Role of Rhizosphere Microorganisms in Endorsing Overall Plant Growth and Development

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Abstract

The rhizosphere, the abutting soil region under living root proximity, is the abode for diverse microorganisms which are distinct in their ecosystem services. Rhizosphere, being a water and nutrient uptake portal, provides a forum for interaction between soil, microorganisms, and living root which brings desirable changes in soil physicochemical properties impacting plant growth, nutrition, and health. Rhizosphere inhabiting microbes have been known for their nitrogen fixation and mineral solubilizing properties since long. In addition to these conventional roles, microbes have been demonstrated to execute multifarious chores. Bacteriogenic phytohormones, exudates, and volatile compounds act as signals for phytostimulation, activating immunity, morphogenesis, and efficiently modulating root system architecture. Novel agricultural applications offered by the rhizosphere microbes could certainly endow manipulation of phenology anticipating changing climatic conditions. Coping up with the adverse effects of environmental stresses on crop development and safeguarding against pests and diseases are the most important agricultural issues being faced by the farming community. Long-term use of chemicals to achieve targeted agro-based demands cannot be an everlasting approach. The use of rhizosphere microbes can circumvent extreme environments limiting crop production. Exploiting microbial potential as biofertilizers, biocontrol agents, and in rhizoremediation can benefit crop growth with lesser environmental hazards. Utilizing rhizosphere microbial potential could be a promising strategy over existing agricultural practices to overcome the challenges and enable sustainable agricultural production.

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U. B. Singh et al. (eds.), *Re-visiting the Rhizosphere Eco-system for Agricultural Sustainability*, Rhizosphere Biology, https://doi.org/10.1007/978-981-19-4101-6_16

16.1 Introduction

Diverse soil-inhabiting organisms are in continuous interaction with field crops. These organisms belong to micro- to macroscopic world comprising of bacteria, fungi, algae, protozoa, nematodes, earthworms, and insects. These organisms exert beneficial, neutral, or harmful effects on the overall growth and physiology of crop plants. Among all soil-inhabiting organisms, a plethora of microbes is present at root–soil interface forming a close association with roots. The microbial association is established on the root surface (rhizoplane), within the root tissue and/or along the immediately adhered root–soil interface (rhizosphere). Microbes colonizing root tissue are called endophytes. These endophytes play a major role in nitrogen fixation by forming root nodules, of which *Rhizobium* spp. in legumes are the most common example. Many of the non-rhizobia endophytes (*Paenibacillus, polymyxa,* and *Paenibacillus* sp.) also induce nodulation and nitrogen fixation in leguminous crops (Ahmad et al. 2019). Some of the endophytes belong to non-nodulating strains like *Endobacter medicaginis, Brevibacillus choshinensis,* and *Micromonospora* spp. (Ramírez-Bahena et al. 2013; Trujillo et al. 2010). Endophytes play important role in amelioration of biotic and abiotic stresses (Waqas et al. 2015; Herrera et al. 2016; de Zélicourt et al. 2018; Sandhya et al. 2017). Endophytic bacteria comprise a much less diverse yet distinct community than the rhizosphere or bulk soil (Dastogeer et al. 2020; Lundberg et al. 2012; Bulgarelli et al. 2012). Some of the endophytic fungi play substantial roles in modification of ecosystem productivity. Endophytic fungus, *Phomopsis liquidambaris,* increased yield, nodulation, and N_2 fixation in peanut (Xie et al. 2019). Soil inoculation with endophytes (Serratia PRE01 or Arthrobacter PRE05) influences several ecological factors such as root morphology, rhizosphere soil properties, bioavailability of heavy metals, composition of endophytic bacterial communities, and phytoremediation (Wang et al. 2020).

Rhizosphere is the home to an enormous diversity of microbiota which offers a variety of ecosystem services to crop plants. Rhizosphere circumscribes nitrogen-fixing bacteria, plant growth-promoting rhizobacteria (PGPR), mycorrhizal fungi, plant growth-promoting fungi (PGPF), biocontrol microbes and protozoa, in addition to soil-borne phytopathogens. Rhizosphere and root microbiota composition is substantially driven by edaphic factors (pH, nutrient content, root exudates, soil texture, temperature, water availability), crop species, crop genotype, stages of crop development (Dastogeer et al. 2020). Cordero et al. (2020) investigated rhizosphere and root interior associated bacterial communities belonging to cereal (wheat), pulses (field pea and lentil), and oilseed (canola) grown at different locations. Distinct rhizosphere bacterial communities were found associated with each crop. The phyla *Acidobacteria, Actinobacteria*, *Bacteroidetes*, *Firmicutes*, *Gemmatimonadetes,* and *Proteobacteria* were the dominant rhizosphere bacteria in the crops studied. Rhizosphere, being colonized by similar bacterial communities, viz. *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, *Acidobacteria*, and *Gemmatimonadetes,* has been reported previously in winter wheat and barley (Mahoney et al. 2017; Bulgarelli et al. 2015). Some studies contextualized the effect of soil type to be more pronounced on rhizosphere microbial communities than plant genotype (Dombrowski et al. 2017; Bulgarelli et al. 2012).

Rhizoshpere, through intricate interactions between plant roots, soil, and soil microbiota, endorsees plant growth by facilitating nutrient acquisition and transport portal, nitrogen fixation, siderophore production, phytostimulation through released exudates, volatile organic compounds and plant growth regulators, ameliorating biotic and abiotic stresses, signal transduction and shaping plant microbiome for sustainable crop production. Intrinsic biological properties of rhizospheric microorganisms such as nitrogen fixation, maintaining soil phosphorus dynamics through phosphate solubilization, hydrogen cyanide, phytohormones and siderophores production, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity are appraised as plant growth promotion (PGP) traits. Several rhizosphere microorganisms have been reported exhibiting various PGP traits (Table 16.1). PGPRs are used as biofertilizer inoculants, bioremediation, and for competitive suppression of pathogens/antibiosis. PGP microbes sequester soil minerals and facilitate their efficient uptake by growing plants. Owing to their multi-faceted role in crop growth, the rhizosphere microbial community makes up the main component of integrated farm/crop management. Rhizosphere microbiota can be harnessed in defining root system architecture and manipulating phonological traits. The utilization of PGP microbes in agriculture offers tremendous potential as a cost-effective, eco-friendly, and sustainable alternative. Understanding the factors promoting diversity and richness of beneficial microbes in the rhizospheric region can supplement conventional agriculture transforming it into a sustainable venture. This chapter provides insight into the role of rhizosphere inhabiting microbes in furnishing overall plant growth through direct (nutrient acquisition and assimilation, phytostimulation through exudation and hormones) and indirect (amelioration of biotic and abiotic stresses) mechanisms and their use as an alternative strategy (biofertilizer, modulating root architecture, manipulating phonological traits) to meet environmental standards besides food security (Summarized in Fig. 16.1).

16.2 Microbial-Based Fertilizers

Rhizosphere microorganisms belonging to several bacterial/fungal genera or kingdom protozoa can be potentially used for the production of microbial-based fertilizers. Microbialfertilizers assist in efficient soil nutrient uptake when delivered through seed or soil. Microbialfertilizers contribute to PGP traits, higher-yielding ability as well as improved soil fertility supporting sustainable agriculture. Several studies indicate the potential of rhizosphere microorganisms as biofertilizers for boosting the growth and nutrient content of crops under field conditions (Majeed et al. 2015; Lally et al. 2017). Wheat seeds inoculated with *Streptomyces nobilis* significantly increased shoot and root length, fresh and dry weight, number of leaves and roots (Anwar et al. 2016) as the rhizobacterial isolates efficiently produce IAA, siderophores, ammonia, and hydrogen cyanide along with possessing phosphate solubilization ability. Plant inoculation in wheat using rhizosphere and root-endosphere bacterial isolates *Stenotrophomonas* spp. and *Acetobacter pasteurianus*

Table 16.1 List of rhizosphere microorganisms with their plant growth promoting (PGP) traits

Crops	Microorganisms	PGP traits	References
Wheat	*Streptomyces* spp.	IAA production, phosphate solubilization, siderophore, ammonia and HCN production, ACC deaminase production	Anwar et al. (2016)
	Stenotrophomonas spp., *Stenotrophomonas rhizophila, Acetobacter pasteurianus*	Phosphate solubilization, production of IAA, enzymatic activity	Majeed et al. (2015)
	Bacillus siamensis (PM13), *Bacillus sp.* (PM15) *Bacillus methylotrophicus* (PM19)	Phosphate and zinc solubilization, production of IAA, ammonia, siderophore, exopolysaccharide, enzymatic activities (ACC-deaminase, catalase, protease)	Amna et al. (2019)
	Pseudomonas libanensis	Solubilization of potassium and zinc, production of siderophores, hydrogen cyanide, ammonia and ACC deaminase	Kour et al. (2019)
Rice	*Pseudomonas* sp. *Bacillus* sp.	Production of IAA, siderophores, ACC deaminase and phosphate-solubilization ability	Xiao et al. (2020)
	Pseudomonas aeruginosa, *Ralstonia* picketti, *Burkholderia cepacia, Klebsiella pneumoniae*	ACC utilization, exopolysaccharide production, P and K solubilization	Gontia-Mishra et al. (2017)
Maize	*Bacillus, Halobacillus Pseudomonas*	P-solubilization activity and IAA production	Mukhtar et al. (2020)
	Bacillus polymyxa, B. pantothenticus, B. anthracis, B. thuringiensis, *B. circulans*, *Pseudomonas cichorii, P. putida*, *P. syringae* and *Serratia marcescens*	Production of ammonia and hydrogen cyanide	Agbodjato et al. (2015)
Chickpea	*Cedecea davisae* RS3	Production of ammonia, IAA, phytase, and solubilization of inorganic phosphate and zinc	Mazumdara et al. (2019)
	Rhizobium leguminosarum, Pseudomonas aeruginosa	Production of phytohormone (IAA) and ammonia, phosphate-solubilization, siderophore and HCN (by P. Aeruginosa)	Yadav and Verma (2014)
Mung bean	*Pseudomonas aeruginosa* BHU B13–398, *Bacillus subtilis* BHU M	P solubilization, production of siderophore, HCN and ammonia	Kumari et al. (2018a)
	Pseudomonas spp., *Bacillus* sp., *Acinetobacter* sp.	IAA production, P solubilization, ammonia production, catalase	Kumari et al. (2018b)

(continued)

Table 16.1 (continued)

Crops	Microorganisms	PGP traits	References
		production, siderophore production, and antagonistic activity against phytopathogenic *Rhizoctonia solani*	
French bean	*Aneurinibacillus aneurinilyticus*, *Paenibacillus* sp.	Production of IAA, siderophore, ammonia, HCN and P and Zn solubilization	Gupta and Pandey (2020)
Soybean	*Streptomyces*	Production of siderophores, ACC deaminase, IAA and phenazines	Horstmann et al. (2020)
Sunflower	*Bacillus licheniformis* AP6 and *Pseudomonas plecoglossicida* PB5	P solubilization, IAA and ACC-deaminase activity	Yasmeen et al. (2020)

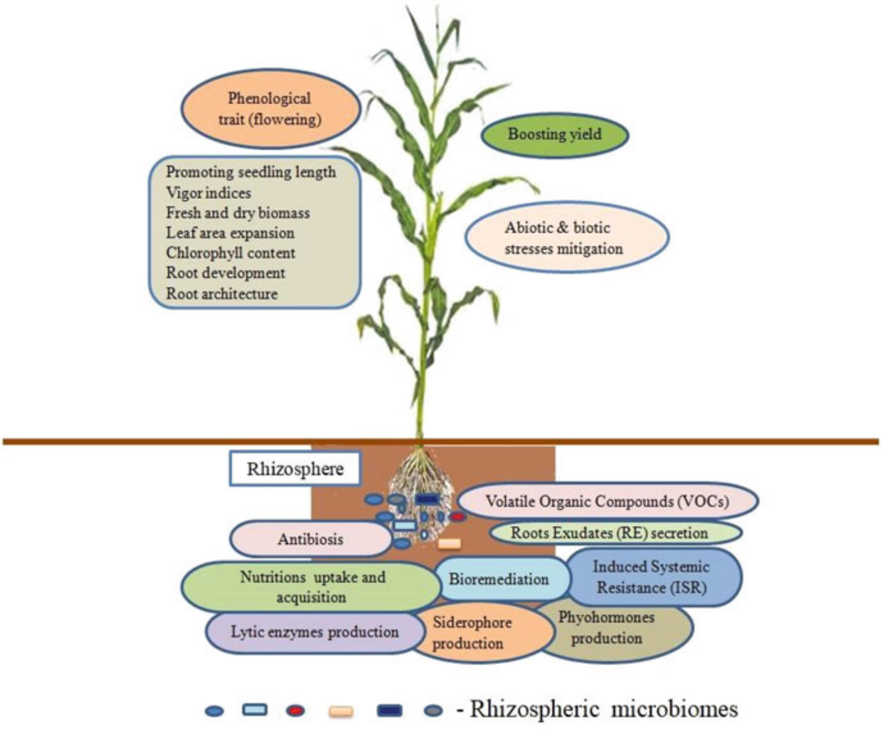

Fig. 16.1 Diverse roles performed by rhizosphere-inhabiting microbes

significantly increased shoot and root length, and shoot and root dry weight, N contents of wheat seedlings in vitro through their role in nitrogen fixation, P-solubilization and IAA-production (Majeed et al. 2015). Seed inoculation with

PGPR strains, viz. *Bacillus licheniformis*, *Bacillus*, *Paenibacillus polymyxa*, *Pseudomonas putida*, significantly increased root and shoot weight in barley (Canbolat et al. 2006). PGPB *Bacillus cereus* and *Klebsiella variicola,* isolated from rhizosphere and root endosphere, respectively increased plant growth and nutrient (iron, zinc, calcium, magnesium, copper, sodium, and potassium) contents significantly in tomato and mungbean. These two PGPB produced IAA, gibberellic acid, and kinetin resulting inenhanced shoot length in tomato and shoot length and dry weight in mung bean (Sunera et al. 2020). Endospore-forming diazotrophic bacilli isolated from the sunflower rhizosphere produced indolic compounds while a few of them exhibited nitrogenase activity as well. *B. mycoides* species significantly promoted N content and shoot dry weights of sunflower (Ambrosini et al. 2016). Application of biofertilizers modulates rhizosphere bacterial communities through changing soil physicochemical properties along with alleviation of mineral phytotoxicity and thus facilitates plant growth (Wang et al. 2019). Besides nutrient supplement to the soil, microbial biofertilizers suppress disease abundance. Fu et al. (2017) reported banana Fusarium wilt to be suppressed by biocontrol inoculant, *Bacillus amyloliquefaciens*. Biofertilizer-amended rhizosphere soils exhibited increased abundances of *Cryptococcus, Dyadobacter,* and *Sphingobium* while lowered abundances of *Burkholderia Fusarium* and *Ralstonia* (Fu et al. 2017).

Microbial-based fertilizers/biofertilizers consist of microorganism formulations developed using a single or cocktail of potential microbial strains. Dal Cortivo et al. (2020) demonstrated effects of bacterial (*Azospirillum* spp., *Azoarcus* spp., and *Azorhizobium* spp.) and mycorrhizal fungal-bacterial consortia on rhizosphere bacterial biomass and on plant growth and grain yield in wheat field trial. Wheat seed application with biofertilizers significantly enhanced plant growth and nitrogen accumulation with small gain in grain yield, upregulated two high-quality glutenin subunits, and increased rhizosphere microbial biomass. Endophytic and rhizospheric *Pseudomonas fluorescens* strains and endophytic microbial consortium were tested under glasshouse and field conditions in *Brassica napus*. PGP determinants (crop height, stem/leaf, pod biomass, seed, and oil yield) were enhanced in field as a result of biofertilizer application (Lally et al. 2017). Biofertilizers, posing low environmental threats, can play a key role in the development of integrated nutrient management systems sustaining agricultural productivity. A better understanding of rhizospheric microbes, their colonizing ability, functional diversity, mode of actions, and strategic application would facilitate their use for far-sighted sustainable agricultural systems.

16.3 Role of Rhizosphere Microorganisms in Nutrient Acquisition and Assimilation (N, P, K, Zn)

16.3.1 Biological Nitrogen Fixers

Nitrogen is an indispensable element required for normal physiological functioning of plants. Atmospheric nitrogen is not accessible to plants directly. Soil inorganic nitrogen available in the form of ammonium and nitrates is absorbed and utilized by plants. Plants procure nitrogen in utilizable form either through manure and/or nitrogen fertilizer or biologically fixed nitrogen. Soil nitrogen fixers (bacteria and *Archaea*) significantly contribute to atmospheric nitrogen fixation by the nitrogenase complex. Nitrogen-fixing prokaryotes are called diazotrophs. These diazotrophs exist either free-living or symbiotically associated with plants. Application of these microbes in the form of bio-inoculant or biofertilizer can reduce dependency on nitrogenous fertilizers. Seed treatment or soil inoculation of endophyte symbiotic microbes such as *Rhizobium* helps in fixation of biological nitrogen in legumes via root nodulation and in non-leguminous crops such as wheat (Yanni et al. 2016) and sorghum (Hara et al. 2019). *Azotobacter, Azospirillum, Clostridium, Gluconacetobacter diazotrophicus,* and *Beijerinckia* are some of the commonly known nonsymbiotic nitrogen fixing bacteria. Dent and Cocking (2017) reviewed the importance of nonrhizobial, nonnodulating BNF bacteria *Gluconacetobacter diazotrophicus* which significantly improves the yields in cereals and oilseed. Saha et al. (2016) applied a consortium of non-rhizobial endophytic microorganisms from *Typha angustifolia* and suggested the consortium to be effective in improving nitrogen uptake, assimilation, nitrogen use efficiency, and plant growth promotion in rice. Bacterial isolates closely related to *Azospirillum, Brevundimonas, Herbaspirillum, Pantoea, Pseudomonas, Rhanella, and Rhizobium* isolated from maize depicted nitrogen-fixing ability by reducing acetylene to ethylene (Montañez et al. 2009). Several studies have been reported where engineering of nitrogenase expression and *nif* gene clusters of endophytic bacteria can deliver higher nitrogen to cereals (Ryu et al. 2020; Li et al. 2016). Apart from bacteria, future research may unfold genetically engineered nitrogen-fixing cereals amenable for nodule organogenesis and infection by nitrogen-fixing bacteria.

16.4 Phosphorus-Solubilizing Microorganisms

Excessive use of inorganic fertilizers to augment agricultural productivity causes water pollution, waterway eutrophication, dwindled soil fertility, and accumulation of toxic elements in the soil (Alori et al. 2017). Phosphate-solubilizing bacteria and fungi facilitate phosphate solubilization and acquisition through conversion of insoluble organic and inorganic phosphates into readily utilizable form. Production of various enzymes (phosphatases, phytases, and lyases), organic/inorganic acids, and ion excretion by these microorganisms facilitate phosphate mineralization in soil (Sindhu et al. 2014). *Bacillus*, *Pseudomonas*, *Rhizobium, Azospirillum, Azotobacter, Enterobacter, Penicillium*, *Aspergillus*, actinomycetes, and arbuscular mycorrhizae are notable PSM genera (Kalayu 2019; Saleemi et al. 2017; Sharma et al. 2017). Srinivasan et al. (2012b) isolated 23 PSB and 35 PSF from salt-affected soil and investigated their phosphate solubilization potential under stress conditions. PSB were identified belonging to genera *Aerococcus, Alteromonas, Bacillus, Enterobacter, Erwinia, Pseudomonas,* and *Xanthomonas,* whereas PSF isolates were identified as *Aspergillus* and *Penicillium*. Fungal isolates were more efficient in terms of P solubilization than bacterial isolates (Srinivasan et al. 2012a).

Inoculation of PSB and vesicular-arbuscular mycorrhizal fungj reduced dependency on phosphorus in soybean–wheat cropping system providing better root property and higher grain yield (Mahanta et al. 2014). Inoculation with arbuscular mycorrhizal fungi (AMF) as biofertilizer improved plant growth and production by facilitating nutrient acquisition, modifying the abundance and diversity of rhizosphere microorganisms and by suppressing soil-borne pathogens acting as a probiotic agent (Liu et al. 2020). Wan et al. (2020) characterized 8 genera of PSB (*Acinetobacter, Arthrobacter, Bacillus, Cupriavidus, Massilia, Ochrobactrum*, *Pseudomonas,* and *Stenotrophomonas*) and their potential in immobilizing soil lead and identified *Acinetobacter pittii* gp-1 as good candidate. Mukhtar et al. (2017) assessed effects of biogas sludge and six phosphate solubilizing strains *Bacillus endophyticus, B. sphaericus, Enterobacter aerogenes* isolated from sugarcane rhizosphere, *B. megaterium,* and *B. safensis* and isolated from wheat rhizosphere and one halophilic strain *Virgibacillus* sp. isolated from *Atriplex amnicola* rhizosphere as biofertilizers on growth and yield of wheat. Under field conditions, enhanced root and shoot dry weights and seed weights were reported by *B. megaterium*, *B. safensis,* and *E. aerogenes* strain using biogas sludge as carrier.

16.5 Potassium-Solubilizing Microorganisms

Potassium is one of the essential macronutrients required by plants for enzyme activation, regulation of stomatal aperture, cell elongation, absorption, and utilization of other plant nutrients and maintaining osmotic balance (Xu et al. 2020). Potassium, like phosphorus, is slowly decomposed in soil matrices thereby its supply to growing crops is relatively low. In the soil matrices potassium is present as: water-soluble, exchangeable, non-exchangeable, and mineral forms (Bahadur et al. 2016). Potassium-solubilizing microorganisms (KSM) solubilize the fixed potassium forms to enhance their availability to crops. KSM are capable of solubilizing unavailable forms of potassium-containing minerals (micas, feldspar, illite, and orthoclases). Production of organic acids (citric acid, ferulic acid, coumaric acid, tartaric acid, oxalic acid, succinic acid, and α-ketogluconic acid), and protons supply by these microorganisms facilitate potassium mineralization in soil (Bakhshandeh et al. 2017; Setiawati and Mutmainnah 2016). *Arthrobacter, Agrobacterium, Acidithiobacillus, Aspergillus, Azospirillium, Bacillus, Burkholderia, Enterobacter, Erwinia, Pantoea, Flectobaccilus, Flavobacterium, Klebsiella, Microbacterium, Myroides, Paenibacillus, Pseudomonas, Rhizobium, Serratia,* and *Stenotrophomonas* are some of the well-known KSM in rhizopshere region (Bakhshandeh et al. 2017; Kour et al. 2020). Inoculation of rice with KSB *Pantoea agglomerans*, *Rahnella aquatilis,* and *Pseudomonas orientalis* enhanced grainyield and K uptake in addition to IAA production and tolerance to different environmental stresses (Khanghahi et al. 2018). *Bacillus* spp. effectively enhanced potassium uptake in the rhizosphere region by production of organic and inorganic acids eventually improving the root architecture system (Yasin et al. 2016). Despite their great relevance in replenishing soil fertility, phosphate−/potassium-solubilizing microorganisms are yet to be incorporated as an integral component of sustainable agriculture.

16.6 Zinc-Solubilizing Microorganisms

Compared to other soil nutrients zinc deficiency is not associated with availability rather solubility, which decreases at higher pH, high organic matter, Mg:Ca ratio, and P, Fe, Mn content in the soil (Nadeem and Farooq 2019). Zinc sulphate, the soluble form of zinc, which is generally applied to soil in agiculture gets converted to different insoluble forms like Zn(OH)2 at higher soil pH, $ZnCO_3$ in calcium-rich alkali soils, $ZnPO_4$ in alkali soils with heavy dose of P fertilizers application (Sarathambal et al. 2010). Plant growth promoting rhizobacteria helps in increasing the bioavailability of native zinc by solubilizing insoluble form (ZnO, $ZnCO_3$) to soluble form. Sindhu et al. (2019) suggested that seed/soil inoculation with ZSB enhances the bioavailability of not only Zn but also other nutrients including P and K, thereby maintaining the plant enzyme functions, oxidative stress, metabolic processes which get affected under deficiency and thus increases the crop yield. Gontia-Mishra et al. (2017) demonstrated ZSB from 4 different genera, namely *Burkholderia cepacia, Klebsiella pneumonia, Pseudomonas aeruginosa, and Ralstonia picketti* to efficiently solubilize ZnO and $ZnCO_3$. Zn solubilization and reduction in pH were positively correlated. Bhatt and Maheshwari (2020) characterized *Bacillus megaterium*, a zinc solubilizing bacteria for its potential in transforming ZnO to available zinc form along with phosphate solubilization and plant growth promotion attributes. *Pseudomonas* sp. and *Bacillus* sp. inoculation increased grain yield and plant growth parameters in chickpea through transforming insoluble forms of P and Zn to available form (Zaheer et al. 2019). Eshaghi et al. (2019) demonstrated with inoculation of siderophore-producing rhizobacterial strains of *Pseudomonas japonica in maize that these strains* can be used as a bio-fertilizer to combat iron and zinc deficiency in crops. The contribution of ZSB *Pantoea, Enterobacter cloacae,* and *Pseudomonas fragi* has been indicated in promoting growth and zinc content of wheat (Kamran et al. 2017). *Bacillus* sp., *Bacillus aryabhattai,* and *Bacillus subtilis* have been identified as ZSB strains with potential to promote maize growth and to be used as bio-inoculants for biofortification (Mumtaz et al. 2017).

16.7 Role of Rhizosphere in Root Development and Defining Root System Architecture

Roots are vital plant organs providing physical and nutritional support. Root system starts developing in the embryo favoring anchoring the plant system, nutrient uptake, and acquisition. The spatial arrangement of root system (primary root, lateral root, root hairs, root tips, crown roots, seminal roots) in the soil matrix is defined as root system architecture (RSA). Adaptation of the RSA helps plants cope with extreme conditions along with nutrient uptake and acquisition. Proper root/rhizosphere management could fortify nutrient use efficiency and crop productivity intensifying sustainable agriculture. Rhizosphere microbiota can modulate root system architecture by promoting root growth and distribution. Several PGPR have been documented modulating RSA through altered cell division and differentiation in primary root affecting lateral root development and root hair formation (Zhao et al. 2018; Ambreetha et al. 2018; Ortiz-Castro et al. 2014). Rhizosphere inhabiting fungi *Trichoderma atroviride* increases root hair length and density (Contreras-Cornejo et al. 2015). Similarly *T. virens* promotes lateral roots by altering auxin-inducible marker *DR5:uidA* in *Arabidopsis* (Contreras-Cornejo et al. 2009). Rice inoculation with PGPR *Bacillus altitudinis* strain FD48 affected root morphogenesis and RSA. Expression of auxin-responsive genes inhibited primary root elongation while promoting formation of lateral roots (Ambreetha et al. 2018). *Rhizobium* sp. IRBG74 suppresses elongation of main root and promotes formation of lateral roots through modulating auxin signaling in *Arabidopsis*. Transcriptome analysis revealed induced expression of auxin responsive reporter *DR5:GUS* in *Arabidopsis* roots (Zhao et al. 2018). Ortiz-Castro et al. (2020) reported *Pseudomonas putida* and *P. fluorescens* stimulated lateral root and root hair formation and increased plant biomass through activation of auxin signaling in *Arabidopsis thaliana*. Auxin signaling modulated auxin-responsive gene expression in roots through production of cyclodipeptides. Similarly, root colonization with *Achromobacter* sp. 5B1 has been demonstrated to influence growth and root architecture in *Arabidopsis thaliana* through auxin perception and redistribution resisting salt stress (Jimenez-Vazquez et al. 2020). Soil protozoa *Acanthamoeba castellanii* has been shown to increase root branching via modulation of auxin IAA metabolism and to foster auxin-producing soil bacteria (Krome et al. 2010).

16.8 Rhizosphere-Mediated Amelioration of Biotic and Abiotic Stresses

Boosting crop yield to meet global food, feed, and fuel demands under continuously changing climate is often threatened by several stresses imposing new challenges for sustainable agriculture. Crop plants are exposed to various biotic (soil pathogens and pests) and abiotic (drought, salinity, heavy metals, acidity, sodicity, temperature extremes, water-logging, submergence) stresses which severely affect crop survival, fitness, and productivity. Crop growth is ceased depending upon the intensity of stress, duration of stress, crop growth stage, crop physiology, and cultivar susceptibility. Mitigation of abiotic stresses employing rhizosphere microbiota has emerged as a potential strategy offering minimal ecosystem disturbance.

16.9 Plant Health and Biocontrol

Synthetic pesticides and fungicides applications have been under common agronomical practices leading to enhanced food production in the last few decades. However, injudicious application of these chemicals has a negative effect on non-target organisms, with future threat of development of resistant pathogen races. Hence microbe-based plant health management and biocontrol agents are gaining attention being a non-chemical alternative. Several rhizosphere dwelling microorganisms have been reported as biological control agents (BCAs) against various soil pathogens in different crops (Table 16.2). Seed coating with biocontrol agents benefits crops by effectively providing disease resilience along with stimulating plant growth. *Pythium*-infested soils challenged with biocontrol agents *Paenibacillus peoriae* and *Streptomyces fulvissimus* strains coated wheat seeds significantly promoted plant height, root weight, and number of heads. Microbial diversity in wheat root and rhizosphere soil was notably influenced as per stages of crop growth under field and greenhouse trials (Araujo et al. 2020). Araujo et al. (2019) employed *Streptomyces* strain as a biocontrol agent in wheat seeds against *Rhizoctonia solani* infested soil in the glasshouse. Biocontrol application promoted plant growth and head maturation along with modulating root endosphere and rhizosphere soil microbiomes. Operational taxonomic units (OTUs) of *Balneimonas, Massilia, Pseudomonas,* and unclassified Micrococcaceae responded as potential protectors against *Rhizoctonia* infestation. The application of biocontrol agents can reduce fungal infestations by promoting a beneficial microbiome contributing to sustainable agriculture. Bio-inoculation with strains belonging to genera *Bacillus*, *Pseudomonas,* and *Rhizobium* promoted plant height, number of nods, fresh and dry weight in bean along with checking growth of *Fusarium solani* f. sp. *phaseoli* (Kalantari et al. 2018). Phagotrophic protists have been reported to protect plants by pathogen suppression and predicting pathogen dynamics through predation-induced shifts (Xiong et al. 2020). These microbiome predators can potentially promote plant performance through microbiome engineering.

16.10 Drought

Drought stress severely affects crop plants by deteriorating their morphological, physiological, and biochemical integrity. Drought hampers water and nutrient uptake, photosynthetic efficiency, stomatal conductance, membrane stability, and transpirational rate resulting in stunted growth, poor biomass, and dropped yield. Drought tolerance is a complex physiological phenomenon involving hormone-regulated modulation of root system architecture, signaling through ROS, osmoregulation, induction of systemic tolerance, and transcriptional regulation of host stress response genes. PGPR application mediates growth promotion as well as alleviation of drought stress in plants. PGPR-mediated stress tolerance in plants includes phytohormone production, enzyme stimulation (nitrogenase, phosphatase, antioxidant enzymes), siderophore and HCN production and regulating endogenous

Table 16.2 Biocontrol agents against soil-borne pathogens

Crop	Biocontrol agents	Source of occurrence	Targeting pathogens	Modes of action	Reference
Bacteria as BCAs					
Wheat	*Lactobacillus plantarum* SLG17 and *Bacillus amyloliquefaciens* FLN13	Rhizophere	*Fusarium culmorum*	Damaged hyphae through digestive enzymes	Baffoni et al. (2015)
	Stenotrophomonas maltophilia *Bacillus cereus* *Trichoderma harzianum*	Rhizophere	*Stenotrophomonas maltophilia* *Bacillus cereus* *Trichoderma harzianum*	Inhibit the mycelial growth	Dal Bello et al. (2002)
Potato	*Serratia plymuthica strain A294, Enterobacter amnigenus strain A167, Rahnella aquatilis strain H145, Serratia rubidaea strain H440, and S. rubidaea strain H469*	Rhizophere	*Pectobacterium spp., Dickeya spp.*	Production of antibiotic compounds, bio-surfactants and siderophores	Maciag et al. (2020)
Tomato	*Bacillus subtilis, Burkholderia cepacia, Bacillus atrophaeus*	Rhizosphere	*Fusarium oxysporum* f. sp. *lycospersici*	Secretion of chitinase and β-1,3-glucanase	Shanmugam and Kanoujia (2011)
	Pseudomonas segetis, P. syringae	Rhizophere	*Dickeya solani, Pectobacterium atrosepticum, P. carotovorum*	Enzymatic deterioration of signal molecules in quorum sensing interaction	Rodríguez et al. (2020)
	Streptomyces atrovirens N23 and *Trichoderma lixii* NAIMCC-F-01760	Rhizophere	*Rhizoctonia solani*	Chitinase, β-1,3-glucanase	Solanki et al. (2019)
	Pseudomonas sp. CHA0	Rhizophere	*Ralstonia solanacearum*	Competition for resources and interference with the pathogen	Hu et al. (2016)

Banana	*Pseudomonas putida* *Achromobacter sp.* *Rhizobium sp.* *Bacillus flexus*	Endophyte and Rhizophere	*Fusarium oxysporum* f. sp. *Cubense*	Inhibition of spore germination and mycelial growth due to antibiosis and antifungal metabolites production	Thangavelu and Gopi (2015)
	Bacillus sp. EPB10, *Bacillus* sp. EPB56, *Pseudomonas fluorescens* Pf1	Rhizosphere	*Fusarium oxysporum* f. sp. *cubense*	Enhances activity of cell wall degrading enzyme	Mathiyazhagan et al. (2014)
Ground nut	Bacillus amyloliquefaciens	Endophyte	*Ralstonia solanacearum*	Release of antimicrobial substances of Surfactin and Fengycin A	Wang and Liang (2014)
Soybean	*Pseudomonas aeruginosa, Bacillus cereus, Bacillus amyloliquefaciens*	Rhizosphere	*Sclerotinia sclerotiorum* *Macrophomina phaseolina*	β-1, 3 glucanase, chitinase, cellulase	Thakkar and Saraf (2014)
Pea	*Pseudomonas* sp., *Bacillus* sp., *Azotobacter* sp., *Azospirillum* sp., Pseudomonas	Rhizosphere	*Sclerotinia sclerotiorum*	Induced systemic resistance	Jain et al. (2015)
Chilli	*Bacillus cereus* *Bacillus subtilis*	Rhizosphere	*Phytophthora Capsici*	Alternation of the soil bacterial community	Zhang et al. (2019)
Fungi as BCAs					
Wheat	*Purpureocillium lilacinum*	Rhizophere	*Tribolium confusum*	Secretion of digestive extracellular enzymes that degrade cuticle	Barra et al. (2015)
	Beauveria bassiana	Rhizophere	*Heterodera filipjevi*	Secrete of chitinases, proteases	Zhang et al. (2020)
Maize	*Trichoderma harzianum*	Rhizophere	*Fusarium graminearum*	Disintegration of the hyphae by lytic enzymes	Saravanakumar et al. (2017)
Tomato	*Purpureocillium lilacinum*	Rhizophere/ egg of *M. incognita*	*Meloidogyne incognita*	Colonize the egg and degrade through lytic enzymes	Singh et al. (2013)
Bean	*Metarhizium* Sp.	Rhizophere	*Fusarium solani* f. sp. *phaseoli*	Secretion of enzyme	Barelli et al. (2020)

(continued)

Table 16.2 (continued)

Crop	Biocontrol agents	Source of occurrence	Targeting pathogens	Modes of action	Reference
Physalis peruviana	*Trichoderma virens* GI006 and *Bacillus velezensis* Bs006	Rhizophere	*Fusarium oxysporum* f. sp. *phaseoli*	Formation of biofilms and production of antimicrobial compounds	Izquierdo-García et al. (2020)
Citrus orchards	*Beauveria bassiana* *Metarhizium anisopliae*	Rhizophere	*Thaumatotibia leucotreta*, *Scirtothrips aurantii* *Planococcus citri*	Secrete of digestive enzyme	Acheampong et al. (2020)

ethylene levels through ACC-deaminase. A consortium consisting of ACC-deaminase-producing rhizobacteria (*Ochrobactrum pseudogrignonense*, *Pseudomonas* sp., and *Bacillus subtilis*) alleviated drought stress along with improved seed germination, dry weight, root, and shoot length in black gram and pea through elevated levels of ROS scavenging enzymes and osmolytes in conjugation with down-regulated ACC-oxidase gene expression (Saikia et al. 2018). ACC-deaminase-producing rhizobacteria *Achromobacter xylosoxidans* in combination with biochar enhanced grain yield, stomatal conductance, photosynthesis, chlorophyll, and carotenoids content in maize under drought stress (Danish et al. 2020).

Selvakumar et al. (2018) evaluated osmotolerant rhizospheric microbial strains toward growth responses and water stress alleviation in tomato for pot culture conditions. Stomatal conductivity, transpiration rate, photosynthesis, relative water contents, biomass, and fruit yield were significantly enhanced as a result of microbial inoculation. *Actinobacterium*, *Citrococcus zhacaiensis*, *Bacillus amyloliquefaciens* were reported as promising strains boosting crop yield. *Bacillus subtilis* inoculation alleviated drought stress and promoted shoot growth of *Platycladus orientalis* seedlings through cytokinin production. Bacterial inoculation significantly increased root exudates such as sugars, amino acids, and organic acids (Liu et al. 2013). *Bacillus cereus*, *B. subtilis*, and *Serratia* sp. were reported to induce drought tolerance in cucumber (Wang et al. 2012). In a similar study by Bresson et al. (2014), *Phyllobacterium brassicacearum* strain has been reported to alleviate drought stress in *Arabidopsis thaliana* through improved water status. Rhizosphere management strategy and rhizosphere engineering/enrichment by addition of drought-tolerant PGPR should be integrated for drought stress mitigation.

16.11 Temperature Stress

Heat stress often occurs in conjugation with other stresses under field conditions, among which drought stress is most common. Sensitivity of crops to heat stress is more during the reproductive phase than the vegetative phase. Seed germination, seedling growth, tillering, pollen fertility, grain filling, grain quality, and yield are hampered under elevated temperature. Bacterial strain *Pseudomonas brassicacearum* along with other PGPRs has been elucidated to reduce heat stress in wheat when applied as bioinoculant as the seedling growth has been promoted due to catalase, oxidases, antioxidant enzymes, proline, and protein content (Ashraf et al. 2019). Seed treatment with strains of *Bacillus amyloliquefacien*s or *Azospirillum brasilense* has been demonstrated effective for heat stress tolerance in wheat corresponding to lesser reactive oxygen species generation and preactivation of certain heat shock transcription factors (Abd El-Daim et al. 2014). Heat tolerant PGPR *Bacillus cereus* has been demonstrated to significantly reduce heat stress in tomato through ACC-deaminase and exopolysaccharide production in the growth chamber resulting in augmented plant growth (Mukhtar et al. 2020). Thermotolerant PGPR *Bacillus tequilensis* improved growth of Chinese cabbage seedlings and soybean under heat stress through elevated levels of jasmonic acid and salicylic acid while down-regulating ABA production (Kang et al. 2019). Thermotolerant *Bacillus cereus* SA1 inoculation has been reported to augment heat stress in soybean through overexpression of stress responsive genes and HSPs along with modulation of auxin, ABA and SA (Khan et al. 2020).

Effect of PGPR *Serratia nematodiphila* was assessed on physio-hormonal attributes of *Capsicum annuum* plants subjected to low-temperature stress. Inoculated plants exhibited higher endogenous GA_4 and ABA levels whereas endogenous jasmonic acid and salicylic acid contents were down-regulated (Kang et al. 2015).

16.12 Salinity

Higher concentration of salt present in soil is one of the major environmental stresses drastically affecting crop productivity. Physiological processes such as respiration, photosynthesis, reproduction, nitrogen fixation, water, and nutrient uptake are impaired under salt stress. Soil salinity leads to osmotic stress, nutrient deficiency/ imbalance, ion toxicity, and oxidative stress on plants. PGPRs and several fungi have been demonstrated for their potential toward alleviation of salt stress in crops (Yasmeen et al. 2020; Hamayun et al. 2017). Inoculation of rice with salt-tolerant PGPRs *Bacillus tequilensis* and *Bacillus aryabhattai* demonstrated improved photosynthesis, transpiration, and stomatal conductance resulting into higher yield corresponding to exopolysaccharide production and sodium ion chelation (Shultana et al. 2020). Abdelmoteleb and Gonzalez-Mendoza (2020) demonstrated that inoculation with two *Tamarix ramosissima* rhizosphere PGPR strains, *Bacillus megaterium* and *Bacillus cereus* significantly increased plant height, root length, root and shoot dry weight, P content and photosynthetic pigments in *Phaseolus vulgaris* under salt stress condition in vivo. Amna et al. (2019) elucidated PGPR *Bacillus siamensis* PM13, *Bacillus* sp. PM15 and *B. methylotrophicus* PM19 strains alleviated the effects of salt stress on wheat seedling through sodium sequestration and ACC degradation. Nawaz et al. (2020) suggested bioinoculation with *Bacillus pumilus*, *Pseudomonas fluorescens,* and *Exiguobacterium aurantiacum* both singly and in consortium can augment yield, nutrient acquisition and plant growth parameters in wheat genotypes. Endophytic fungus, *Aspergillus flavus* (isolated from *Chenopodium album* roots) ameliorated adverse effects of salt stress by down-regulation of ABA and JA synthesis and elevated activities of various antioxidant enzymes (catalase, peroxidase, polyphenoloxidase, and superoxide dismutase) in soybean plant apart from growth promoting activities (Asaf et al. 2018). Another endophytic fungus *Porostereum spadiceum* has been reported mitigating salt stress by modulation of endogenous phytohormones (GAs, JA, and ABA) and isoflavones in soybean seedlings (Hamayun et al. 2017).

16.13 Metal Toxicity

Heavy metals such as arsenic, lead, copper, cadmium, mercury, aluminum are soil pollutants having phytotoxic effects. These heavy metals get accumulated in plant tissues hampering crop productivity. Heavy metal accumulation interrupts enzymatic activity and causes chlorosis, stunted growth and ROS generation in plant system (Tiwari and Lata 2018). PGPRs can effectively immobilize heavy metals and reduce their translocation in plants via precipitation, chelation, complex formation, and adsorption. Rhizobia possess phytoremediation and plant growth-promoting mechanisms besides nitrogen fixation. Brígido et al. (2017) characterized a collection of native Portuguese chickpea *Mesorhizobium* isolates to evaluate their potential toward PGP traits and tolerance to different metals. Most of the bacterial isolates exhibited IAA synthesis, siderophore production, P solubilization, acid phosphatase and cytokinin activity and tolerance to Zn or Pb indicating their potential as PGP rhizobacteria as well as in phytoremediation. *Pseudomonas aeruginosa* and *Burkholderia gladioli* enabled tomato seedlings to reduce cadmium stress (Khanna et al. 2019). PGPR *Bacillus toyonensis* strain Bt04 enhanced growth and root development under aluminum toxicity through production of IAA, a non-indole phenylacetic acid cytokinins and increasing protection against oxidative stress in maize (Zerrouk et al. 2020). Auxin transport pathway has been demonstrated crucial for aluminum-induced stress response post PGPR inoculation (Zerrouk et al. 2020). Kang et al. (2017) explored the ameliorative capacity of PGPR *Leifsonia xyli* against copper stress in tomato. Detrimental effects of copper stress were relieved through modulation of endogenous amino acids contents (arginine, glutamic acid, glycine, threonine, phenylalanine, and proline) and phytohormones gibberellic acid and IAA. Bio-inoculation increased P and Fe content, stimulated total polyphenol and flavonoid content whereas reduced superoxide dismutase activity in plants grown under elevated Cu stress. Similarly *Paenibacillus polymyxa* and *Bacillus circulans* inoculation conferred copper toxicity resilience to maize plants through decreased malondialdehyde and copper content in root and shoot tissues due to better antioxidant enzymes activities and osmolyte regulation (Abdel Latef et al. 2020).

16.14 Phytostimulation Through Exudation and Hormones

Rhizosphere microbiome exert phytostimulatory effect through releasing various root exudates, volatile organic compounds (VOCs), and hormones such as auxin, gibberellins, cytokinin, and ethylene. Root exudates modify soil properties, nutrient acquisition and enable crop survival under extreme environmental conditions through mechanisms such as (1) changing soil pH for mineral solubilization, (2) chelating toxic compounds, (3) recruiting rhizosphere microbiota, or (4) releasing toxic substances for pathogens, etc. Root exudation and its composition are affected by physical, chemical, and biological agents. Root exudates include carbohydrates, amino acids, and organic acids (primary metabolites) and flavonoids, glucosinolates, auxins (secondary metabolites) depending up on the quantity of release. Abiotic stresses, nutrient availability, and several other physical, chemical, and biological factors affect root exudation process. Bacteriogenicindole-3-acetic acid (IAA) controls lateral root formation, primary root elongation, and root hair synthesis which ultimately enhances root length and surface area coverage, improving water and nutrient acquisition and overall plant growth. Gibberellic acids (GAs) promote shoot elongation, germination, flowering, and leaf growth. Cytokinin triggers proliferation of root hairs and promotes cell division and acts antagonistically with auxins by inhibiting lateral root formation and primary root elongation.

16.15 Auxin

Seed bacterization with PGPR of the genera *Escherichia*, *Micrococcus*, *Pseudomonas,* and *Staphylococcus* significantly increased shoot length, pod number, biomass, and grain weight of mungbean through IAA production in the presence of L-tryptophan (Ali et al. 2010). Bose et al. (2016) reported bacterial isolate *Enterobacter cloacae* exhibiting maximum IAA production along with other PGP traits. Seed bioinoculation with this siderophorogenic auxin producer enhanced seed germination and plant vigor under in vivo condition of different cereals (rice, wheat, and maize), pulse (mung), and oilseed (groundnut). IAA-producing Bacillus strains have been demonstrated to stimulate growth in wheat (Ravari and Heidarzadeh 2014). Bhattacharyya et al. (2015a, b) reported that volatile indole produced by rhizobacterium *Proteus vulgaris* stimulated plant growth through hormonal interplay of auxin, cytokinin, and brassinosteroid in *Arabidopsis thaliana. Arabidopsis thaliana* Col-0 seedlings exposure to volatile indole for 2 weeks resulted in overexpression of *small auxin up RNA, histidine kinase1*, and *brassinosteroid biosynthetic cytochrome P450* genes. Auxin-producing microorganisms strengthen crops to withstand various abiotic stresses besides stimulating growth. Auxin-producing PGPR of the genera *Bacillus*, *Enterobacter*, *Moraxella*, and *Pseudomonas* have been effective in mitigating drought stress in wheat (Raheem et al. 2017). *Pseudomonas* strains (*P. aureantiaca* TSAU22, *P. extremorientalis* TSAU6, and *P. extremorientalis* TSAU20) effectively alleviated salinity stress on wheat seed dormancy (Egamberdieva 2009). *Pseudomonas fluorescens* Ms-01 and *Azospirillum brasilense* DSM1690 have been reported prominent to neutralize salinity stress in wheat and promoting plant growth due to production of auxin and P solubilization (Kadmiri et al. 2018).

16.16 Ethylene

Crop growth and productivity are often impeded by environmental stress induced ethylene content. Under such circumstances bio-inoculation with bacteria-producing ACC deaminase could be an effective approach to mitigate abiotic stress and promote plant growth with lowered endogenous ethylene level. Bacteria-producing 1-aminocyclopropane-1-carboxylate deaminase enzyme actively modulates ethylene levels and facilitates plant growth under adverse environmental conditions. ACC deaminase-producing bacteria prevent flower wilting, promote rooting, and facilitate nodulation of legumes (Gamalero and Glick 2015). Seed bacterization employing rhizobacterial strains *Aneurinibacillus aneurinilyticus* and *Paenibacillus* sp. isolated from *Allium sativum* rhizosphere significantly alleviated salt stress stimulated ethylene levels and its associated growth inhibition by virtue of their ACC deaminase activity in french bean seedlings. In addition to this, bacterial consortia treatment facilitated PGP parameters (fresh weight, shoot and root biomass and chlorophyll content) through PGP traits (Gupta and Pandey 2019). Similarly, Gupta and Pandey (2020) demonstrated that consortium inoculum formulated with two salt-tolerant strains *Aneurinibacillus aneurinilyticus* and *Paenibacillus* sp. markedly improved seed germination, root/shoot length, fresh and dry weight, water content, chlorophyll and carotenoid content, osmoprotectants (proline and total soluble sugar) levels of salt exposed plants due to down-regulated ethylene levels in common bean under saline conditions. Co-inoculation with halotolerant IAA and ACC deaminase-producing bacterial strains belonging to genera: *Achromobacter, Enterobacter*, *Microbacterium*, *Pseudomonas,* and *Serratia* improved seedling emergence, biomass and SOD activity under saline conditions in wheat (Barra et al. 2016). Rice seedlings inoculated with ACC deaminase-producing salt-tolerant *Burkholderia* sp. improved seedling growth exposed to salt stress through mechanisms involving reduced ethylene levels, scavenging ROS and proline and IAA production (Sarkar et al. 2018). ACC-deaminase-producing PGPR *Achromobacter xylosoxidans* and *Enterobacter cloacae* in combination with biochar help ameliorate drought stress in maize (Danish et al. 2020).

16.17 Gibberellins

Gibberellin-producing microorganisms have been isolated from soil and rhizosphere having a beneficial effect on plant growth. GA secreting rhizobacterium *Leifsonia soli* sp. SE134 culture filtrate prompted biomass and root lengths of cucumber seedlings, growth of rice seedlings, growth promotion in tomato and radish (Kang et al. 2014). Bacterial endophyte *Bacillus amyloliquefaciens* improved growth parameters and physiology of rice plants through GA production. Inoculated rice plants exhibited higher endogenous salicylic acid and lower abscisic and jasmonic acid (Shahzad et al. 2016). Tomato plants inoculated with PGPR *Promicromonospora* sp. SE188 exhibited higher shoot length and biomass due to up-regulated GA biosynthesis pathway. Abscisic acid was decreased whereas salicylic acid was profoundly higher in inoculated tomato plants (Kang et al. 2012). do Amaral et al. (2014) reported that endophytic diazotrophic bacterium, *Herbaspirillum seropedicae,* modulated expression of gibberellin biosynthesis pathway genes and NADPH oxidase transiently in maize root. Inoculated seedlings had a higher number of lateral roots. Quantification of transcript levels of ten maize genes revealed *ent-kaurene oxidase* and *respiratory burst oxidase protein C* to increase in inoculated seedlings.

PGPR *Leifsonia xyli* SE134 effectively ameliorates copper stress on tomato through modulating GAs and IAA metabolism along with endogenous amino acids (arginine, glutamic acid, glycine, threonine, phenylalanine and proline) contents (Kang et al. 2017). GA and ABA released by *Azospirillum* significantly contributes to the alleviation of water stress in maize (Cohen et al. 2009). Gibberellin-producing PGPR *Serratia nematodiphila* helps in mitigating low-temperature stress in pepper plants owing to higher endogenous GA and ABA levels and reduced jasmonic and salicylic acid levels (Kang et al. 2015).

16.18 Cytokinin

Phytohormone-producing PGPR possesses phytostimulatory potential. Phytohormones, especially cytokinin, have been studied for their biocontrol mechanisms and environmental resilience in addition to developmental regulation and governing plant physiology. Großkinsky et al. (2016) demonstrated *Pseudomonas fluorescens* G20–18 in biocontrol of *P. syringae* infection in *Arabidopsis* where cytokinin has been identified as being the key determinant. Inoculation of *Platycladus orientalis* seedlings with *Bacillus subtilis* improved leaf water potential and relative water content while decreased root/shoot ratio under water-stressed conditions due to higher cytokinin and abscisic acid content (Liu et al. 2013). Rhizosphere bacterial strains, belonging to the genera *Pseudomonas*, *Bacillus,* and *Azospirillum* have been screened for their phytostimulatory effect through phytohormones (cytokinins and IAA) production. Bacterial cytokinin stimulated shoot length, fresh and dry weight under axenic conditions while bacterial IAA negatively correlated to root length and positively to the number of roots. Inoculated plants exhibited an increase in spike length, tillering and seed weight under natural conditions (Hussain and Hasnain 2011a). Cyanobacteria possess phytostimulatory and biofertilization ability in addition to nitrogen-fixing ability. Cyanobacteria, viz. *Anabaena*, *Chroococcidiopsis*, *Oscillatoria*, *Phormidium*, and *Synechosystis* have been reported to release cytokinin (Hussain et al. 2010). Rhizospheric and free-living cyanobacteria *Chroococcidiopsis* sp. and *Anabaena* sp. improved seed germination, shoot length, spike length, number of tillers, number of lateral roots, and grain weight of inoculated wheat plants owing to phytohormones cytokinin and IAA (Hussain and Hasnain 2011b). PGPR *Bacillus aryabhattai* strain SRB02 promotes growth and tolerance to heat stress in soybean through phytohormones, viz. abscisic acid, IAA, cytokinin, jasmonic acid, and gibberellic acids (Park et al. 2017).

16.19 VOCs

Rhizospheric microorganisms can alter plant morphology, physiology, and phenology through the emission of volatile organic compounds (VOCs). Emission of VOCs by rhizosphere inhabiting microbes promotes growth and flowering of various crop plants. VOCs emitted by the phytopathogen *Alternaria alternata* triggered photosynthesis and cytokinin and sugars accumulation in *Arabidopsis* through modulating the expression of genes involved in photosynthesis, growth, and flowering (Sánchez-López et al. 2016). Microbial volatiles induce plant growth through phytohormonal regulation. *Bacillus subtilis* strain SYST2 induced growth in tomato through regulation of endogenous auxin, gibberellins, cytokinin, and ethylene levels. Albuterol and 1,3-propanediole were the main VOCs which promoted growth through phytohormonal regulation (Tahir et al. 2017). Venneman et al. (2020) demonstrated that VOCs from roots of endophytic fungus *Serendipita* spp. improve *Arabidopsis* seedling performance in terms of plant biomass, petiole elongation, leaf area expansion, lateral root extension, enhanced quantum efficiency of photosystem II. Fungal respiratory CO_2 along with methyl benzoate and other volatile compounds elicited plant growth promotion.

Microbial VOCs induce tolerance to abiotic stresses and defense against various biotic stresses. Volatiles (hexanedioic acid and butanoic acid) from *Alcaligenes faecalis* strain improved growth performance of *Arabidopsis thaliana* under salt stress through mediating auxin, gibberellins, and brassinosteroid pathways (Bhattacharyya et al. 2015b). *Bacillus amyloliquefaciens* strain emitted VOCs, diacetyl modulates immune system and phosphate-starvation response system in *Arabidopsis thaliana* through salicylic acid- and jasmonic acid-mediated immunity (Morcillo et al. 2020). Despite diverse roles offered by microbial VOCs we are still lagging in implementation of current knowledge of microbial VOCs as phytostimulants to support intensified sustainable agriculture.

16.20 Manipulating Phenological Traits (Flowering) and Heterosis

Though modulation in plant phenology is largely determined by environmental factors, several recent findings reported soil microbial communities to act as possible drivers of flowering time (Wagner et al. 2014; Lu et al. 2018). The role of rhizosphere microbiota in triggering and driving plant phenology has emerged as the latest area of interest to the scientific community. Rhizosphere microbiota can play an important role in modulating flowering time and contributing to phenotypic plasticity equipping crop plants to withstand climatic perturbations and increased crop production. Application of PGPRs consortium (*Azotobacter chroococcum*, *Bacillus subtilis, Pseudomonas florescens,* K-mobilizing bacteria, and AM fungi) in different combinations along with soil solarization significantly improved yield, phenological and pomological attributes of strawberry besides promoting rhizosphere microbial count in calcareous soils (Kumar et al. 2020). Lu et al. (2018) documented the role of rhizosphere microorganisms in delaying the flowering of *Arabidopsis thaliana* through conversion of tryptophan to IAA. Prolonged nitrogen bioavailability stimulated vegetative growth as the flowering genes were downregulated. Wagner et al. (2014) suggested soil microbes contribute to phenotypic plasticity of flowering time and reproductive fitness of *Boechera stricta.* Panke-Buisse et al. (2015) reported microbial inoculation shifted flowering time in

Arabidopsis thaliana and *Brassica rapa*. Host plants inoculated with late-flowering-associated microbiomes showed increased inflorescence biomass correlated with higher soil nitrogen mineralization resulting due to enhanced microbial enzyme activities.

Rhizosphere microbial communities have been reported to be associated with heterosis (Wagner et al. 2020). The rhizosphere of inbred lines and hybrids harbored different bacterial and fungal communities besides leaf-associated fungal communities. Microbiome composition is affected by heterotic host traits. Wagner et al. (2020) pinpointed the role of natural selection behind heritable components of microbiome variation reflecting plant–microbe interactions.

16.21 Conclusion

Augmenting crop yield and production in a sustainable way to meet raised demands of ever-growing global population under climate change scenario is an acquainted concern. Under such circumstances rhizosphere inhabiting microbes render a natural yet potent strategy to confront forthcoming challenges. These invisible forms of life can bring out visible and discernible changes by unlocking the gateway to sustainable agriculture. Advances in the next-generation sequencing platform, genome editing technologies (CRISPR/Cas9), bioinformatics and omics-based approaches are some of the genetic tools that would buttress efficient utilization of rhizosphere microbiome as "bioguards" against stresses and sustainable food production.

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