Chapter 11
Microbial Consortium of Plant Growth-Promoting Rhizobacteria Improves the Performance of Plants Growing in Stressed Soils: An Overview

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Abstract Soil and associated stress conditions not only influence dwelling microbial populations and soil ecosystems but also affect growth and yield of plants. Major soil stress includes salinity, drought, and metal contamination. Due to burgeoning populations and expanding food demands, it has become imperative to alleviate the stressful soil conditions so that the crop production is increased and, consequently, the food demands are fulfilled. Different strategies are followed to resolve this problem, and one such approach involves exploiting microbial potential for plant's benefit. The multifunctional microscopic life-forms are already known for their applications in industries, medicine, and agricultural field. One of the major attributes of microbes from agronomic point of view is their ability to solubilize difficultly available forms of soil phosphorus. Phosphate-solubilizing microbes are also known to produce enzymes, siderophores, and growth hormones; embellish plant growth and biocontrol activity; and improve soil properties. Such microorganisms possessing attributes, beneficial for plants are termed as plant growth-promoting rhizobacteria (PGPR). There are plentiful reports on bacterial-mediated plant growth promotion under nonstressed conditions although fewer reports are available on their effects under stressed condition. The bacterial ability to enhance tolerance of plants in stressed soils and the impact of PGPR consortium (mixture) on different crops are highlighted. The major idea here is to consolidate the fact that PGPR consortium can be used directly in stress-affected soil with an aim to refurbish soil conditions to foster crop productivity in stressed soils.

Keywords PGPR • Microbial consortium • Siderophores • Biocontrol • Soil stressors

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11.1 Introduction

Soil inhabits different life-forms including plants, animals, and microorganisms and is a nutrient hoarded treasure, a support system (for plant) furnishing with plentiful crops and yields. Any change in soil conditions eventually affects plant growth. Human activities and ever-increasing populations are continuously exploiting this natural system, consequently affecting the growth and productivity of plants. However, there are certain soil factors which negatively affect plant growth. These are (1) moisture content, (2) salt, (3) nutrient pool of soils, (4) microbial composition and their functional variation, and (5) soil pollution especially deposition of toxicants (heavy metal and pesticides) in soil. When deviated from optimal conditions, these factors cause adverse effects and are specified as stress conditions for soil. The deleterious impacts of these stresses include dwindling productivity, burden on delimited resources, and economic fall. Considering these threats, researchers from different fields are working in unison to avert such problems. One such area involves the exploitation of microbiological resources of soils. Microorganisms are known to be omnipresent and possess multifunctional characteristics even though the full potential of microorganisms is still unrevealed. Most of the chemical reactions occurring in soil leading to nutrient availability are mediated by different microorganisms like N_2 fixers, P solubilizers, or decomposers (Powlson et al. 2001). Considering the available information and application of microorganisms, there has been greater interest in using such organisms to restrain the adverse effects also (Vassilev et al. 2012).

Microorganisms colonizing the rhizospheres are known to have beneficial effects on the nutrient acquisition, mineral solubilization, disease resistance, and stress tolerance and are collectively described as plant growth-promoting rhizobacteria (PGPR) (Kloepper and Schroth 1978; Vessey 2003). Reports are available in the literature on the effectiveness of rhizospheric microorganisms as plant growth promoters as well as on their potential for imparting stress resistance or improving stress tolerance in plants, presenting PGPR as viable option to cope with these problems (Yang et al. 2009; Zelicourt et al. 2013; Ahemed and Kibret 2014). Another aspect of exploiting microbial potential is to combine the attributes of different microbes to get an outcome encompassing numerous or complementing beneficial effects. Microorganisms are known to have attributes like cooperation/ mutualism where they benefit each other or other life-forms to enhance the positive outcomes (Singh et al. 2010). Multiple properties of resistance/tolerance and plant growth promotion, therefore, serve as an appraisal and make PGPR one of the most suitable choices to manage these problems (Bano and Fatima 2009; Egamberdieva and Kucharova 2009; Zelicourt et al. 2013). Judicial application of the stress-tolerant PGPR consortium can be a viable solution and need to be further strengthened through field trials. The present chapter gathers reports on the experimental studies done on PGPR consortium helping plant/crops cope with stressful soil conditions. Also, the focus is given here on soil stress and associated effects including mechanisms of PGPR in stress alleviation.

11.2 Stresses Occurring in Soils

Soil can be defined as upper layer of earth where plant grows and have their roots (Brady 1974). Soil indeed is the habitat for both microscopic (millions of microorganisms) and macroscopic (insects, animals, plants) life (Pelczar et al. 1993; Saika 2013). The plants along with soil inhabiting microbes affect the soil structure, fertility, and porosity; prevent erosion; and serve as source of organic matter; likewise, any alteration in soil influences these life-forms. Soil stress is one of the abiotic factors and can be defined as environmental variables affecting soil, which can induce potentially injurious effects on the growth and yield of plants. Stress in plants is mainly measured in relation to survival, growth, crop yield, biomass, and primary assimilation processes associated with growth (Oliveira et al. 2013). These abiotic stresses also reduce the number, activity, and diversity of soil microflora, which in turn may limit the crop production (Sgroy et al. 2009).

11.2.1 Types of Soil Stresses

Soil stresses involve drought stress (decreased water availability to plants), salt stress (increase salts in soil solution), heavy metal stress (excessive toxic metals in soil), nutrient stress (insufficient nutrients in soil), and temperature stress (extremes of temperature both high and freezing). Of these, drought is one of the most important stresses followed by salinity stress (Kinje 2006; Carmen and Roberto 2011). Extensive areas of land are affected by these two stresses and are reported to have maximum deleterious effects on the agricultural productivities (Oliveira et al. 2013). The effects of drought and salt stress are highly interrelated and influence practically almost every aspect of plant. The effects of stresses on plants involve disrupted photosynthesis leading to leaf senescence, accumulation of excessive reactive oxygen species (ROS), nutrient deficiency, and destruction of cellular organelles and metabolism leading to decreased plant growth. The after-effect includes both physiological and metabolically disturbed homeostasis of plant (Carmen and Roberto 2011; Oliveira et al. 2013). Metal stress is another important soil stress, which is becoming increasingly intensive due to numerous anthropogenic factors (Glick 2010). Unchecked increase in population and industrial revolution is resulting in accumulation of toxic metals and organic wastes in soil making it unsuitable for agricultural practices and also harmful to all life-forms (Glick 2010). Some of the effects of these stresses are briefly outlined in Fig. 11.1.

11.2.1.1 Drought Stress

Water comprises 80–90 % of the plant biomass and plays central role in all major physiological processes of the plants involving nutrient uptake and photosynthesis.

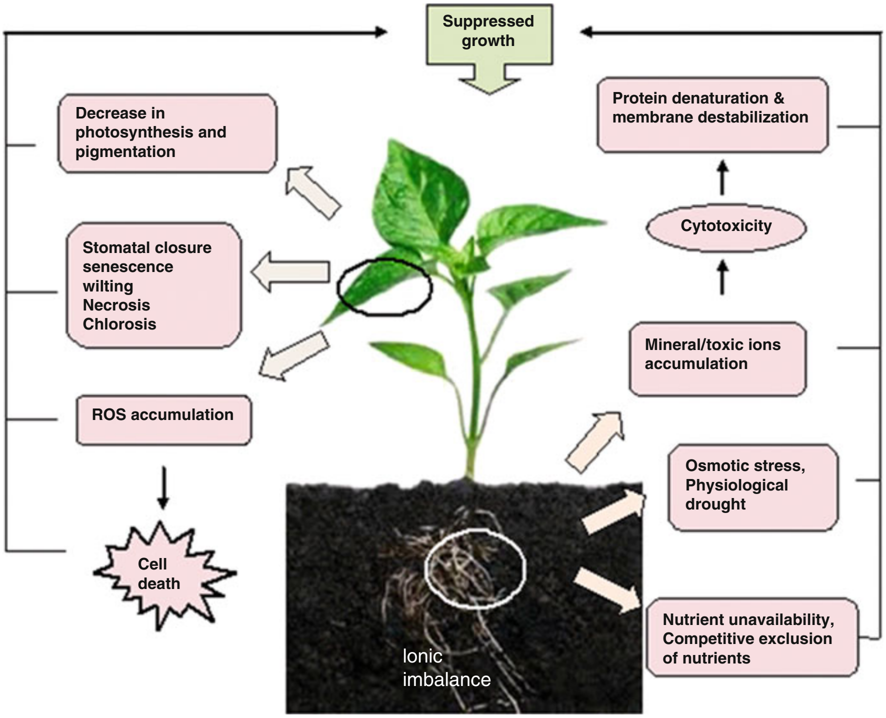

Fig. 11.1 An overview of stress effects on the plant. Effects include a combinatorial picture of salt and metal stress (ionic imbalance) and drought stress (osmotic stress) on physiological and metabolic aspects of plants focusing mainly on leaves and root-associated processes which ultimately lead to inhibition in growth

Drought stress can be defined as low water or moisture content in soil, not enough to fulfill the plant requirements. When the water loss occurs due to metabolic processes and transpiration exceeds the water availability for absorption or when water content of plant gets low enough to interfere with normal plant processes, water deficit/stress is created. It can also result from reduced moisture of soil, due to less rainfall or supplemental irrigation. Water stress has been found as an important factor affecting deleteriously various stages/metabolic processes of plants (Upadhyay and Panda 2013). For example, water stress reduces the water potential of plant cell and thus enhances the solute concentration, which further hinders cell enlargement, stem proliferation, and root elongation, thereby hampering the plant growth (Akinci and Losel 2012). However, when plants are growing under stressed situation, it exhibits visible symptoms. As an example, "wilting" is the condition of plants where the non-wooden parts of the plants become nonrigid due to low turgor pressure and is one of the most common symptoms of water stress (Correia et al. 2001; Cabuslay et al. 2002). Also, water stress may cause stomata closure. Accumulation of plant hormone, for instance, abscisic acid (ABA), is responsible for the stomatal closure (Socias et al. 1997). This further reduces gaseous exchange, transpiration, and CO_2 assimilation during photosynthesis (Cornic 2000). Also, water stress results in reduced chlorophyll content, inhibits chloroplast activity and disorganizes thylakoid membranes, decreases the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase and other enzymes in carbon reduction cycle (Reddy et al. 2004), impairs electron transport, and increases the concentration of ROS. The imbalance in scavenging and formation of ROS and increased O_2 photoreduction in chloroplast results in ROS accumulation (Robinson and Bunce 2000). The ROS damages photosynthetic apparatus, cell membrane, and macromolecules. DNA nicking, denaturation of structural and functional macromolecules, lipid peroxidation, oxidation of amino acids and proteins, and photosynthetic pigments are some of the effects of ROS accumulation (Lisar et al. 2012). Stomata closure under drought stress is also found to be related to altered nutritional status, xylem sap pH, and hydraulic conductivity as well as declines water content in leaf (Oren et al. 1999). Summarily, drought stress interrupts the enzymatic reactions mainly involved in CO_2 fixation and ATP synthesis and thus affects the plant by altering (1) photosynthesis, (2) transpiration, (3) nutrient uptake, (4) hormone production, (5) homeostasis, and (6) other metabolic processes.

11.2.1.2 Saline Stress

In agricultural terms, salinity can be defined as salt level exceeding the plant requirements (Yadav et al. 2011). In other words, it can also be defined in terms of dissolved mineral salt concentration, i.e., electrolytes of cations and anions where major cations involve Na^+, Ca^{2+}, Mg^{2+}, and K^+ and anions involve Cl^-, SO_4^{2-}, CO_3^{2-}, HCO_3^-, and NO_3^-. According to USDA Salinity Laboratory (Seidahmed et al. 2013), saline soil is defined as soil having electrical conductivity 4 dS m^{-1} or higher. The excessive concentrations of salt change the physicochemical properties of soil and affect the nutrient uptake from soil, making nutrients inaccessible for plants. Some of the effects of salt stress on plants include deteriorated growth, nitrogen content, photosynthetic capacity, and metabolic processes including protein and lipid metabolism (Upadhyay et al. 2011). Salt stress has been reported to drastically affect the growth and yield of several crops (Parida and Das 2005; Ondrasek et al. 2011). Broadly, effects of salt stress can be categorized as (1) unavailability of water causing drought-like conditions; (2) high salt content in plants, i.e., Na^+ and Cl^-, leading to disrupted physiological and biological processes; and (3) high salt content affecting availability of other soil nutrients. One of the most dominant symptoms of salt stress involves stunted growth. Cessation of leaf expansion and reduction in dry weight and fresh weights of stem, roots, and leaves are some other effects of the salt stress (Hernandez et al. 1999; Wang and Nil 2000). Salt stress affects largely the shoot growth compared to root growth and hence influences both vegetative and reproductive stages of plants. It creates osmotic and ionic stress due to less water content and high salt concentration, respectively. The osmolarity of external tissues results in decreased growth of plant (Munns 2002), whereas the ionic effect leads to ion (mainly Na^+) accumulation mainly in leaf tissues leading to necrosis. "Necrosis" is death or degeneration of tissue, visible as yellowing or dark patches on plant leaves. Due to excessive salt in soil, the required nutrient becomes unavailable for plants. The salt ions (Na^+) intervene the transporters of root plasma membrane and hamper root growth, thus obstructing the nutrient uptake by plants (Yadav et al. 2011). Salt stress causes water deficit, which results in oxidative stress due to formation of ROS, causing membrane dysfunction and cell death (Parida and Das 2005). Lipids also act as a target for oxidative reactions and, being structural constituent of membranes and insulator for internal organs, damage the cellular structure aggravating negative effects of the salt stress (Singh et al. 2002). The high concentration of solutes in root medium interferes with the water absorption by roots and reduces root conductivity. These effects further lead to decreased plant growth and photosynthetic rate. The chlorophyll and carotenoid content in leaves decline under salt stress. Symptoms of chlorosis appear on leaves due to the reduction of photosynthetic pigments. Salt stress affects different physiological processes such as cessation of carbon assimilation in leaves, reduction in permeability due to dehydration, closure of stomata affecting chloroplast activity, senescence, ionic leakage into the cytosol leading to inactivation of photosynthetic and respiratory electron transport (Allakhverdiev et al. 2000; Parvaiz and Satyawati 2008), and altered enzyme activity due to change in cytoplasmic structure.

11.2.1.3 Metal Stress

Heavy metals (HM) can be defined as elements with metallic properties and higher range of molecular weight and include transition elements. The industrial revolution and anthropogenic activities have dramatically raised the metal concentration in soil (Yan-de et al. 2007; Oves et al. 2012). Among these metals, iron (Fe), molybdenum (Mo), and manganese (Mn) are known as essential micronutrients required by the plants, while a few, for example, cadmium (Cd), do not have any biological activity. Other metals like chromium (Cr), copper (Cu), mercury (Hg), lead (Pb), and nickel (Ni) are also common in soil. Based on the requirement, HM can be divided into essential and nonessential elements, although the excessive accumulation of both of these in soils adversely affects the plants (Wani et al. 2012; Morsy et al. 2013) as well as soil microflora (Oliveira and Pampulha 2006; Wani and Khan 2010). The plentiful HM in soil is absorbed and translocated to various organs of plants and impairs plant metabolism and growth (Bingham et al. 1986; Cheng 2003; Ahmad et al. 2012b). The excessive metals in soil also affect soil properties and fertility, making it unsuitable for agricultural activities.

The possible toxic impact of heavy metals on plant includes (1) disintegration of cell organelles and (2) disruption of membranes and physiological processes like (a) photosynthesis, (b) inactivation of protein synthesis, (c) inactivation of respiration and carbohydrate metabolism, and (d) nutrient uptake (Jing et al. 2007; Wani et al. 2007; Wani et al. 2008; Khan et al. 2012). Metal accumulation also results in reduced microbial population (Wani and Khan 2013) thereby affecting the soil fertility and making it unsuitable for sustainable agriculture (Cheng 2003). Germination rate and root vitality of the plant are also affected by the metal stress (Shu et al. 1997). Heavy metals were also known to affect the cell division by causing inhibition of DNase and RNase activity; damaging nucleolus and disrupting DNA synthesis; and causing chromosomal aberration, coagulation, and fragmentation (Yang and He 1995; Musarrat et al. 2011). Reduced cell division and elongation along with decreased cell membrane integrity are some other effects of membrane toxicity. Some of the visible symptoms include interfoliar chlorosis, wilting, necrosis, crinkling of leaf, reddening, and purpling (Reichman 2002). Lessened chlorophyll content, reduced photosynthetic rate, and augmented carotenoid breakdown are also some of the results of metal toxicity. Accumulated metals are believed to replace Mg ion of the chlorophyll molecule thus affecting photosynthesis (Kupper et al. 1996). Heavy metals are also known to disrupt the photosystems ensuing decreased proton availability, consequently affecting photosynthesis. Reduced ATP synthesis and disrupted activity of chloroplast are some other effects reported for metal toxicity by disruption of enzymatic systems (Teige et al. 1990). Like any other stress, free radical production is increased in plant as a response to metal stress. The concentration of metal plays an important role here as at low concentration the protective antioxidant enzymes balance the effect, but at higher metal toxic condition these accumulated free radicals damage membranes by lipid peroxidation (Yadav 2010) followed by injury to surrounding cells. Free radicals also damage macromolecules like nucleic acids and proteins, thus disrupting normal metabolism and leading to cell death. Leaf senescence is another effect of oxidative damage due to ROS accumulation (Luna et al. 1994). Since growth, yields, and many other physiological functions of plants are affected negatively by toxic metals (Yadav 2010; Selvakumar et al. 2012), remedial measures are urgently required for its cleanup from the contaminated sites (Khan et al. 2011; Zaidi et al. 2012). In this context, scientists around the world have attempted to use molecular tools and breeding programs for exploiting physiological traits of plants, developing new stress-tolerant crop varieties, altering crop calendars, and managing agronomic resources to circumvent stress-related impact on plants. Another well-considered option in this direction is the use of microorganisms for combating stress (Khan et al. 2009). In this regard, reports on the individual/combined use of metal-tolerant/normal microorganisms in growth promotion and other positive effects on plants are available (Selvakumar et al. 2012; Ahmad et al. 2013; Oves et al. 2013).

11.3 Plant Growth-Promoting Rhizobacteria

Soil is inhabited by numerous microorganisms, which can be categorized as beneficial or detrimental based on their effect on the soil, plants, and ultimately plant's yield (Singh et al. 2011a). The diverse microbial population of soil plays a pivotal role in processes determining soil fertility and plant's productivity (Tilak et al. 2005). Soil microorganisms participate in processes like decomposition, mineralization, and nutrient availability, improve soil structure (soil aggregation by production of polysaccharides), increase the nutrient acquisition efficiency of the plants, and improve plant health through growth hormone production (Hayat et al. 2010; Singh et al. 2011b). Microbial populations having the ability to colonize root surface and imparting beneficial effects to plants are known as plant growth-promoting rhizobacteria (PGPR) (Kloepper and Schroth 1978; Joshi and Bhatt 2011). Plant growth-promoting rhizobacteria facilitate plant growth both directly and indirectly (Glick 2012). Some of the notable PGPR belong to genera *Arthrobacter* (Banerjee et al. 2010), *Azotobacter* (Ponmurugan et al. 2012), *Azospirillum* (Jacoud et al. 1999), *Bacillus* (Kumar et al. 2011), *Enterobacter* (Shoebitz et al. 2009), *Pseudomonas* (Noori and Saud 2012), and *Serratia* (Zhang et al. 1997). Based on the proximity with the plant roots, PGPR can be divided into (1) extracellular PGPR, existing in rhizosphere, rhizoplane, or spaces between root cortices, and (2) intracellular PGPR, present within roots or nodules of the plant. Also, based on the mode of action, PGPR have been classified as (1) bio-stimulants which promote plant growth via phytohormone production, including auxins IAA and similar compounds like abscisic acid, gibberellic acid, cytokinins (Carmen and Roberto 2011); (2) biofertilizers which enable nutrient availability and acquisition via N_2 fixation (Mohammadi and Sohrabi 2012) and P solubilization (Khan et al. 2007; Zaidi et al. 2009; Khan et al. 2010; Das et al. 2013); and (3) bioprotectants which provide protection to plants against phytopathogens via production of antibiotics (Labuschagne et al. 2011), siderophores (Glick 2012), and induced systemic resistance (Figueiredo et al. 2011).

11.3.1 Direct Mechanisms

11.3.1.1 Production of Plant Growth Regulators

Microorganisms are known to produce plant growth-stimulating substances such as phytohormones, for example, auxins (Spaepen and Vanderleyden 2011), cytokinins (Nieto and Frankenberger 1990), gibberellins and abscisic acid (Singh 2013), etc., as well as certain volatiles (Ryu et al. 2003). The phytohormone-producing microorganisms include *Acetobacter diazotrophicus* (Patil et al. 2011), *Azospirillum brasilense* (Perrig et al. 2007), *Herbaspirillum seropedicae* (Bastian et al. 1998), *Bacillus pumilus* and *B. licheniformis* (Gutirrez-Manero et al. 2001), etc.

11.3.1.2 Nitrogen Uptake

Specialized microorganisms have capability to fix atmospheric N (biological nitrogen fixation; BNF) and maintain the balance of N in soil ecosystem. Nitrogen fixers are categorized into two groups: (a) symbiotic nitrogen fixers and (b) nonsymbiotic nitrogen fixers. *Rhizobium* and *Frankia* belong to symbiotic N_2 fixers that associate with legumes, whereas nonsymbionts are free-living N_2 fixers which interacts with nonleguminous plants (Ahemed and Kibret 2014). Numerous PGPR are also known to possess this attribute although the mechanism responsible for their growth promotion is not N_2 fixation. Some of these PGPR are *Azotobacter* (Kizilkaya 2009), *Bacillus* (Ding et al. 2005), *Clostridium*, *Klebsiella* (Iniguez et al. 2004), *Alcaligenes*, *and Arthrobacter* (Mohammadi and Sohrabi 2012).

11.3.1.3 Increased Mineral Uptake

Plant growth-promoting rhizobacteria are reported to provide nutrients to plants via mineralization/solubilization of unavailable minerals like P (Khan et al. 2007). Also, the siderophores, secreted by PGPR strains, play important roles in mineral transport (Vessey 2003; Ahmad et al. 2013). Mineralization process involves conversion of organic P into soluble forms through enzymes like phytases and phosphatases (Walpola and Yoon 2012), whereas in solubilization the inorganic P is transformed into soluble forms via organic acid production, acidification of medium (Park et al. 2009; Khan et al. 2010), chelation, and exchange reactions (Walpola and Yoon 2012). Both solubilization and mineralization mechanism can occur in one bacterial species also. Some of the phosphate solubilizing (PS) bacteria include *Acinetobacter* (Rokhbakhsh-Zamin et al. 2011), *Burkholderia* (Gupta et al. 2012), *Enterobacter* (Gupta et al. 2012; Maheshwari and Sudha 2013), *Klebsiella* (Ahemad and Khan 2011), *Pseudomonas* (Rajkumar and Freitas 2008), and *Stenotrophomonas* (Mehnaz et al. 2010). Numerous studies have been conducted globally to analyze the effects of various P solubilizers on growth, yield, and other important parameters of plants (Khan et al. 2009; Ahmad et al. 2012a). Some of the examples supporting the effectiveness of these micro-organisms against different crops are listed in Table 11.1.

11.3.2 Indirect Mechanisms

11.3.2.1 Antibiotic Production

Antibiotics are defined as heterogenous low molecular weight organic compounds secreted by microorganism, having destructive/inhibitory effects on the growth and metabolism of other microorganism/s (Duffy 2003; Beneduzi et al. 2012). PGPR are also known to produce antibiotics and other small molecules preventing plants from damage caused by the plant pathogens. These antibiotics are categorized as (A) nonvolatiles including polyketides (e.g., pyoluteorin), heterocyclic nitrogenous compounds such as phenazine derivatives, phenylpyrrole (e.g., pyrrolnitrin), lipopeptides (e.g., bacillomycin), aminopolyols (e.g., zwittermicin A) and (B) volatile antibiotics such as hydrogen cyanide (HCN), aldehydes, sulfide,

Table 11.1 Examples of P-solubilizing microorganism and their effects on the plants

P solubilizer	Plants	Effect	Reference
Bacillus megaterium	Sugarcane (*Saccharum officinarum*)	Enhanced sugarcane and sugar yield, P content in soil	Sundara et al. (2002)
Bacillus sp.	Banana cultivars (*Musa paradisiaca*)	Improved yield and mineral content, fresh biomass (aerial and root), aerial dry mass, diameter, and foliar surface	Jaizme-Vega et al. (2004)
Pseudomonas sp.	Tomato (*Solanum lycopersicum*)	Enhanced growth	El-Tantawy and Mohammed (2009)
Pantoea eucalypti	Slender trefoil (*Lotus tenuis*)	Enhanced growth	Castagno et al. (2011)
Variovorax paradoxus	Pea (*Pisum sativum)*	Increased root-shoot biomass, stomatal conductance, enhanced nutrient availability, and P accumulation	Jiang et al. (2012)
Burkholderia multivorans WS FJ9	Poplar (*Populus euramericana cv.*)	Increased height, root collar diameter, biomass, P content	Li et al. (2013)
B. tropica KS04	Chili (*Capsicum frutescens L. cv. Hua Rua*)	Significant increase in height, fresh weight, root and shoot dry weight, as well as number of flowers	Boonlue et al. (2013)

ketones, and alcoholic compounds (Fernando et al. 2006). Some of the antibiotics like 2,4-diacetylphloroglucinol (Shanahan et al. 1992), phenazine-1-carboxylate (Chin-A-Woeng et al. 2001), pyoluteorin (Howell and Stipanovic 1980), pyrrolnitrin (Thomashow and Weller 1988), and HCN are produced by *Pseudomonas* sp. (Hass and Defago 2005); bacillomycin (Volpon et al. 1999), kanosamine (Milner et al. 1996), and iturin A (Constantinescu 2001) are produced by *Bacillus* sp. (Fernando et al. 2006). Toluene, dimethyl disulfide, and terpenoid compounds like α-pinene and limonene are the other volatiles produced by *Burkholderia* sp. (Tenorio-Salgado et al. 2013).

11.3.2.2 Siderophore Production

Siderophores are low molecular weight peptide molecules with side chains and functional groups acting as ligand for Fe^{3+} (Beneduzi et al. 2012). Siderophores are also known as “iron carriers” and act as biocontrol agents by sequestering iron (Fe), required for phytopathogens. By limiting the iron availability, siderophores inhibit the growth of phytopathogens in immediate vicinity of plant and hence indirectly protect plant from pathogen damage (Glick 2012). Siderophore-producing PGPR, for example, *Pseudomonas* sp. and *Enterobacter* sp. (Gram-negative bacteria) and

Bacillus sp. and *Rhodococcus* sp. (Gram-positive bacteria) (Saharan and Nehra 2011) also deprive native microflora from available iron and thus outnumber the native microbes and exhibit plant growth-promoting effect (Kloepper et al. 1980).

11.3.2.3 Induced Systemic Resistance

Induced systemic resistance (ISR) is another indirect mode of action where PGPR or nonpathogenic rhizobacteria act as stimuli, and in response, plants develop enhanced resistance to pathogens. ISR involves actions of nonpathogenic bacteria and is mainly dependent on jasmonic acid and ethylene signaling in plants (Lugtenberg and Kamilova 2009). Some of the putative mechanisms responsible for enhanced resistance include accumulation of phenolic compounds, increased activity of defense enzymes, enhanced lignifications, etc. Many *Pseudomonas* sp. and *Bacillus* sp. are recognized to act as biocontrol agents and protect plant from pathogens through this mechanism (Kloepper et al. 2004). PGPR-mediated ISR against bacteria, fungi, and viruses has already been reported (Niranjan et al. 2005).

11.4 Microbial Consortium

"Consortium" is a Latin word, which stands for partnership, association, or group, that works for common interest. From the microbiological perspective, consortium constitutes a group of compatible organisms belonging to different species in contact with one another, implicated in different biological processes ranging from sewage treatment to metabolic processes in rumen (Mark 2009). Two or more microorganisms living in symbiosis can be called as consortium. Microbes with different attributes can be used as consortium, which can work synergistically promoting each other's beneficial effects. Some of the PGPR consortium-related studies are summarized in Table 11.2. A study involving N_2 fixing, *R. leguminosarum* bv. *viceae* (LB-4); P solubilizing, *B. megaterium*; and PGPR, LK-786 (*Kurthia* sp.) and LK-884 (*Pseudomonas diminuta*) was carried out to ascertain their effects on lentil (*Lens culinaris*) crop following single and dual culture inoculation (Kumar and Chandra 2008). Maximum increase in dry weight, yield, mineral uptake, and nodule number was reported in case of all microbial combination as compared to dual combinations of *Rhizobium* + *B. megaterium or Rhizobium* + LK-884/LK-786 (*Kurthia* sp.), whereas no positive effects were observed in uninoculated controls. A similar study was carried out using consortium of *Burkholderia gladioli* 10242, *Enterobacter hormaechei* 10240, *Pseudomonas synxantha* 10223, and *Serratia marcescens* 10241, for their effect on the *Aloe vera* plants. The result indicated augmented biomass as well as aloin-A content of the plants (Gupta et al. 2012). An experimental study was conducted on the evaluation of effects of PGPR consortium comprising FCA-8, FCA-56, and FCA-60 of *P. putida* and arbuscular mycorrhizal fungi (AMF) on citrus (*Citrus*

Table 11.2 Examples of PGPR consortium effects on various crops

PGPR	Crop/plant	Effects	Reference
Rhizobium + *B. megaterium or Rhizobium* + LK-884 (*P. diminuta*)/LK-786 (*Kurthia sp.*)	Lentil crop (*Lens culinaris*)	Increased dry weight, yield, mineral uptake, and nodule number	Kumar and Chandra (2008)
A. brasilense strain Az39 and *B. japonicum* strain E109	Soybean (*Glycine max*) and corn/maize (*Zea mays*)	Augmented germination rate, shoot-root length, dry weight, and nodulation	Cassan et al. (2009)
A. lipoferum, *P. fluorescens*, and *P. putida*	Maize (*Zea mays*)	Improved biomass and yield	Adjanohoun et al. (2011)
PGPR strains FCA-8, FCA-56, FCA-60 of *P. putida* and AM-fungi	Citrus (*Citrus volkameria*)	Plant height, stem-base diameter, root length and volume, biomass, and colonization similar to fertilization	Chiquito-Contreras et al. (2012)
Different combinations of PGPR	Artichoke (*Cynara scolymus*)	Increased shoot length, root and shoot weight, vigor, germination percentage, and mean time of germination	Jahanian et al. (2012)
Pantoea cypripedii and *Enterobacter aerogenes*	Chickpea (*Cicer arietinum*)	Increased P uptake by plant	Singh et al. (2013)
Trichoderma viride, *P. fluorescence*, and *A. chroococcum*	Chili (*Capsicum annum* L.)	Improved growth and yield	Sateesh and Sivasakthivelan (2013)

volkameriana) (Chiquito-Contreras et al. 2012). The study involved consortium treatment with 50 % fertilization, whereas control involved no PGPR inoculation with 100 % fertilization. Different parameters studied involved plant height, stem-base diameter, root length and volume, biomass, and colonization; results so obtained were similar to the effects obtained with control, suggesting that their effectiveness is similar to fertilizers.

Besides agricultural crops, PGPR were also found effective in facilitating the growth of flower crops (Kumari et al. 2013). One such study involved the combination of four PGPR (*A. chroococcum*, *A. lipoferum*, *B. megaterium*, and *P. fluorescens*) on rose plants (*Catharanthus roseus*). Mixed inoculation enhanced growth, vigor, nutrient content (P, K, and N by 2.34 %, 2.2 %, and 0.34 %, respectively), and chlorophyll content (Lenin and Jayanthi 2012). Another comparative experiment involving single, double, and consortium inoculation of *A. chroococcum*, *P. fluorescence*, and *T. viride* was carried out for chili crop (*Capsicum annum* L.). Maximum growth and yield were recorded for consortium cultures relative to single and double inoculation (Sateesh and Sivasakthivelan

2013). Phosphate-solubilizing *Pantoea cypripedii* and *Enterobacter aerogenes* used together increased P uptake by 53 % in chickpea crop compared to control (Singh et al. 2013).

11.5 PGPR and Stress Alleviation

Different studies have suggested that such microorganisms can also divulge some degree of tolerance to the plants thus imparting resistance to these plants. Tolerance can be defined as microbe's intrinsic property to encounter stressful conditions, whereas resistance is microorganism's ability to withstand stressful conditions by certain mechanisms. Some of the experimental evidence indicates that microorganisms with tolerance/resistance abilities can help plants to successfully adapt to different stressed situations. Therefore, the organisms endowed with tolerance/resistance abilities can be used effectively as beneficial inoculants for enhancing crop production in stressed/derelict soils (Khan et al. 2011; Milosevic et al. 2012). Some of the mechanisms by which PGPR ameliorate stress situations are discussed in the following section and are illustrated in Fig. 11.2.

11.5.1 Mechanisms and Role of PGPR in Stress Alleviation

11.5.1.1 Exopolysaccharide Secretion

Microorganisms belonging to different functional groups for example rhizobia secrete exopolysaccharides (EPS), which provide resistance to cell against different stressors and thus protect the microorganism from stress. The EPS also improve the soil structure by forming macroaggregates with soil, which further increase the water retention ability of soil (Alami et al. 2000). Macroaggregates uphold equilibrium in aerobic and anaerobic conditions in soil and also ascertain gradual uptake of nutrients from soil. In case of salt stress, these aggregates help by binding cations making them unavailable to plants (Haynes and Swift 1990). The rhizobacteria have the ability to form biofilms by secreting polysaccharides and proteins, the matrix so formed limits the diffusion of compounds like plant growth hormones and nutrients from the plant's vicinity, thus promoting plant growth by alleviating stress conditions (Timmusk et al. 2013).

11.5.1.2 Accommodation: Accumulation and Sequestration of Metals

Plant growth-promoting rhizobacteria produce metal-chelating agents, known as siderophores, an iron-chelating agent, which can make the required iron available to plants and hence prevent plants from becoming chlorotic and indirectly

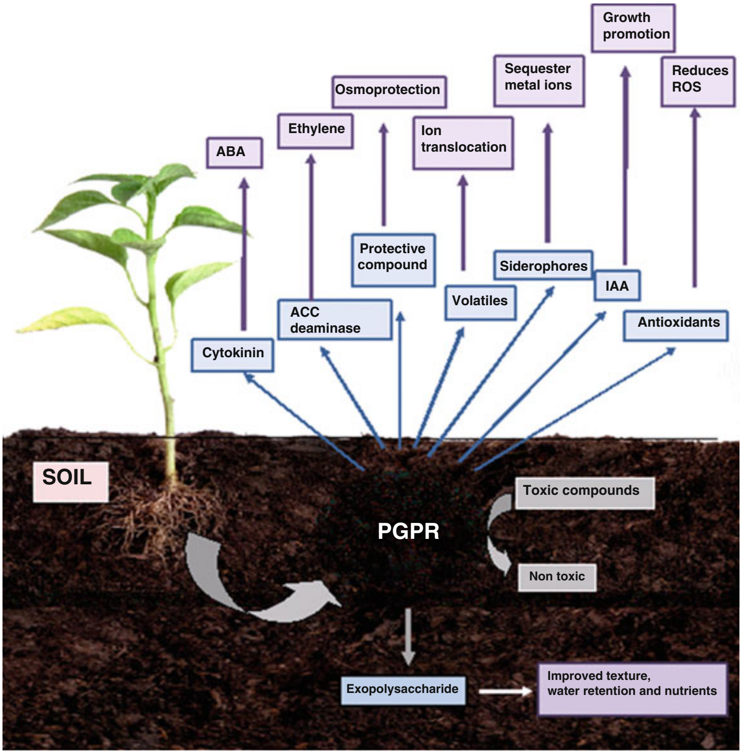

Fig. 11.2 Stress alleviation modes of PGPR (modified from Yang et al. 2009). *ABA* abscisic acid, *IAA* indole acetic acid, *ROS* reactive oxygen species

ameliorating metal stress. The siderophores also bind to other metals like Mg, Mn, and Cr and chelate the solubilized/leached metals (Akhtar et al. 2013). Siderophore-producing PGPR can therefore be used to remove toxicants (metals) from metal polluted soil (Mani et al. 2010). Along with metal stress, siderophore-producing rhizobacteria also inhibit the phytopathogen (Kloepper et al. 1980; Glick 2012) as discussed in Sect. 11.3.2.2.

11.5.1.3 Biotransformation: Conversion of Toxic Forms to Less Toxic Forms

Microorganisms especially PGPR can help in relieving metal toxicity by transforming highly toxic metals to less toxic forms or in forms more readily accessible to plant roots (Khan et al. 2009). The conversion of metals involves mainly a change in the valence state of metals, for example, change of organic selenium to selenate or organo-selenium (Zayed et al. 1998) which can easily be taken up by plants. This feature of PGPR has been well exploited in phytoremediation technology for enhancing metal removal by plants (Jing et al. 2007). Furthermore, rhizobacteria affect the adsorption/desorption of metals by altering their chemical properties, pH, organic matter content, redox state, etc., consequently affecting their solubility and mobility (Gray et al. 1998). PGPR also improve the efficiency of phytoremediation strategy of metal cleanup by increasing the hyper-accumulating abilities of certain plants through their rapid growth in metal stress (Varsha et al. 2011).

11.5.1.4 P Solubilization

The amount of P available to plants is very less as compared to total soil P pool. One of the important attributes of PGPR is phosphate solubilization and the group of microorganisms capable of converting inorganic P into soluble forms is known as P-solubilizing microorganisms (Khan et al. 2007). Along with P assimilation, these microorganisms release a fair amount of soluble P into soil which can be used as P source by the plants. The most efficient PS bacterial strains are *Pseudomonas* (Das et al. 2003) and *Rhizobium* (Sridevi and Mallaiah 2009), whereas *Penicillium* (Chai et al. 2011) and *Aspergillus* (Singh and Reddy 2011) are the most powerful fungal PS strains (Khan et al. 2010; Brahmaprakash and Sahu 2012).

11.5.1.5 Improves Plant Defense Mechanisms Under Stressed Environment

Modulating Enzyme: 1-Aminocyclopropane-1-Carboxylate Deaminase

Under normal condition, plant maintains its homeostasis by producing a hormone “ethylene” which plays important role in various developmental processes. Under stress conditions, the amount of ethylene produced by plant increases due to which it is also known as “stress ethylene.” At higher concentrations, it decreases root and shoot growth and also induces defense responses of plant to mitigate adverse effects. Plant growth-promoting rhizobacteria produce an enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which degrades ACC, the precursor for ethylene, into ammonia and α-ketobutyrate. Bacteria utilize ammonia as N source thereby restricting the ethylene accumulation consequently rescuing the plant growth from the stress (Khan et al. 2009). Also, PGPR synthesize growth hormone IAA from tryptophan produced in plant root exudates which in turn enhances both plant growth and activates enzyme ACC synthase involved in ACC production. ACC so produced is then exuded from the plant roots and acted upon by the bacteria (Selvakumar et al. 2012).

Volatile Production

PGPR are known to produce volatile organic and inorganic compounds which can affect the plant growth and resistance/tolerance against biotic and abiotic stresses via different mechanisms. Some of the volatile compounds produced by different PGPR include 3-hydroxy-2-butanone (acetoin) and 2,3-butanediol by *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a (Ryu et al. 2003) and C-13 hydrocarbon tridecane by *Paenibacillus polymyxa* E681 (Lee et al. 2012). These volatile compounds were found to affect the tissue-specific regulation of high-affinity K^+ transporter 1 (HKT1), which is further involved in the regulation of Na^+ homeostasis in salt stress. The volatiles downregulate hkt1 in roots but upregulate them in the shoot, lowering Na^+ levels and recirculation of Na^+ levels in plant (Yang et al. 2009). Other mechanisms include enhanced iron uptake by upregulating FIT1 (Fe-deficiency-induced transcription factor) during metal stress and production of compatible solutes like betaine under oxidative stress (Farag et al. 2013). These volatiles are also found to have negative effects on the plant growth under certain circumstances (Bailly and Weisskopf 2012). Some of the volatiles involved in stress resistance against biotic factors like pathogens have been already discussed in Sect. 11.3.2.1.

Synthesis of Auxins and Similar Compounds

Microbial auxins can affect the plant's auxins governed developmental processes such as root development including root length, surface area, and number of root tips. This root development further enables nutrient uptake by plants, thereby improving plant health in the presence of inhibitory compounds or under stress conditions (Egamberdieva and Kucharova 2009). Plant exudates contain tryptophan, which is when acquired by rhizobacteria converted to IAA. The microbial IAA along with plant's pooled auxins stimulates plant growth and proliferation (Glick 1995).

Protective Compounds

Microorganisms are known to produce osmo-protectants such as proline, betaine, trehalose, and glutamate which modulate their cytoplasmic osmolarity and hence protect plants from stress conditions (Blanco 1994). Plant also produces protective compounds or compatible osmolytes in response to stress conditions, mainly salt stress. Some of these compounds include amino acids, imino acids, amides, proteins, quaternary ammonium compounds, and polyamines (Carmen and Roberto 2011). Increased production of proline in response to stressors has been reported (Lalelou et al. 2010; Marin et al. 2010) which plays a role in osmo-adaptation in salt stress (Meloni et al. 2001), and as a molecular chaperone it protects and stabilizes macromolecules like proteins during dehydration and also acts as a scavenger for hydroxyl radical, thus protecting from osmotic stress (Csonka 1989; Upadhyay et al. 2012).

Antioxidative Enzymes

Another mechanism of PGPR to counteract stress involves the production of ROS scavengers. Enhanced production of ROS, such as H_2O_2, hydroxyl radicals, singlet oxygen, and superoxide, ensues oxidative damage to DNA, proteins, and lipids. This response is mainly an outcome of imbalance in production and scavenging of ROS due to stress condition. Major ROS scavengers include catalase, superoxide dismutase, and ascorbate peroxidase. PGPR, for instance, *Serratia* sp., *Rhizobium* sp. (Han and Lee 2005), *Bacillus* sp., *Arthrobacter* sp. (Upadhyay et al. 2012), *Azospirullum* sp., and *Pseudomonas* sp. (Baniaghil et al. 2013), are reported to enhance the production of these antioxidant enzymes responsible for ROS degradation/breakdown, thereby helping plants to ameliorate stress response and also growth promotion (Kohler et al. 2009; Carmen and Roberto 2011).

Induced Systemic Tolerance

Similar to ISR for biotic factors, another term “induced systemic tolerance (IST)” had been proposed for abiotic stress alleviation by PGPR. IST is defined as physical and chemical changes elicited by PGPR in response to abiotic stresses such as salt stress, drought stress, temperature stress, metal stress, or nutrition deficiency (Yang et al. 2009). These microbial communities follow different mechanisms such as production of (1) volatiles to modulate Na^+ homeostasis under salt stress (Farag et al. 2013); (2) abscisic acid causing closure of stomata, thus preventing water loss in drought stress; (3) antioxidant enzymes like superoxide dismutase and catalase, which degrade the reactive oxygen species, bringing down cell damage (Selvakumar et al. 2012); (4) IAA, cytokinins, and other metabolites stimulating root growth, thus helping nutrient acquisition combating nutrient deficiency; etc. (Yang et al. 2009). Some of the PGPR reported for IST include *B. cereus*, *B. subtilis*, *Serratia* sp. (Wang et al. 2012), *Paenibacillus polymyxa* (Timmusk and Wagner 1999), *Achromobacter piechaudii* (Mayak et al. 2004), etc.

11.6 PGPR Consortium Application in Plants Growing in Stressed Soils

11.6.1 Drought Stress

The consortia of *Paenibacillus polymyxa* (DSM 36) and *P. polymyxa* Loutit (L) along with *Rhizobium tropici* (CIAT 899) significantly increased growth, N content, and nodulation of common bean (*Phaseolus vulgaris*) growing under drought stress conditions (Figueiredo et al. 2008) compared to plants inoculated only with *Rhizobium*. However, negative effects of drought stress on the measured parameters were observed suggesting that the mixture of bacteria had a positive mitigating impact on stressor. Single and multiple inoculations with different *Pseudomonas* sp. were carried out to study the effect on Asparagus (*Asparagus officinalis*) cultivars (Guelph millennium and Jersey giant) under both drought and flood stress up to 8 weeks. The results so obtained were significantly convincing in one of the cultivars in case of both single and multiple inoculation (Liddycoat et al. 2009). Five drought-tolerant bacterial strains, namely, *Pseudomonas entomophila* strain BV-P13, *P. monteillii* strain WAPP53, *P. putida* strain GAP-P45, *P. stutzeri* strain GRFHAP-P14, and *P. syringae* strain GRFHYTP52, were used to inoculate maize grown under water-deficit conditions. The PGPR inoculation reduced the drought stress damage and improved plant biomass, leaf water potential, relative water content, aggregation stability, sugars, amino acids, and proline content. The effects also included decreased electrolyte leakage and water loss from leaves (Sandhya et al. 2010). In other experiment, three plant growth-promoting strains—*B. cereus AR*156, *B. subtilis* SM21, and *Serratia* sp. XY21—decreased wilting symptoms and leaf monodehydroascorbate in cucumber (*Cucumis sativus*) plant, while they showed 3.45-fold increase in proline content along with increased SOD activity, supporting the hypothesis of induced systemic tolerance in drought stress (Wang et al. 2012). The combined application of PGPR (*A. brasilense*, *B. lentus*, and *Pseudomonades* sp.) improved antioxidant activity and also indicated better photosynthetic capacity and improved photosynthetic pigments in Basil (*Ocimum basilicum*) (Heidari and Golpayengani 2012), while the combined inoculation of different PGPR strains increased superoxide dismutase and peroxidase activity along with better chlorophyll content and transpiration in runner bean plants (*Phaseolus coccineus* L.) (Stefan et al. 2013).

11.6.2 Salt Stress

Effects of dual inoculation of *Serratia* sp. and *Rhizobium* sp. on the growth and other parameters of lettuce plant grown under salt stress were variable. PGPR negated the effects of salt stress on the antioxidant enzymes and on photosynthesis, mineral content, and growth (Han and Lee 2005). And hence, the consortia of microbial cultures showed both growth-promoting activity and the stress alleviation activity. Another greenhouse study was carried out on two legumes like common bean and soybean under moderate salt conditions (25 mM) where rhizobial strains *R. tropici* (CIAT899) or *R. etli* (ISP42) and *Ensifer fredii* (*Sinorhizobium*) SMH12 and HH103 along with PGPR *Chryseobacterium balustinum* Aur9 strains were used both individually and in combination to determine their effects on nodulation and growth. The coinoculation significantly increased the nodule primordial formation in common bean and showed better nodulation and shoot-root growth in both crops (Estevezi et al. 2009). In yet other report, the coinoculation of *Pseudomonas* sp. and *Rhizobium* sp. showed maximum increase in growth (dry weight and height), mineral accumulation, ion uptake, chlorophyll content, and proline content in maize (cv. Agaiti 2002 and Av 4001) plants grown under salt stress compared to single inoculations of either culture (Bano and Fatima 2009). The consortia of EPS producing salt-tolerant PGPR strains comprising of *Bacillus* sp., *Burkholderia* sp., *Enterobacter* sp., *Microbacterium* sp., and *Paenibacillus* sp. increased the biomass of wheat (Upadhyay et al. 2012). The mixture of salt-tolerant bacteria such as strains of *Brachybacterium saurashtrense* (JG-06), *Brevibacterium casei* (JG-08), and *Haererohalobacter* (JG-11) augmented the water content, metal ion ratio K^+/Na^+, and mineral and auxin content and decreased the electrolyte leakage and oxidative damage in peanut (*Arachis hypogaea*) plants compared to uninoculated control plants (Shukla et al. 2012). In a similar study, Nadeem et al. (2013) observed a significant increase in germination rate and percentage, growth, yield, and nutritional status of wheat inoculated with consortia of *Enterobacter cloacae*, *Pseudomonas putida*, *P. fluorescens*, and *Serratia ficaria*, when grown under saline-stressed environment. The co-culture of *Pseudomonas syringae* Mk1, *P. fluorescens* Mk20, and *P. fluorescens Biotype* G Mk25 in combination with *R. phaseoli* (M1, M6, and M9) increased the shoot weight, root weight, number of pods, and total dry weight of mung bean plants by 145 %, 173 %, 150 %, and 269 %, respectively, when grown in saline condition. Furthermore, the seedling growth, nodulation, and mineral uptake were significantly enhanced following mixture of PGPR where there was a substantial reduction in salt stress due to microbial application (Ahmad et al. 2012a; Aamir et al. 2013). Two bacterial strains *A. brasilense* and *Pantoea dispersa* showed a significant increase in dry weight and K^+/Na^+ level of salt-sensitive sweet pepper (*Capsicum annuum*) compared to uninoculated controls. The net assimilation rate remained unaffected even at higher salinity level (80 mM) in case of inoculated plants. Inoculated plants were also found to have higher stomatal conductance at higher stress (Amor and Cuadra-Crespo 2012).

11.6.3 Metal Stress

Plant growth-promoting attributes of metal-tolerant *Flavobacterium* sp., *Rhodococcus* sp., and *Variovorax paradoxus* were found to stimulate the root growth of rapeseed both in the presence and the absence of Cd, supporting their role as promoters under metal-stressed situation (Belimov et al. 2005). A study on the effect of metal-tolerant PGPR *Burkholderia* sp. CMBM40 and *Methylobacterium oryzae* CMBM20 inoculation on tomato plants grown in Ni- and Cd-treated soil was carried out. The PGPR were found to decrease the metal uptake by plants and also enhanced the plant growth by producing growth hormones (Madhaiyan et al. 2007). Consortia of *Bradyrhizobium* sp. with metal-tolerant PGPR *Pseudomonas* sp. and *Ochrobactrum cytisi* significantly improved biomass, yield, and N content of metal accumulating *Lupinus luteus* plants but they decreased metal accumulation within plants (Dary et al. 2010). Likewise, the metal-tolerant PGPR consortia significantly increased root length, shoot length, biomass, and chlorophyll content of mung bean by 138 %, 88 %, 256 %, and 54.1 %, respectively, when grown in chromium-treated soils (Singh et al. 2010). Similar enhancement in some cereals, for example, wheat following metal-tolerant PGPR, *B. thuringiensis* and *P. fluorescens* (Shahzadi et al. 2013) and *A. brasilense* and *A. chroococcum* (Janmohammadi et al. 2013), has been reported. The PGPR *Ralstonia eutropha* (B1) and *Chryseobacterium humi* (B2) inoculated sunflower (*Helianthus annuus*) plants when grown in Zn- and Cd-contaminated soil had decreased metal concentration inside plant tissues, suggesting that metal-resistant PGPR might have served as effective stabilizers for plants grown in metal-contaminated soil (Marques et al. 2013).

11.7 Conclusion

Among various abiotic stresses, drought, salinity, and metal pollution are the most stronger and stringent ones, which restrict the overall performance of plants growing in such derelict soils. The sole or composite (consortia) application of PGPR is an emerging area of interest because these microbes have been found to enhance the growth and development of plants both under conventional and stressed environments in different production systems across varying ecological niches. Moreover, microbial inoculation is cost effective, environmentally friendly, and easy option for farm practitioners. However, before they are made commercially available, more field trials are needed to get the full benefit of this strategy in combating stress-related problems caused to agronomically important crops. Considering the available information, it is believed that the practice of PGPR consortium application is likely to grow faster and agricultural practices will slowly be able to shifting its focus from fertilizer to efficacious use of PGPR.

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