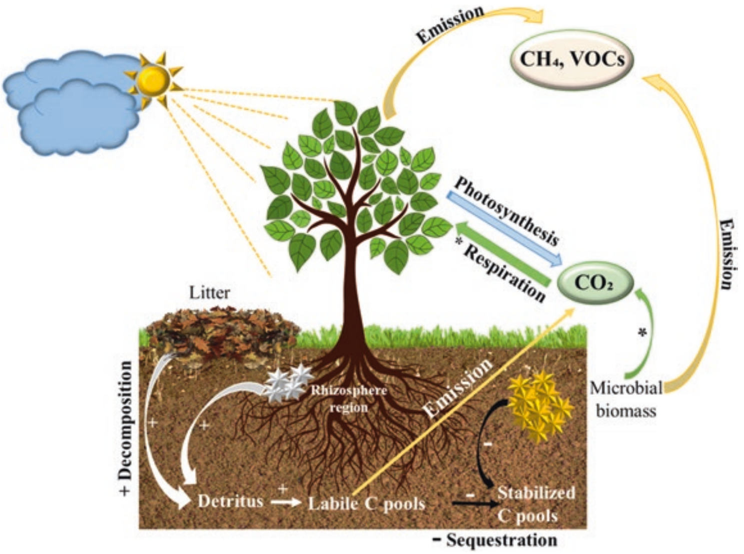

Fig. 7.1 Interaction of rhizosphere region with the other components of the plant ecosystem

The belowground diversity of the plant may perform as insurance under the different conditions of the environment for maintaining the productivity of the plants (Wagg et al. 2011). The rhizospheric microbes are considered as the soil quality bioindicators for the plants (Schnitzer et al. 2011; Yadav et al. 2020b). These rhizospheric microorganisms protect plants from the attack of the phytopathogens (Lugtenberg and Kamilova 2009). These include abiotic stress and disease control, root growth stimulation, biofertilization, and rhizoremediation (Kumar et al. 2019a, c). They can also facilitate the trace elements uptake, i.e. iron. In soil, iron is an abundant element under the conditions of alkaline and neutral (Andrews et al. 2003; Buckling et al. 2007). The interaction of the rhizosphere region with the other components of the plant ecosystem is illustrated in Fig. 7.1.

7.3 Engineering of Rhizosphere

Plant preservation is essential because of various reasons as it provides feed, food, fuel, aid in regulating carbon as well as the water cycle, climate, nutrition entrapment, and serve as habitat for wildlife. Considering, the massive diversity in the genotype of collected as well as generated plant species, the assessment of their genetic diversity of these plants has become highly important (Shishido et al. 2019). It could maintain the plant ecosystem and its values by stabilizing and generating stress tolerance in both cultivated and native ecosystem, and by retaining both cultivation and functioning of the ecosystem. These opinions direct that the selection of both species and genotypes should be taken into consideration while designing the breeding programme (Turnbull et al. 2016).

Hence, plant ecosystems can be engineered to improve carbon storage involving the allocated carbon in both above and belowground biomass for separating into the structural form or transport them to the soil for the conversion of recalcitrant minerals like calcite (Nogia et al. 2016). In 2010, Jansson and his colleagues comprehended and reviewed the potential of engineered plants in enhancing the carbon storage capacity and also introduced the term "phytosequestration"(Jackson and Baker 2010), whereas another group of scientists discussed the potential of terrestrial ecosystems in improving carbon storage. In the long run, storage of carbon in soil will become necessary. Therefore, a better understanding of the metabolic processes of microbial communities in rhizosphere and their interaction with the host plant and mechanism involved in carbon deposition is required (Dignac et al. 2017).

7.4 Plant Metabolism Through Rhizosphere Engineering

The conventional approach of plant breeding and advanced plant genetic engineering has been a success to accumulate desirable genes associated with stress response and tolerance in the plant genome. Most commonly employed strategy by plants to modify the rhizosphere is by altering exudation potential of roots; in view of this, researchers have attempted to develop transgenic plants that can alter the rhizospheric region by regulating the efflux of organic anions and H^+ in roots (Backer et al. 2018). Since the identification of several genes involved in root exudation, it has become possible to regulate the expression of those genes in plants for the incorporation of new features in the redesigned rhizosphere (Mark et al. 2005). For example, insertion of Arabidopsis vacuolar H^+ pyrophosphatase gene AVP1 in tomato and rice plants resulted in enhanced malate and citrate efflux, approximately 50%, on treatment with $AlPO_4$. This can be attributed to the increase of the tolerance in Al^{+3}-induced stress conditions and enhance the utilization of the insoluble form of phosphorus (Pasapula et al. 2011; Singh et al. 2020b). However, rhizosphere engineering is a complex process depending on several factors such as (1) inactivation of the engineered trait of the plant in the soil; (2) inability of the low rate of root exudation to affect the rhizosphere; (3) limited information about the composition of root exudates; and (4) variation in concentration and release time of root exudates during the development of plant and external stimuli.

Another approach involves exploring genetically diverse crops with desirable characters for partitioning and allocation of carbon (Canarini et al. 2019). It is debatable that increased distribution of photosynthate in rhizosphere will occur at the expense of carbon partitioning into harvestable compounds. However, reports suggest that inadequate sink demand can inhibit the process of photosynthesis through feedback response and make it sink limited. Thus, there is an immense potential for belowground allocation of carbon for long-term storage without imperilling crop productivity (Kaiser et al. 2015).

7.5 Genetic Modification of Rhizospheric Microbes

Genetic modification of microorganisms presents a unique opportunity to promote plant growth, confer resistance towards various diseases, and induce stress tolerance. Till now, numerous bacterial species have been identified to possess many advantageous effects but selecting and engineering a sustainable organism remains a challenge (Ortíz-Castro et al. 2009). For example, considering the inhabitation of two microbes in a niche, there can be six broad ecological interactions between them, namely commensalism, competition, predation, amensalism, cooperation, and null interaction. With the increase in microbial species in a niche, the perplexity of the ecological interactions among them increases linearly (Mougi 2016). The major challenge is to maximize positive interactions like cooperation and eliminate negative interactions like competition and parasitism. In view of this, it is an arduous task to minimize the competition between two strain co-cultures. The rate of plant growth, rate of seeding, sensitivity to pathogenic organisms, stabilization in adverse conditions, and sustainability of the microbiota are greatly influenced by the environmental factors such as pH, temperature, availability of nutrients, and exudates of the host plant (Bashey 2015). Besides these challenges, knowledge about interactions of natural soil microorganisms, including PGPR, can be exploited to develop a synthetic microbial community with desirable traits.

Numerous rhizosphere colonizing microorganisms have been identified as belonging to a wide range of genera whose genome sequences are publicly available, which are amenable to genetic modifications (Devi et al. 2020; Jacoby et al. 2017). These genera comprise of *Pseudomonas, Streptomyces, Rhizobium,* and *Bacillus.* Complete genetic sequences are available for *Streptomyces* spp., especially the ones used as PGPR. Still, they have certain limitations such as they have large genomes and possess mobile components which pose difficulty in engineering. *Bacillus* species are considered as an ideal organism to develop the synthetic microbial community as it is comparatively easy to modify genetically, has detailed information on genome sequences, contains many strains that promote plant growth, and are currently utilized as biocontrol agents (Vurukonda et al. 2018; Subrahmanyam et al. 2020). A consortium comprising of three different microbes, genetically modified *Bacillus* spp. and two other nitrogen-fixing microbes (natural or engineered) like *Bradyrhizobium, Pseudomonas,* and *Rhizobium* can provide many of the advantages of the complex natural microbiota of rhizosphere (de Souza et al. 2015; Yadav 2020).

To promote cooperation over competition, each strain can be engineered to make it deficient in certain essential genes such as elimination of gene synthesizing an essential enzyme or co-factor that is required by all strains (Hibbing et al. 2010). For instance, this could be understood as the system where *Bacillus* requires a co-factor produced by *Pseudomonas*, on the contrary, the *Pseudomonas* depends on the genes of *Rhizobium*, and *Bacillus* has the ability to remediate the waste generated by *Rhizobium* and recycle it for mutual use. This functional interaction among the strains on subsequent addition of the other strains as a consortium of three strains will have >729 predicted interaction, whereas a consortium of four strains will have about 531,441 predicted interaction (Gupta and Diwan 2017).

Hence, there is a need to limit the strain number to three in synthetic microbial community system so that their interaction among each other and with host plant could be controlled. In order to design the microbial consortium for an engineered rhizosphere, some critical realms need to be followed for their competence (McCarty and Ledesma-Amaro 2019; Mondal et al. 2020). Numerous traits need to be assessed prior to their selection for developing engineered microbial consortium: (a) Proficiency of microbes on colonizing the host plant roots in the rhizosphere, (b) Do the microbes colonize effectively on the host plant? (c) Are the microbes capable of surviving as well as competing with the other microbes in the consortium? (d) Is the adherence of microbes with the surface of root effective? (e) Does the microbe aid in promoting the plant growth or enhancing the growth of member of the consortium? (f) Do the microbes multiply themselves to reach the desired density? (g) Do the strains involved in consortium enable them to survive under abiotic stress? (Compant et al. 2019). The most important factor is the growth density irrespective of the reason that microbes will have a positive effect on the plant or not.

For instance, *Pseudomonas* spp. requires the growth density about 10^5–10^6 CFU/g of root to save the plant pathogens like *G. tritici* as well as *Pythium* spp. (Kwak and Weller 2013). If these standards are taken into consideration, then these microbial consortia could be used in the engineered rhizosphere, and these microbial consortia will help the plant in tolerating the effects induced by fertilizers, herbicides, and pesticides without losing their beneficial effects (Woo and Pepe 2018).

7.6 Molecular Mechanisms in the Rhizosphere

Previous studies mentioned the potential of PGPR in improving the growth of plants under stress conditions. Even advancement in molecular techniques has unveiled information regarding the genetic basis of PGPR that is showing the advantageous effect on plants (Shivakumar and Bhaktavatchalu 2017). Some of the studies that provide information regarding the molecular basis of PGPR have been comprehended in Table 7.1. Therefore, screening of the mechanism regulating the activities of PGPR will open the new avenue for genetic modifications of the microbe and host plant to improve their plant growing ability, especially under stress conditions.

In a study reported by Wang and collaborators, a microarray-based study was conducted to expand their knowledge about biochemical and physiological changes that take place in the plant. For this, they inoculated *Pseudomonas fluorescens* strain FPT9601-T5 (PGPR) in *Arabidopsis* plant. The result obtained on the analysis revealed that 200 genes out of 22,810 genes of *Arabidopsis* plant were showing different expression, i.e. two-fold increase in expression in PGPR-treated plant (Wang et al. 2005). Later, the majority of genes were found to be involved in different cellular processes like metabolic processes, stress response, and signal transduction. Moreover, upregulation of auxin-regulated genes, as well as nodulin-like genes and downregulation of ethylene-responsive genes, was observed (Markakis et al. 2012).

Table 7.1 The molecular studies involving PGPR under stress conditions

Species of plant	Microbial species	Molecular method used	References
Arabidopsis thaliana	*Bacillus megaterium* BP17	Microarray	Vibhuti et al. (2017)
Arabidopsis thaliana	*Bacillus subtilis* GB03	RT-PCR	Zhang et al. (2010)
Arabidopsis thaliana	*Pseudomonas fluorescens* FPT9601-T5	Microarray	Wang et al. (2005)
Arabidopsis thaliana	*Pseudomonas fluorescens* strain SS101	Microarray and LC-QTOF-MS	van de Mortel et al. (2012)
Arabidopsis thaliana	*Pseudomonas putida* MTCC5279	Microarray	Srivastava et al. (2012)
Cucumis sativus	*Acinetobacter calcoaceticus* SE370 and *Burkholderia cepacia* SE4	GC and enzyme-based assay	Khan et al. (2014)
Abelmoschus esculentus	*Enterobacter* sp. UPMR18	RT-PCR	Habib et al. (2016)
Piper nigrum	*Bacillus licheniformis* K11	2D-PAGE and PCR	Lim and Kim (2013)
Oryza sativa	*Azospirillum brasilense* Sp245	qRT-PCR	Vargas et al. (2012)
Saccharum officinarum	*Gluconacetobacter diazotrophicus* PAL5	Illumina sequencing	Vargas et al. (2014)
Triticum aestivum	*Dietzianatronolimnaea* STR1	qRT-PCR	Bharti et al. (2016)
Triticum aestivum	*Acinetobacter guillouiae* EU-B2RT.R1	16S rRNA-PCR	Rana et al. (2020b)
Triticum aestivum	*Pseudomonas libanensis* EULWNA-33	16S rRNA-PCR	Kour et al. (2020d)
Setaria italica	*Acinetobacter calcoaceticus* EU-LRNA-72	16S rRNA-PCR	Kour et al. (2020e)
Sorghum bicolor	*Streptomyces laurentii* EU-LWT$_3$–69	16S rRNA-PCR	Kour et al. (2020c)

Whereas another group of researchers with the help of RNA-Seq technology, i.e. Illumina, revealed that the inoculation of *Gluconacetobacter diazotrophicus* strain PAL5 in sugarcane triggered the ABA-dependent signalling genes and made its resistance to drought (Vargas et al. 2014). In 2015, Kim and his group showed that VOCs synthesized by *Bacillus subtilis* strain JS influenced the gene expression profiles of the tobacco. The upregulation in genes related to photosynthesis pathways was observed, signifying the VOC-mediated improvement in the growth of the plant (Tahir et al. 2017).

Other than the previous studies discussing gene expression profiles, proteomic analysis has also been conducted to gather more information about proteins as well as pathways triggered during host–PGPR interaction. As recognition of candidate protein among different PGPR could serve as a valuable resource for promoting the growth of the targeted plant in the near future (Singh et al. 2017). In 2008, Buensanteai and collaborators conducted an experiment on *Bacillus* *amyloliquefaciens* strain KPS46 inoculated in soybean plant to investigate the role of synthesized extracellular protein in improving plant growth and inducing systemic resistance (Radhakrishnan et al. 2017). For the separation of extracellular proteins synthesized by strain KPS46 (wild-type), KPS46 (mutant-type), N19G1, the methods like mass spectrometry (MS), two-dimensional polyacrylamide gel electrophoresis (2D–PAGE), and exploring of protein database were employed. The results obtained showed the presence of 20 extracellular proteins which could have a role in inducing resistance and plant development (Atshan et al. 2015). Another study revealed the presence of six different stress proteins on the molecular assessment of the pepper plant inoculated with *Bacillus licheniformis* strain K11 under drought stress. Even though there are technical constraints of using proteomic techniques for assessing the PGPR–host interaction but advancement in molecular techniques involving top-down proteomics and MALDI-TOF promises to extend our knowledge about the molecular basis for PGPR–host plant interaction in the near future (Lim and Kim 2013).

Furthermore, metabolic profiling of bacteria and plant is an alternative approach to understand the mechanism of symbiotic interactions. For instance, GC–MS analysis of drought-stressed wheat seedlings revealed the presence of seven stress-related VOCs in the rhizosphere and secondary metabolites were found to be β-pinene, benzaldehyde, and geranyl acetone. These three VOCs are likely to be considered as a promising candidate for rapid assessment of crop under drought stress. Hence, the deep insight about the genes, secondary metabolites, and proteins involved in plant–PGPR interaction and are responsible for abiotic stress resistance can be used for developing engineered plants. These engineered plants will harbour genes that control stress or microbes that alleviate the stress (Vaishnav et al. 2017).

7.7 Role of Rhizospheric Microbes for Agricultural Sustainability

7.7.1 Mutual Plant–Microbe Interactions

To overcome the adverse effects caused by environmental stresses, various strategies have been demonstrated. Transcriptome engineering is one such method to develop crops tolerant to abiotic stress (Cohen and Leach 2019). To date, the commonly used strategy to combat environmental stress in plants is to overexpress the single genes that encode for enzymes involved in the transportation of ions and scavenging of ROS. The application of this approach is limited due to the resultant pleiotropic effects on growth of the plant and comprehended multiple pathways in response to environmental stress (Xie et al. 2019). Utilization of agrochemicals is another method to enhance crop productivity in boosting crop productivity, but it is cost-intensive and has adverse effects on the environment on long-term use (Aktar et al. 2009). Employment of beneficial microbes in the rhizosphere of plants is another strategy to reduce the harmful effects of climatic fluctuations on the growth of plants and crop productivity. Mutualistic plant–microbe interaction in the

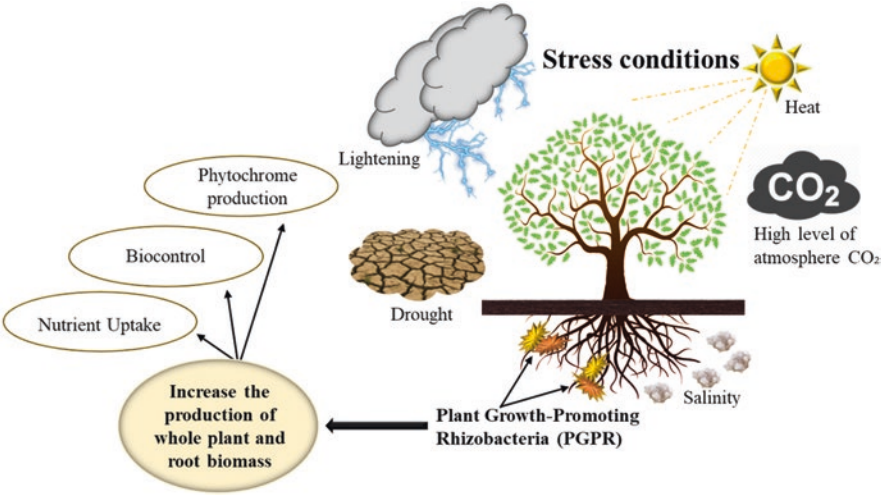

Fig. 7.2 Role of PGPR under the stress conditions

rhizosphere can enhance the nutrient uptake from roots, improve the biomass productivity and potentially, the ability to tolerate environmental stress (Igiehon and Babalola 2018). Bioprospecting, the rhizospheric microorganisms with the ability to confer tolerance towards stress to host plant and using their symbiotic interaction with plants to improve the overall plant growth and crop productivity, could significantly aid in decreasing the adverse effects of stress on plants. This approach has several advantages such as the ability of PGPR to confer multiple environmental stress tolerance to host plant, their application to diverse plant hosts and enhanced crop productivity as illustrated in Fig. 7.2 (Odelade and Babalola 2019).

7.7.2 Mitigation of Drought Stress

Among the environmental factors, drought is considered as the most critical factor that hampers plant growth and threatens crop productivity. Drought stress can be attributed to climatic changes, agronomic and edaphic factors (Rastegari et al. 2020a). Researchers predict that in the future, drought stress will worsen if the global supply of freshwater and climatic hitches remain a hurdle (Nadeem et al. 2019). In view of fluctuations in precipitation and global temperature, drought will hinder the production of biomass, feed, and most importantly, food. Thus, to ensure food security, the development of drought-tolerant crops becomes a necessity for a sustainable future. Most bioenergy crops used for biofuel production are tolerant towards drought conditions like poplar, miscanthus, etc. Therefore, there is an urgent need to enhance the tolerance of bioenergy crops towards drought and significantly improve their water use efficiency (WUE) for sustainable production of biomass in semi-arid and arid regions (Von Cossel et al. 2019).

Genetic engineering techniques have been extensively used to induce drought tolerance in plants, despite the efforts, there has been slow progress owing to the involvement of numerous genes and sophistication associated with the traits (Khan et al. 2019a, b; Rastegari et al. 2020b). It has been observed that the rhizosphere and microbiota associated with it play a vital role in constraining the capability of plants to manage the drought stress (Kour et al. 2019a; Verma et al. 2014, 2019; Yadav and Yadav 2018). The rhizosphere of plants is colonized by diverse microorganisms including plant growth-promoting rhizobacteria (PGPR) which provides them with the ability to cope with drought by aiding in the production of exopolysaccharides (EPS), phytohormones, and volatile organic compounds (VOCs) (Naseem et al. 2018; Tiwari et al. 2020). They also help in accumulating various antioxidants and osmolytes. Moreover, they can also alter the morphology of root in response to stress and regulate the stress-responsive genes (Sharma et al. 2019). For instance, it has been observed that the drought tolerance of wheat plant was enhanced by the inoculation of indole acetic acid (IAA) producing *Azospirillum* species which improved the growth of roots and induced lateral roots formation (Vurukonda et al. 2016). Similarly, the growth of *Lavandula dentata* in drought was stimulated by IAA producing plant growth-promoting bacteria, *Bacillus thuringiensis* that increased nutrient availability and improved the metabolic activities of the plant (Armada et al. 2016). In another study, grapevine and *Arabidopsis* plants were able to adapt to drought conditions when they were inoculated with GFP-labelled *Pseudomonas species* and *Acinetobacter species* which induced a water-stress mechanism to cope with drought (Rolli et al. 2015).

Upon inoculation of leaves of *Platycladus orientalis* with *Bacillus subtilis,* an increase in ABA concentration in shoots and stomatal conductance was observed, that provided drought resistance to the plant. Due to increased ABA levels, the water content in leaves enhanced, water potential improved, and cytokinin levels increased drastically (Liu et al. 2013). In another study, an isolate from the rhizosphere of *Brassica napus*, *Phyllobacterium brassicacearum* strain STM196 inoculated in *Arabidopsis* plants aided in acclimation of drought stress by enhancing ABA concentrations, reducing transpiration in leaves and increasing tolerance towards osmotic stress (Ahkami et al. 2017). Also, an inoculation of soybean plants with gibberellin-producing rhizobacterium, *Pseudomonas putida* strain H-2–3, an increase in fresh weight and length of shoots under drought conditions was reported (Kang et al. 2014b). In response to drought stress, they produced more chlorophyll, abscisic acid, and salicylic acid in comparison to control plants (Radhakrishnan et al. 2014).

7.7.3 Mitigation of Salinity Stress

Salinity is another major environmental factor that adversely affects the productivity of plants globally. Presence of salt in excess in the soil creates ionic imbalance and ion toxicity in plants which further triggers water deficiency in plants due to hyperosmotic stress and induces an imbalance in the metabolic activities (Shrivastava and Kumar 2015; Rajawat et al. 2020; Yadav et al. 2015; Kang et al. 2014a). Plants cope with stress due to salinity in various ways such as by producing polyamines and osmolytes, triggering defence mechanisms, preventing deposition of reactive oxygen species and regulating the transport of ions (Khan et al. 2019a, b; Gaba et al. 2017; Yadav et al. 2020a).

A study demonstrated that uptake of Na^+ ions by the plant was reduced significantly and the production of biomass enhanced when the wheat seedlings were subjected to the application PGPR like *Paenibacillus, Enterobacter, Bacillus,* etc. that synthesized exopolysaccharides (EPS) under highly saline conditions (Egamberdieva et al. 2019). In another study, PGPR inoculation in tomato plants reduced the adverse effects of ethylene, released under stress conditions, on the growth of roots by the activity of enzyme ACC deaminase which resulted in improved plant growth in water-deficit and saline conditions (Ilangumaran and Smith 2017). A recent study described the use of *Dietzia natronolimnaea* strain STR1, i.e. carotenoid producing and halotolerant, in combating the effects of salinity in wheat plants. Wheat plants inoculated with halotolerant PGPR showed higher levels of proline and production of numerous antioxidants that conferred salinity tolerance to the plants. Moreover, application of PGPR activated certain pathways in a plant-like ABA signalling, Fe transport, SOS pathways, etc. (Bharti et al. 2016).

In comparison to the uninoculated peanut seedlings, the inoculated peanut seedlings showed enhanced ion homeostasis, less accumulation of ROS, and improved growth under saline conditions. Another study showed the synergistic action of *Bacillus drentensis* and *Enterobacter cloacae* to aid in withstanding salinity in mung beans with foliar application of silicon (Ahkami et al. 2017). Moreover, when peanut seedlings inoculated with *Haererohalobacter*, *Brachybacterium saurashtrense,* and *Brevibacterium casei* were subjected to highly saline conditions by incorporation of 100 MNaCl, grown plants showed overall improved growth (Shukla et al. 2012).

7.7.4 Mitigation of Heavy Metals Stress

Heavy metals like Ni, As, Cr, Cd, Cu, Pb, Zn, etc. at low concentrations are essential to microbes and plants for the growth and metabolic activities but can present a major challenge if the concentration exceeds the tolerance limits (Singh et al. 2011). The presence of toxic heavy metals in soil greatly influence the characteristics of the plant and phytoremediation potentials; however, bacteria present in soil can significantly enhance the phytoremediation potential of the plant through synergistic action and hence the term, microbe-assisted phytoremediation (Ojuederie and Babalola 2017; Sharaff et al. 2020).

Reports suggest that PGPR also aid in protecting host plant from ill effects of toxicity caused by heavy metals. PGPR are known to possess this ability to cover a wide range of genera such as *Bradyrhizobium, Mesorhizobium, Sinorhizobium, Rhizobium, Pseudomonas, Azotobacter,* and *Bacillus* (Wani et al. 2008; Rai et al. 2020). For instance, a study showed that application of *Bacillus licheniformis* could significantly improve the germination of rice plant seed and enhance the biochemical characteristics of rice when subjected to stress induced by Ni. Therefore, highlighting the potential of the strain in protecting the rice plant from heavy metal toxicity (Jamil et al. 2014). Like most microorganisms, PGPR has also evolved in certain unique ways to tolerate heavy metals such as mobilization, immobilization, and transformation of heavy metals into either inactive form or less toxic utilizable form (Tiwari and Lata 2018). PGPR are known to follow five mechanisms broadly to increase heavy metal resistance: (1) Extrusion of heavy metals by transportation through efflux pumps; (2) Exclusion of heavy metals by direct removal from target sites; (3) Inactivation of heavy metals through the formation of complexes like the formation of thiol-containing complex structures; (4) Biotransformation of heavy metals from a toxic oxidation state to a less toxic oxidation state such as the conversion of highly toxic Cr^{+4} into less toxicCr^{+6}; and (5) Addition or removal of methyl from heavy metals, i.e. methylation and demethylation (Ma et al. 2016).

Similarly, plants also possess various mechanisms to cope with heavy metal resistance; however, the process by which microbes and plants interact at the molecular level to combat heavy metal toxicity remains unclear. Furthermore, increasing the knowledge about plant–microbe interactions, genes involved, and mechanisms of regulation, it would be possible to engineer plants for enhanced growth heavy metals contaminated sites (Mishra et al. 2017).

7.7.5 Mitigation of Heat Stress

Temperature is one of the abiotic stresses which negatively impact the growth, homeostasis, and metabolic activities of plants and microorganisms. Bioprospecting PGPR with the ability to promote plant growth at alleviated temperatures would possibly enhance global crop productivity, especially concerning the increased rate of global warming (Kour et al. 2020a). The experimental evidence supporting the effect of PGPR isolates in enhancing crop production at high temperatures is less. Till now, thermostable PGPR isolates stable even at 60 °C (Rodriguez et al. 2008) have been reported in the literature, but they lack the ability to provide thermostability to host plant. Nonetheless, some studies have shown the application of PGPR isolates to cope with the negative impacts due to low temperature-induced stress (Barka et al. 2006; Dimkpa et al. 2009). Low temperature-induced stress has resulted in enhanced synthesis of certain compounds like proline, sugar, anthocyanin, etc. (Dimkpaet al. 2009). In a study, grapevine plants inoculated with *Burkholderia phytofirmans* lead to increased production of carbohydrates, proline, and phenols along with the improved accumulation of starch (Barkaet al. 2006; Kumar et al. 2019b). However, PGPR-inoculated grapevine plant showed reduced biomass production and imbalance of electrolytes when subjected to low temperature (4 °C).

7.7.6 Combating Elevation CO_2 Levels

The process of photosynthesis plays a significant role in the uptake of atmospheric CO_2 and its conversion to organic carbon in plants biomass. The rise in CO_2 levels in atmosphere enhances the photosynthetic process in C3 plants, helping the proliferation of rhizospheric bacteria with enhanced localization of photosynthate in soil. Climatic fluctuations greatly influence the composition of plants as well as the diversity that threatens the soil microbes and edaphic characteristics of soil, including quality and quantity of organic matter in the soil. It also has a negative impact on various nutrient cycles like the carbon cycle, methane cycle, nitrogen cycle, and terrestrial ecosystem climates (Dorrepaal et al. 2009; Malyan et al. 2019). The PGPR utilization has enhanced the grassland management technology (Antoun et al. 1998; Van Der Heijden et al. 2006), restoration of the ecosystem (Requena et al. 2001), and reforestation (Chanway 1997). The PGPR have a remarkable ability to improve the accumulation of carbon in terrestrial systems by enhancing crop productivity and reducing the carbon loss through respiration in microbial systems at alleviated atmospheric CO_2 levels (Nie et al. 2015). However, the possibility of escalation of atmospheric CO_2 concentrations in future will broaden the horizon of PGPR application. The impact of microorganisms on the host plant through plant–microbe interactions is well known, but the mechanisms involved at the molecular level still remain unclear. Thus, it becomes important to study the plant growth dynamics and mechanism of rhizobacteria colonization to exploit the potential of PGPR further.

7.8 Conclusion and Future Prospects

Increasing crop productivity has become a global necessity. There is a need to improve environmental management practices, revert the effects of changing climate, and forecast the interaction and impact of plant ecosystems on atmospheric processes. To meet the ecological requirements, there is a need to understand plant ecosystem dynamics in stressful environments. The emerging field of engineering of ecosystems and rhizosphere marks a promising opportunity to fill critical research gaps and to develop solutions. The interactions within ectophytic and endophytic microbial communities along with mycorrhizal–rhizospheric relationship to promote plant growth and enhance nutrient uptake still remain unknown. Plant–microbe interactions is the key to understand the mechanism of rhizosphere priming, management of the carbon cycle in soil, and improve the crop productivity under current and future climatic conditions. Recent advancement in genetic engineering offers an exciting opportunity to fulfil the research gaps. Future studies will explore the synthetic approaches, which improves the production of bioenergy crops under abiotic and biotic conditions.

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