Rhizobacteria as Bioprotectants Against Stress Conditions

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Abstract

The area around the plant which is under the influence of plant roots, known as the rhizosphere, is an attractive habitat for soil microorganisms. However, although a variety of root-colonizing bacteria exist, the beneficial bacteria also called plant growth-promoting bacteria (PGPR) or rhizobacteria essentially serve as bioprotectants against stress conditions. Environmental abiotic stresses such as drought, salinity, and metal contamination, as well as biotic stresses from opportunistic pathogens, present a major challenge as it reduces the potential yields of food production. Rhizobacteria are of immense interest because they compete with indigenous bacteria and increase plant resistance against stress conditions. These bacteria have a number of traits that contribute to root colonization such as the presence of specific cell surface components, pili, fimbriae, chemotaxis toward plant exudates, ability to use specific components of plant exudates, protein secretion property, ability to form biofilms, and quorum sensing. The production of biologically active metabolites and the regulation of ACC deaminase are some of the principal mechanisms by which rhizobacteria modify the rhizosphere environment thereby enhancing plant growth. This article seeks to give an overview of mechanisms in rhizobacteria proposed to enhance stress tolerance conditions.

Keywords

Rhizobacteria · Abiotic stress · Stress tolerance · Plant growth

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R. Z. Sayyed et al. (eds.), *Plant Growth Promoting Rhizobacteria for Sustainable Stress Management*, Microorganisms for Sustainability 12,
https://doi.org/10.1007/978-981-13-6536-2_9

9.1 Introduction

The ever-increasing rise in world population has made the task of feeding the global population extremely difficult. Biotic stresses such as phytopathogens and herbivory and abiotic stresses such as flooding, drought, heating, freezing, radiations, and salinity variations due to global warming and climate change further challenge the agriculture industry. Environmental stresses are believed to reduce the potential yields by as much as 70% in crop plants and therefore constitute a major problem for sustainable food production. According to the current scenario, it has been estimated that food production needs to be increased as much as 50% by 2030. However, since food production is sensitive to environmental conditions, alternate strategies such as the systematic identification of bacterial strains that can help farmers reduce the anticipated adverse impacts of multiple stressors from global warming are highly valuable for agricultural production. Although a variety of bacteria exist, the root-colonizing nonpathogenic bacteria also called as plant growth-promoting bacteria (PGPR) or rhizobacteria hold promise, as they can increase plant resistance to biotic and abiotic stress factors, thereby essentially serving as bioprotectants against stress conditions. Here, we present an overview of current progress on the use of rhizobacteria under stress conditions and the modes of action of these bacteria in the mitigation of abiotic stresses.

9.2 Soil as an Ecosystem

The soil is a dynamic living matrix whose complexity is determined by the interplay of physical, chemical, and biological components, which is a manifestation of environmental conditions prevalent at that time (Buscot 2005). The soil matrix together with the physical properties like texture, porosity, and moisture holding capacity and chemical properties such as the amount of organic matter in the soil, its pH, and redox conditions influences the dynamics of structure and function of the microbial communities in soils (Lombard et al. 2011). Soil ecosystem is directly influenced by climate changes. Any increase in temperature would result in an increase in the microbial activity resulting in an altered microbial community. Another important factor which influences microbial community structure is the water content. Turnover of organic matter due to microbial activity is directly influenced by the water potential (Thomsen et al. 1999). Even the rate of respiration in soil depends upon the soil moisture content, temperature, and organic matter. Therefore any changes in temperature, salinity, and an increase in metal content due to pollution would result in manifesting as a stressful environment for plants. Under stress, there is a reallocation of resources from growth pathways in microorganisms to producing protective molecules, which could also benefit plants. However, ecologically it results in substantial amounts of C and N being vulnerable to loss (Schimel et al. 2007).

9.3 Root Exudates and Microbial Community Structure

Soil having more vegetation harbors a greater microbial population, compared to soil devoid of plants. The higher number of bacteria in the rhizosphere (the narrow region of soil that is directly influenced by root secretions and associated soil microorganisms) and rhizoplane (the external surface of roots together with closely adhering soil particles and debris) is because the rhizosphere region is rich in total organic carbon from root exudates and sloughed-off root cells and tissues (Barber and Martin 1976). Roots have been estimated to release between 10 and 250 mg C/g or about 10–40% of the total photosynthetically fixed carbon (Newman 1985). The products released by the roots in the surrounding soil are called rhizodeposits (McNear 2013). Rovira (1969) defined rhizodeposits based on their chemical composition and mode of release and function to include sloughed-off root cap and border cells, mucilage, and exudates. According to Walker et al. (2003), plant roots are not passive targets for soil organisms. This is evidenced as soon as a seed starts to germinate; the plant roots nurture a tremendous diversity of microbes via exudation of a wide variety of compounds such as carbohydrates, amino acids and proteins, organic acid anions, phytosiderophores, vitamins, purines, nucleosides, phenolics, and mucilage, which serve as chemical attractants and repellents in the rhizosphere (Bais et al. 2001; Estabrook and Yoder 1998; Stintzi and Browse 2000; Stotz et al. 2000). Del Gallo and Fendrik (1994) and Bell et al. (2013) attributed the regulation of soil microbial community to direct conflict and competition between the different species for nutrient acquisition and colonization, and differential growth patterns of the large population of microorganisms attracted to the exudates in the vicinity of the roots. According to Bais et al. (2004), root exudates promote beneficial microbial colonization on root surfaces (e.g., *Bacillus subtilis*, *Pseudomonas fluorescens*). Recently, the root-specific transcription factor MYB72 which regulates the excretion of the coumarin scopoletin, an iron-mobilizing phenolic compound with selective antimicrobial activity, has been reported by Stringlis et al. (2018) to shape the root-associated microbial community.

Dakora and Phillips (2002) explained how in low-nutrient environments, root exudates act as mediators of mineral acquisition by releasing extracellular enzymes such as acid phosphatases which mobilize phosphorus from organic compounds; as also molecules such as phytosiderophores increase iron availability through chelation. Organic acids such as malic and citric acids released into the rhizosphere from root exudates have been shown to effectively reduce the rhizosphere pH and solubilize unavailable soil Ca, Fe, and Al phosphates. Similarly, inorganic ions (e.g., HCO_3^-, OH^-, H^+) and gaseous molecules (CO_2, H_2) from root exudates could also modify the rhizosphere pH (Dakora and Phillips 2002). The mode of alteration of rhizosphere pH is linked to the form of nitrogen available in the soil. Plants respond differently when nitrogen in the form of ammonium is present. Since ammonium has a positive charge, the plant expels one proton (H^+) for every NH_4^+ taken up resulting in a reduction in rhizosphere pH; but when nitrogen in the form of NO_3^- is present, there is an increase in the rhizosphere pH due to the release of bicarbonate (HCO_3^-). Such alterations in pH can influence the availability of essential micronutrients such as Mg, Zn, and Ca for plants (McNear 2013).

Root exudates are also beneficial as chemical signals for the attraction of symbiotic partners such as *Rhizobia*. Peters et al. (1986) reported that flavonoids present in the root exudates of legumes were responsible for activating *Rhizobium meliloti* genes that help in nodulation. Where N_2 is reduced to ammonia, aldonic acids and phenolics exuded by roots of N_2-fixing legumes have been reported to serve as signals to *Rhizobiaceae* bacteria for the formation of root nodules.

Root exudates also serve as defense mechanisms against pathogenic microorganisms in the rhizosphere. Brigham et al. (1999) and Bais et al. (2002) reported biologically active compounds having antimicrobial activity in the root exudates of hairy root cultures, such as naphthoquinones of *Lithospermum erythrorhizon* and rosmarinic acid (RA) of sweet basil (*Ocimum basilicum*), respectively. Walker et al. (2003) and Doornbos et al. (2012) suggested that it is also possible that roots may develop defense strategies by secreting compounds into the rhizosphere that interfere with bacterial quorum-sensing responses such as signal blockers, signal mimics, and signal-degrading enzymes. Flores et al. (1999) attributed the survival of delicate unprotected root cells which are continuously under attack by pathogenic microorganisms to the secretion of defense proteins, phytoalexins, and other unknown chemicals. Thus, the plant may be in a positive or negative association with its microbial community, based on factors prevalent in the rhizosphere and the symbiotic or defensive role played by root secretions.

9.4 Plant Growth-Promoting Rhizobacteria

Plant growth-promoting rhizobacteria were first defined by Kloepper and Schroth (1978) as organisms that, after being inoculated on seeds, could successfully colonize plant roots and positively enhance plant growth (McNear 2013). Plant growth-promoting rhizobacteria (PGPR) are nonpathogenic, free-living soil and root-inhabiting bacteria that colonize seeds and root tissue (endophytic/epiphytic) or enhance production of root thereby promoting plant growth. Root-colonizing bacteria establish on or in the root or rhizosphere to multiply, survive, and colonize along the growing root in the presence of the indigenous microflora, thereby exerting beneficial traits on plant growth and development. Some examples of rhizosphere bacteria that have been found to have beneficial effects on various plants include species of the genera *Acinetobacter*, *Agrobacterium*, *Azotobacter*, *Arthrobacter*, *Alcaligenes*, *Azospirillum*, *Acetobacter*, *Actinoplanes*, *Bacillus*, *Bradyrhizobium*, *Cellulomonas*, *Clostridium*, *Enterobacter*, *Erwinia*, *Frankia*, *Flavobacterium*, *Pasteuria*, *Pseudomonas*, *Rhizobium*, *Serratia*, *Thiobacillus*, *Xanthomonas*, and others (Gray and Smith 2005), as well as *Streptomyces* spp. (Tokala et al. 2002; Dimkpa et al. 2008a, 2009b). To be an effective PGPR, bacteria must be able to colonize roots because bacteria need to establish themselves in the rhizosphere at population densities sufficient to produce the beneficial effects. However, the beneficial effect of the bacterial strains of a particular genus and species is not always the same for all plants and may even be negligible in some plants. According to Glick et al. (1999), the mechanism by which the bacteria promote plant growth may be directed by facilitating uptake of nutrients or by supplying a particular growth promoting substance synthesized by the bacteria, for example, volatile compounds of *Bacillus methylotrophicus* M4-96 increased shoot biomass and chlorophyll content (Pérez-Flores et al. 2017), or indirectly by acting as biocontrol agents against phytopathogens. Effective rhizosphere colonization by bacteria can be beneficial to plants to control diseases by producing antifungal factors; it can bring about phytostimulation by the production of phytohormones, fertilization by increasing the availability of nutrients, bioremediation of hazardous chemicals in the environment (Dekkers et al. 1999), and assist in mitigating stress.

9.5 Role of Microorganisms in the Rhizosphere

Microbial communities can be considered as architects of soils (Rajendhran and Gunasekaran 2008). There is a dynamic interaction between soilborne microorganisms, plant roots, and soil constituents at the root-soil interface. Root exudates and decaying plant material provide sources of carbon compounds for the heterotrophic biota (Barea et al. 2005; Bisseling et al. 2009), while in turn, the probiotic root microbiome members such as the rhizobacteria modulate their metabolism to optimize the acquisition of nutrients, protect the host plant against pests and pathogens, encourage beneficial symbioses, change the chemical and physical properties of the soil, inhibit the growth of competing plant species, and promote plant growth (Nardi et al. 2000; Hardoim et al. 2008). For the bacteria to establish themselves in the rhizosphere, certain cell surface structures such as pili, fimbriae, and flagella facilitate movement, attachment, and colonization on root surfaces (Merritt et al. 2007; Fernàndez and Berenguer 2000). Persello-Cartieaux et al. (2003) showed that bacterial flagella possess adhesive properties, but Tokala et al. (2002) observed that rhizobacteria such as *Streptomyces* spp. that do not possess flagella could still establish beneficial interactions with plants via development of hyphae in plant tissues.

Other traits that are useful for bacteria for competitive colonization are the O-antigen of lipopolysaccharide, amino acids, and vitamin B1, and root mucilage as a source of carbon (Dekkers et al. 1999).

9.6 Mitigation of Stress

Under stress conditions, plants recruit the help of microorganisms to change the chemical environment of the rhizosphere and alter the root morphology. They differentially recognize pathogenic or beneficial rhizobacteria by detecting diffusible substances, such as the quorum-sensing compounds such as N-acyl-L-homoserine lactones, which induces changes in the root secretion profile (Mathesius et al. 2003; Ortiz-Castro et al. 2011) and activates plant immunity (Schuhegger et al. 2006).

The presence of EPS from microorganisms has been implicated in symbiosis, protection from predation, biofilm formation, and stress conditions. After establishing themselves in the rhizosphere, bacteria form a mutualistic relationship with the plant roots. Although the exact mechanisms of plant growth stimulation under stress conditions remain largely speculative, it is known that they differ between bacterial strains and most certainly depend on the various compounds released by the different microorganisms. One of the mechanisms by which they stimulate plant growth is by phosphate solubilization. Rhizosphere bacteria from the genera *Pseudomonas*, *Bacillus*, and *Rhizobium* are among the most powerful phosphate solubilizers. The principal mechanism for mineral phosphate solubilization is the production of organic acids, and acid phosphatases play a major role in the mineralization of organic phosphorus in the soil. Stress-induced phosphate solubilization by *Arthrobacter* sp. and *Bacillus* sp. isolated from tomato rhizosphere was reported by Banerjee et al. (2010).

Another mechanism by which rhizobacteria can promote plant growth is by nitrogen fixation. Plant growth-promoting rhizobacteria (PGPR) strains *Serratia liquefaciens* and *Serratia proteamaculans* were reported to increase nodulation, nitrogen fixation, and total nitrogen yield in two soybean cultivars in a short season area (Dashti et al. 1998). Sharma and Johri (2003) reported that maize seeds inoculated with siderophore-producing pseudomonads were better suited for iron uptake under iron-stressed conditions.

Rhizobacteria are known to stimulate plant growth (Patten and Glick 2002; Joo et al. 2005; Ryu et al. 2005; Aslantaş et al. 2007; Dimkpa et al. 2009a) via secretion of phytohormones – auxins, cytokinins, gibberellins, abscisic acid (ABA), and ethylene (Arkhipova et al. 2007; Dobbelaere et al. 2003; Forchetti et al. 2007; Perrig et al. 2007), which act directly or in concert with other bacterial secondary metabolites. In low concentrations auxins, specifically indole acetic acid (IAA), are reported to be produced in the plant shoot and transported basipetally to the root tips (Martin and Elliott 1984), where they enhance cell elongation, resulting in enhanced root growth and the initiation of lateral roots. Promotion of root growth results in a larger root surface, and can therefore have positive effects on water acquisition and nutrient uptake. However, when the concentrations of auxin are too high in the root tips, they are said to have an inhibitory effect on root growth. When the plant is exposed to different types of stress, ethylene synthesis is reported to increase, and it plays a key role in stress-related signal transduction pathways (Wang et al. 2002).

Haas and Défago (2005) showed that the production of siderophores confers competitive advantages to rhizobacteria, excluding other microorganisms from this ecological niche. A pseudobactin siderophore produced by *P. putida* B10 strain was reported by Kloepper et al. (1980) to suppress *Fusarium oxysporum* in soil deficient in iron. Under highly competitive conditions, the ability to acquire iron via siderophores may finally determine the survival of microorganisms competing for different carbon sources from rhizodeposition (Crowley 2006).

9.7 Role of Rhizobacteria in Mitigating Abiotic Stresses

Environmental stress plays a crucial role in productivity, survival, and reproductive biology of plants. Plants are subjected to many forms of environmental stress, which can be categorized into two broad areas: abiotic (e.g., physical stress due to drought, high temperature, chilling and freezing, UV-B radiation, salinity, and heavy metals) and biotic stress (e.g., pathogen, herbivores). Plant growth-promoting rhizobacteria (PGPR) could play a significant role in the alleviation of stress in plants (Table 9.1).

9.7.1 Water Stress

In order to survive, plants require a certain amount of water. Too much water (flooding stress) may cause cells to swell and burst, whereas too little water (drought stress) can cause the plant to dry up. Drought stress results in various physiological and biological changes in plants (Rahdari et al. 2012) because it influences the availability and transport of soil nutrients, water being the medium by which nutrients are carried through the roots (Selvakumar et al. 2012). Drought also induces free radicals formation such as hydroxyl radicals, hydrogen peroxide, and superoxide, which at high concentrations cause damage at various levels of organization (Smirnoff 1993). Deterioration of plant cell membrane, lipid peroxidation, and

Table 9.1 Mitigation of various stresses

Stress	Stress
Salinity	Drought
ACC deaminase reducing ethylene production	ACC deaminase reducing ethylene production
Increased P, Ca^{2+}, and K^+ uptake	Increased osmolyte production
Increased water use efficiency	IAA stimulated root growth
Removal of salt suppression of photosynthesis	Nitric oxide stimulated root growth
IAA stimulated root growth	Induced changes in root cell wall/cell membrane
Nitric oxide stimulated root growth	EPS production
Osmolyte production	Synthesis of antioxidative enzymes
EPS production	Change in transpiration rate
Synthesis of antioxidative enzymes	Improved nutrient uptake
Ion homeostasis	Reproductive delay
Improved nutrient uptake	Improved photosynthetic pigment
	Production of volatile organic compounds
Temperature stress	Heavy metal stress
ACC deaminase reducing ethylene production	ACC deaminase reducing ethylene production
Induced changes in root cell wall/cell membrane	IAA stimulated root growth
Upregulation of stress genes	Nitric oxide stimulated root growth

degradation of proteins, lipids, and nucleic acids are some of the effects of oxidative stress reported by Hendry (2005), Nair et al. (2008), and Sgherri et al. (2000). Marulanda et al. (2010) studied the possibility of increasing drought tolerance of plants growing in arid or semiarid areas by inoculation of plants with native beneficial microorganisms. Beneficial microorganisms such as *Bacillus amyloliquefaciens*, *Bacillus licheniformis*, *Bacillus thuringiensis*, *Paenibacillus favisporus*, and *Bacillus subtilis* were found to colonize the rhizosphere of plants and promote growth under stress conditions. Heidari and Golpayegani (2012) showed that inoculation with rhizobacteria effectively improved plant growth by increasing antioxidant status especially of glutathione peroxidase and ascorbate peroxidase, and photosynthetic pigments in basil *(Ocimum basilicum)*. Another mechanism by which rhizobacteria are reported to impart drought tolerance is by producing exopolysaccharides (EPS). *Bacillus* spp. secrete conspicuous amounts of EPS under stress conditions (Vardharajula et al. 2010). EPS forms an organo-mineral sheath around the cells, favoring increased macroaggregate formation, which helps in the survival of plants under drought stress by increasing water stable aggregates and root-adhering soil per root tissue (RAS/RT) ratio (Alami et al. 2000). PGPR play a significant role in alleviating environmental biotic-abiotic stress conditions by the production of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase. Figueiredo et al. (2008) reported a link between ACC deaminase activity of the rhizobacterium *Rhizobium tropici* and reduction in drought stress in *Phaseolus vulgaris* L. Similar instances of enhanced drought tolerance were reported in tomato plant due to the PGPR *Bacillus cereus* AR156 (Chun Juan et al. 2012) and in *Arabidopsis thaliana* by *Paenibacillus polymyxa* (Timmusk and Wagner 1999). ACC serves as the precursor of the plant hormone ethylene synthesized in plant tissues during stressful conditions. PGPR also colonize the rhizosphere/endo-rhizosphere of plants and impart drought tolerance by producing volatile compounds (Naznin et al. 2012), inducing accumulation of osmolytes, upregulation, or downregulation of stress-responsive genes and alteration in root morphology. IAA stimulates stress tolerance because of physical and chemical changes in the plant caused by these PGPR (Marulanda et al. 2009) (Table 9.2).

9.7.2 Temperature Stress

Freezing stress can affect the amount and rate of uptake of water and nutrients, leading to cell desiccation, starvation, and death. Intense heat can cause plant cell protein denaturation or affect cell wall and membrane permeability. Inoculation of *Pseudomonas* sp. strain AKM-P6 and *P. putida* strain AKM-P7 enhanced the tolerance of sorghum and wheat seedlings to high-temperature stress due to the synthesis of high-molecular-weight proteins and also improved the levels of cellular metabolites (Ali et al. 2009, 2011). Production of ACC deaminase by rhizobacteria also helped the plant to withstand extreme temperatures (Table 9.3).

Table 9.2 Role of PGPR in ameliorating water stress

Stress condition	Rhizobacterial inoculant	Plant species	Mechanisms	References
Water stress	*Acinetobacter* sp. and *Pseudomonas* sp.	Grapevine	Siderophore release and solubilization of inorganic phosphate compounds, EPS production	Rolli et al. (2015)
Water stress	*Citrobacter freundii* J118	Tomato	Increased uptake of nutrients	Ullah et al. (2016)
Water stress	*Brevibacillus brevis*	Cotton	Phosphate solubilization, IAA production, acetylene reduction, and antifungal activity	Nehra et al. (2016)
Water stress	*Pseudomonas putida*	*Arabidopsis thaliana*	Auxin secretion	Shah et al. (2017)
Water stress	*Bacillus megaterium BOFC15*	*Arabidopsis thaliana*	Spermidine secretion (a type of polyamine)	Zhou et al. (2016)
Water stress	*Acinetobacter pittii* JD-14	Alfalfa	Improved the relative water content; chlorophyll a; chlorophyll b; carotenoid contents; nitrogen (N), phosphorus, and potassium contents	Daur et al. (2018)

Table 9.3 Role of PGPR in ameliorating temperature stress

Stress condition	Rhizobacterial inoculant	Plant species	Mechanisms	References
Temperature stress	*Burkholderia phytofirmans* strain *PsJN* (*Bp PsJN*)	*Arabidopsis thaliana*	Differential accumulation of pigments; cell wall strengthening in the mesophyll	Su et al. (2015)
Temperature stress	*Burkholderia phytofirmans* strain PsJN	Potato	ACC deaminase	Bensalim et al. (1998)
Temperature stress	*Bacillus safensis* and *Ochrobactrum pseudogrignonense*	Wheat	Increased redox enzyme activity and accumulated osmolytes like proline and glycine betaine; maintained cell viability, restored chloroplast structure	Sarkar et al. (2018a, b)
Temperature stress	*P. putida*	Canola	ACC deaminase	Cheng et al. (2007)

9.7.3 Salinity Stress

High amounts of salt taken up by a plant can lead to cell desiccation, adversely affecting biochemical processes. Mahmood et al. (2016) showed that inoculation of mung bean with EPS-producing *Enterobacter cloacae* P6 and *Bacillus drentensis* P16 increased water and nutrient availability to crops due to the formation of biofilm on the root surface. Bacterial exopolysaccharide (EPS) produced by plant growth-promoting rhizobacteria was reported to help mitigate salinity stress by reducing the content of sodium available for plant uptake (Upadhyay et al. 2011) while increasing the uptake of phosphorus and potassium. Ashraf and McNeilly (2004) explained how EPS reduces sodium uptake and transfer to leaves thereby alleviating salt stress. Kasotia et al. (2016) proposed that plant-microbe biofilm on the surface of seedlings resulted in a lesser flow of sodium to the steel, insulating from NaCl toxicity. *Enterobacter* sp. P23 was shown to promote rice seedling growth under salt stress, and this effect was correlated with a decrease in antioxidant enzymes and stress-induced ethylene production. These bacteria possessed ACC deaminase activity and therefore could use ACC as a nitrogen source preventing ethylene production since ACC is a precursor of ethylene (Sarkar et al. 2018a, b).

Bacterial IAA is also shown to stimulate (ACC) deaminase activity for degradation of the ethylene precursor ACC (Glick 2005). Bianco and Defez (2011) also proposed that the toxic effects of salinity could be reduced by modulation of major plant hormones such as IAA. Mansour (2000), Hare and Cress (1997), Kavi Kishor et al. (2005), and Verbruggen and Hermans (2008) attributed salinity tolerance to the accumulation of nitrogen-containing compounds such as the amino acid proline in plants. The activities of the antioxidative enzymes such as catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (POX), glutathione reductase (GR), and superoxide dismutase (SOD) increase under salt stress in plants, and a correlation between these enzyme levels and salt tolerance has been described (Apel and Hirt 2004). PGPR strains producing IAA showed high antioxidant enzyme activity in *Medicago* plants which were found to enhance their protection against salt stress (Bianco and Defez 2009). Wang et al. (2016) reported that *V. paradoxus* 5C-2 mitigated salt stress by improving water relations, ion homeostasis, and photosynthesis in pea plants. Rhizobacteria were also found to increase the water use efficiency in saline environments and to help alleviate salt suppression of photosynthesis (Table 9.4).

9.7.4 Ultraviolet-B Radiation Stress

UV-B radiation can affect the production of secondary metabolites such as flavonoids (Takshak and Agrawal 2014b), tannins, and lignins which act as defense compounds in plants. It is also known to impact metabolism and cause morphogenetic defects, such as a reduction in IAA oxidase and the cumulative antioxidative potential (CAP), protein and chlorophyll content, and various enzymes of the phenylpropanoid pathway. Supplementary UV-B has been known to cause an increase in the concentrations of reactive oxygen species (ROS) in leaves but a decrease in roots of

Table 9.4 Role of PGPR in ameliorating salinity stress

Stress condition	Rhizobacterial inoculant	Plant species	Mechanisms	References
Salinity	*Pseudomonas fluorescens* MSP-393	Pea	Osmolyte synthesis, alanine serine, threonine, aspartic acid, glycine, glutamic acid; osmoprotectants, protein stabilizing	Paul and Nair (2008)
Salinity	*Pseudomonas fluorescens* MSP-393	Rice	Protein stabilization and alteration of cell envelope composition; altered expression of proteins, periplasmic glucans and capsular, exo- and lipopolysaccharides	Paul et al. (2006)
Salinity	*Pseudomonas putida* FBKV2	Maize	Production of exopolysaccharides; enhancing water retention and regulating the diffusion of carbon sources	Vurukonda (2016a, b)
Salinity	*Dietzia natronolimnaea* STR1	Wheat	Modulation of transcriptional machinery of stress-related antioxidant genes	Bharti et al. (2016)
Salinity	*Bacillus megaterium*	Maize	Increased ability of the root to absorb water	Marulanda et al. (2010)
Salinity	*Pseudomonas* sp.	Pistachio	Increased protein content, antioxidant activity, ACC deaminase activity	Azar et al. (2016)
Salinity	*Enterobacter cloacae* and *Bacillus drentensis*	Mung bean	Modified stomatal conductance, transpiration rate, water relations, and synthesis of photosynthetic pigments	Mahmood et al. (2016)
Salinity	*P. pseudoalcaligenes* and *Bacillus pumilus*	Rice	Increased concentration of glycine betaine-like quaternary compounds	Jha et al. (2011)
Salinity	*Enterobacter* sp.UPMR18	Okra	ROS scavenging enzymes	Sheikh et al. (2016)
Salinity stress	*Arthrobacter protophormiae (SA3) and Dietzia natronolimnaea (STR1)*	Wheat	Enhance photosynthetic efficiency; increase indole-3-acetic acid; modulating expression of a regulatory component (CTR1) of the ethylene signaling pathway and DREB2 transcription factor	Barnawal et al. (2017)

(continued)

Table 9.4 (continued)

Stress condition	Rhizobacterial inoculant	Plant species	Mechanisms	References
Salinity stress	*Achromobacter piechaudii* and *Bacillus subtilis*	Tomato (*Lycopersicon esculentum*)	Degradation of reactive oxygen species	Mayak et al. (2004), Zhang et al. (2008), and Yang et al. (2009)
Salinity	*Enterobacter* sp. (MN17) *Bacillus* sp. (MN54)	*Chenopodium quinoa*	ACC deaminase activity, exopolysaccharide secretion, and auxin production	Yang et al. (2016)

Table 9.5 Role of PGPR in ameliorating oxidative stress

Stress condition	Rhizobacterial inoculant	Plant species	Mechanisms	References
Oxidative stress	*Azospirillum* spp.	Maize	Phytohormone production and induction of plant-stress tolerance and defense genes	Fukami et al. (2017)
Oxidative stress	*P. agglomerans* RSO6 and RS07 *B. aryabhattai* RSO25	*Spartina densiflora*	Regulation of antioxidant enzyme activity	Paredes-Páliz et al. (2018)
Oxidative stress	Rhizobacteria	*Oryza sativa*	Enzyme activities related to oxidative stress induced such as ascorbate peroxidase, guaiacol peroxidase, glutathione reductase, superoxide dismutase	García-Cristobal et al. (2015)
Oxidative stress	*Burkholderia cepacia* SE4, *Promicromonospora* sp. SE188, and *Acinetobacter calcoaceticus* SE370	*Cucumis sativus*	Reduced activities of catalase, peroxidase, polyphenol oxidase	Kang et al. (2014)

Withania somnifera (an indigenous medicinal plant); however, the enzymatic antioxidant activity increases under UV-B treatment (Takshak and Agrawal 2014a). The adverse effects of UV-B radiation on growth characteristics of *Brassica campestris* were said to be reduced upon application of IAA at 10^{-7} M (Lal et al. 2011). However, IAA is reported to be susceptible to UV-B-induced damage via direct photodegradation and enhanced activity of IAA oxidase enzyme (Huang et al. 1997) (Table 9.5).

9.7.5 Heavy Metal Stress

Heavy metals like lead, nickel, cadmium, copper, cobalt, chromium, and mercury which are known as environmental pollutants cause toxic effects in plants, thereby lessening productivity. They affect the basic physiological and biochemical activities in plants such as photosynthesis. PGPR is known to precipitate and remove toxic metals from the surroundings by mechanisms such as intracellular sequestration or sorption to cell components. Rizvi and Khan (2018) showed that plant growth-promoting *Azotobacter chroococcum* produced siderophores, ammonia, and ACC deaminase under metal pressure and enhanced growth and yield of maize in the presence of both Cu and Pb. Also, the melanin extracted from *A. chroococcum* revealed metal chelating ability. *Kluyvera ascorbata* SUD165, a PGPR resistant to the toxic effects of Ni^{2+}, Pb^{2+}, Zn^{2+}, and CrO^{4-}, producing siderophore(s) and displaying ACC deaminase activity, was capable of promoting growth in plants in the presence of nickel by its ability to lower the level of stress ethylene induced by the nickel (Burd et al. 1998). Dell'Amico et al. (2008) also showed that inoculation with cadmium-resistant strains *Pseudomonas tolaasii* and *Pseudomonas*

Table 9.6 Role of PGPR in ameliorating heavy metal stress

Stress condition	Rhizobacterial inoculant	Plant species	Mechanisms	References
Metal stress	*P. tolaasii*	Canola (*Brassica napus*)	ACC deaminase activity	Dell'Amico et al. (2008)
Metal stress	*P. fluorescens*	Canola (*Brassica napus*)	Indole acetic acid (IAA) and siderophore production	Dell'Amico et al. (2008)
Metal stress	*Bacillus* sp.	*Rice*	Superoxide dismutase	Asch and Padham (2005)
Metal stress	*Kluyvera ascorbata*	Tomato, canola, and Indian mustard seeds	Siderophore production	Burd et al. (2000)
Metal stress	*Pseudomonas libanensis*	*Brassica oxyrrhina*	Production of indole-3-acetic acid, siderophore, and ACC deaminase	Ma et al. (2016)
Metal stress	*Pseudomonas fluorescens*	Maize	Production of IAA	Zerrouk et al. (2016)
Metal stress	*Pseudomonas stutzeri* A1501	*Rice*	Transcription and translation of acdS gene, ACC deaminase	Han et al. (2015)
Metal stress	*P. aeruginosa* strain OSG41	Chickpea	IAA, PO_4 solubilization, EPS production, siderophores, salicylic acid, 2,3-Dihydroxybenzoic acid, HCN, and NH_3 production	Oves et al. (2013)

fluorescens enabled *Brassica napus* to grow under cadmium stress by the production of IAA, siderophores, and ACC deaminase. Siderophores also play a key role in the regulation of auxin level in plants growing in metal-contaminated sites. Metals are known to inhibit auxin synthesis. Dimkpa et al. (2008b) proved that siderophores complexed with toxic metals, thereby decreasing the concentration of free metals and attenuating metal inhibition of auxin synthesis (Table 9.6).

9.8 Conclusion

PGPRs have the ability to act as bioprotectants under abiotic stress and can enhance plant growth. Because of their rhizoremediating and phytostimulating properties, they could be beneficial in replacing chemical fertilizers and supporting eco-friendly sustainable food production. Due to their worldwide importance and acceptance, PGPR are the future of sustainable agriculture.

Acknowledgments The author is grateful to the Principal of P.E.S's RSN College for his support.

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