Role of Plant Growth-Promoting Rhizobacteria in Combating Abiotic and Biotic Stresses in Plants

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Muhammad Zahid Mumtaz, Maqshoof Ahmad, Khadija Mehmood,
Ahsan Sattar Sheikh, Arif Malik, Azhar Hussain,
Sajid Mehmood Nadeem, and Zahir Ahmad Zahir

Abstract

Global climate change accelerates the coincidence of a variety of abiotic stresses, viz., salinity, drought, flooding, high and low temperature, and biotic stresses, viz. phytopathogens which degrade agricultural productivity. In such circumstances, plant growth-promoting rhizobacteria (PGPR) are eco-friendly and sustainable candidates to combat these stresses. Several PGPR with the ability to support plant growth under various stressed conditions have been commercialized. The current chapter is mainly restricted to beneficial effects of PGPR on plant growth and development under environmental and biotic stresses. It begins with the description of various abiotic and biotic stress factors affecting plant growth and their tolerance achieved by both physiological and molecular mechanisms of adaptation. The use of PGPR helps ameliorate these stresses in rhizosphere by using several mechanisms and has beneficial effects on plant growth after efficiently colonizing the root surface. Plant growth stimulation through PGPR is the net result of multiple mechanisms of action that may be activated simultaneously. Such bacteria are more likely to be used for stress

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M. Z. Mumtaz · A. S. Sheikh · A. Malik
Institute of Molecular Biology and Biotechnology, The University of Lahore, Lahore, Pakistan

M. Ahmad (✉) · K. Mehmood · A. Hussain
Department of Soil Science, The Islamia University of Bahawalpur, Bahawalpur, Pakistan

S. M. Nadeem
University of Agriculture Faisalabad, Sub-Campus Burewala-Vehari, Burewala, Vehari, Punjab, Pakistan

Z. A. Zahir
Institute of Soil and Environmental Sciences, University of Agriculture Faisalabad, Faisalabad, Punjab, Pakistan

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tolerance to fulfill the need for food production under extreme environmental conditions. The bacterial inoculants also enhance nutrient uptake and crop growth. They are also involved in biocontrol so they may be good supplements to chemical fertilizers and agrochemicals. This chapter discusses the potential and key mechanisms used by PGPR under stress conditions for sustainable agricultural productivity followed by their prospects.

Keywords

ACC-deaminase activity · Beneficial bacteria · Environmental sustainability · Integrated stress · Phytohormones · Plant tolerance

2.1 Introduction

Global warming leads to abiotic and biotic stresses that are affecting crop productivity all over the globe. Abiotic stresses include salinity, drought, flooding, heavy metals, heat, and cold stress, while biotic stresses are caused by the attack of insects, pests, and microbial infection. Such abiotic and biotic stresses are collectively known as integrated stresses (Flynn 2003; Brown et al. 2017). Abiotic stresses are also known as environmental stresses that drastically reduce plant growth by disrupting metabolic and biochemical attributes of a plant (Suzuki et al. 2014). Abiotic stresses induce plant responses through modification in cellular metabolism, reduction in plant growth, and modulation in biochemical attributes (Singh 2015). Many studies have illustrated the effect of selective abiotic stresses such as salinity (Mumtaz et al. 2018; Sapre et al. 2021), heavy metals (Thakare et al. 2021), drought (Mumtaz et al. 2020; Ansari et al. 2021), flooding (Bal and Adhya 2021), heat (Sarkar et al. 2021), and cold (Vega-Celedón et al. 2021) on the growth of different plants.

Microorganisms can be handy in mitigation of abiotic and biotic stresses. Beneficial bacteria which constitute up to 2–5% of the total bacterial population in soil are beneficial for plant growth even under adverse environments (Nazli et al. 2020). Millions of microorganisms colonizing the rhizosphere form a complex biological community with a plant root system and stimulate plant growth through their metabolic activities (Schmidt et al. 2014; Zvinavashe et al. 2021). Plant growth promoting bacteria (PGPR) improve plant nutrient availability and help in sustained crop yields (Hayat et al. 2010) through efficient nutrient solubilization and mobilization, providing biocontrol against phytopathogens, improving soil structure and quality by sequestrating toxic salt ions, and even degrading various xenobiotic compounds (Braud et al. 2009; Koskey et al. 2021). The application of such inoculants is a promising strategy for the amelioration of various stresses and improving plant health (Ahmad et al. 2013a). Bioaugmentation of PGPR modulates environmental stresses through direct and indirect mechanisms that induce systemic tolerance (Yang et al. 2009). Production of phytohormones and 1-amino-cyclopropane-1-carboxylic acid (ACC) deaminase activity by various PGPR has a crucial role in plant growth under environmental as well as biotic stresses. It activates the radicular system and promotes root elongation through the development of apical meristem and lateral roots, thus improving plant access to soil nutrients (Vessey 2003; Liu et al. 2021). In the current chapter, we have discussed the status of various abiotic and biotic stresses and their effects on plant growth. We have also discussed the potential of PGPR for remediation of these stresses. Abiotic stress induced by salt, drought, flooding, heat, and cold factors and biotic stress due to fungal, bacterial, and nematode pathogen have been reviewed. Various direct and indirect mechanisms used by PGPR for amelioration of these stresses have also been discussed.

2.2 Plant Responses to Stress

Plant stress is a condition in which plants are developed in non-ideal circumstances for their growth. It could be due to various external biological and non-biological factors that lead to a direct effect on plant growth. Biological stresses are also known as biotic stress, observed on plants due to plant interactions with pathogenic bacteria, fungi, virus, nematodes, weeds, and/or insects. Non-biological stress could be due to physical factors such as deficiency or toxicity of nutrients, high or low temperature, limited water availability or excess of water conditions, etc. (McKersie and Lesheim 1994). Non-biological factors result in non-favorable conditions to plants and enforce them under a state of stresses known as abiotic or environmental stresses. Mostly, abiotic stresses have a huge impact on plants by causing up to a 50% reduction in growth. Both biotic and abiotic stresses could affect plant growth for short or long periods depending on the exposure level (Mosa et al. 2017). Plants are exposed to abiotic and biotic stress factors, collectively called stressors that deviate plant’s optimal growth conditions. Stressors damage plant growth up to certain tolerance limits and, after that, may cause death. Stressors are interconnected to each other and affect plants by causing osmotic stress, ion imbalance, disrupting plant metabolism, production of ethylene, reactive oxygen species (ROS), and cell homeostasis. Many groups of genes have also shown changes in their expression patterns due to various stressors (Mittler 2006; Ramegowda et al. 2020; Kusale et al. 2021; Sofy et al. 2021).

Plants use a stress-sensing mechanism that depends on plant species and type of stress. Plant response to stress can be categorized into alarming, resistance, exhaustion, and regeneration (Mosa et al. 2017). In initial stress exposure, distinguishable changes from optimal plant growth in terms of functional deviation, declining vitality, and increase in catabolism take place. If stressors continue, these affect plant growth and productivity, and plant responds through stress adaptation, repair, and hardening processes. To minimize damage caused by various stresses, plant activates a complex signaling cascade of defense and specific ion channels; generates ROS and phytohormones, and expresses various stress-related genes that improve plant stress tolerance (Ramegowda et al. 2020; Tanveer and Ahmed 2020; Salvi et al. 2021). Every plant species has a certain limit for resistance against stresses that cannot be extended through external modification. Further increase in stress dosage beyond the plant resistance will cause loss of vitality, severe cell damage, and plant death (Mosa et al. 2017). Before complete senescence, plants can regenerate their physiological standards that allow plants to survive under various stresses. However, if stressors cause permanent damage, then it will not recover. A plant can survive under stress conditions but with limited growth and reproduction ability. These responses usually involve physiological-, biochemical-, and molecular-level actions (Kranner et al. 2010; Brunetti et al. 2019; Ansari et al. 2021). Plant response to stress can be modified/improved through exogenous application of various chemicals, phytohormones, and/or by modification of growing conditions. Rhizosphere microbiome engineering has also been studied as an eco-friendly, economical, and sustainable approach by the soil microbiologists.

2.3 Strategies for Stress Amelioration

Several strategies have been proposed by plant scientists to ameliorate stress. These strategies are comprehensively reviewed and available in literature (Glick et al. 2007; Saharan and Nehra 2011; Nadeem et al. 2014). Certain chemicals are used to reduce the impact of stresses on plant growth. These chemicals can reduce the negative impact of ethylene on plant growth by inhibiting its excess production under stress. Important chemicals reported in the literature are silver ions (Ag^+), cobalt ions (Co^{2+}), and aminoethoxyvinylglycine (AVG) which improve plant growth by suppressing ethylene production (Coupland and Jackson 1991; Mckeon et al. 1995; Kim and Mulkey 1997). Savvides et al. (2016) reported that plant priming with chemical agents, hydrogen peroxide, melatonin, polyamines, sodium hydrosulfide, and sodium nitroprusside, can improve multiple-stress tolerance. Priming with γ-amino butyric acid and β-amino butyric acid also induces promising tolerance in plants against abiotic stresses (Vijayakumari et al. 2016). Soaking seed with these priming agents shows greater stress tolerance by improving metabolic events and shows early seed germination and seedling emergence as compared to non-primed seeds (Ashraf et al. 2018). These chemicals also improve antioxidative enzymes, proline, malondialdehyde, and improve stress-responsive proteins (Thakur et al. 2019; Buttar et al. 2020).

The use of chemicals in agriculture is, however, expensive and deteriorates the plant, soil, and human health (Dodd et al. 2004; Pahalvi et al. 2021). These chemicals can increase crop yield but reduce farm profitability. Scientists have also raised certain environmental issues due to the persistence and toxicity of these chemicals for the natural habitat (Ahmadi et al. 2009). The use of osmoprotectants and potassium to reduce the negative effects has also been reported. However, the use of chemicals cannot reduce the negative effects of ion toxicity caused by salinity or root desiccation under osmotic stress. Although plants employ some specific mechanisms to cope with stresses, the presence of beneficial microbes can be helpful to combat the negative effects of stresses on plant growth. Rhizosphere engineering by using PGPR can therefore be exploited as a useful strategy to ameliorate the negative effects on plant growth. It could be the most important approach to remediate multiple stresses for sustainable agriculture. Recently, such beneficial bacteria have been acknowledged by scientists for their capability to improve crop productivity as well as raise stress tolerance in various crops (Goyal et al. 2019; Njeru and Koskey 2021).

2.4 Role of Plant Growth-Promoting Rhizobacteria to Combat Stresses in Plants

Plants are associated with soil microorganisms in a symbiotic relationship; thus there is a strong plant-microbe interaction in the rhizosphere. Such symbiotic free-living soil microorganisms inhabiting the rhizosphere of many plant species having diverse beneficial effects on host plants are known as PGPR. Their interactions with plants are commercially explored and have biotechnological applications for sustainable agriculture to improve plant health in an eco-friendly manner (Gonzalez et al. 2015; Gouda et al. 2018). Biological activities of soil microbiome in the ecosystem make it vigorous for sustainable agriculture production. The PGPR dwell in plant roots and improve plant growth through various mechanisms including nitrogen (N) fixation (Kuan et al. 2016; Aasfar et al. 2021), solubilization of phosphorus (P) (Selvakumar et al. 2009; Kusale et al. 2021); potassium (K) (Ahmad et al. 2016) and zinc (Zn) solubilization (Mumtaz et al. 2017, 2019); production of siderophores (Gouda et al. 2018); ACC-deaminase (Misra et al. 2017; Ansari et al. 2021; Vega-Celedón et al. 2021); and phytohormones, e.g. indole-3-acetic acid (IAA) (Kim et al. 2017; Khan et al. 2020a, b; Kusale et al. 2021), cytokinins (CK) (Liu et al. 2013; Ilyas et al. 2020), gibberellins (GA) (Gutiérrez-Mañero et al. 2001; Khan et al. 2020a, b), abscisic acid (ABA) (Belimov et al. 2014; Kang et al. 2019), hydrogen cyanide (HCN) (Kremer and Souissi 2001), and antibiotics and/or lytic enzymes (Gouda et al. 2018; Migunova and Sasanelli 2021). They also possess more specific plant growth-promoting (PGP) traits that can ameliorate/reduce environmental stresses such as heavy metals, salinity, and drought stress and biological control of phytopathogens (Egamberdieva and Lugtenberg 2014). Such PGPR are classified into two main types: (1) the extracellular PGPR that can colonize the rhizoplane and (2) intracellular PGPR that colonize inside the root cortex or nodule cells (Bhattacharyya and Jha 2012).

The PGPR possess several PGP characteristics that are involved in enhancing plant physiology under normal as well as stress conditions through various mechanisms (Ahmad et al. 2011; Zakry et al. 2012; Asghari et al. 2020). They produce volatile organic compounds (VOCs) and enzymes for biocontrol of phytopathogens and neutralize abiotic and biotic stresses. However, different PGPR have different modes of action which differ under certain circumstances according to their host plant, abiotic and biotic factors, plant defense and developmental stages, and presence of competition for microflora (Garcia et al. 2015). They can support plant growth and development through enhancing nutrient availability by nitrogen fixation, solubilization of minerals, mineralization of nutrients, and production of phytohormones and siderophores (Bhardwaj et al. 2014). Such mechanisms improve plant growth directly and may contribute according to the ability of microbial strains. In the presence of PGPR, improved individual ion fluxes at the root surface enrich nutrient uptake (Gouda et al. 2018). The PGPR may indirectly improve plant growth and development by producing suppressive compounds that prevent the phytopathogen attack on plants (Singh and Jha 2015; Migunova and Sasanelli 2021). This process actively helps plants grow under biotic stresses (Akhgar et al. 2014). In this mechanism, PGPR contribute through the production of chitinases, cellulases, proteases, and other hydrolytic enzymes and production of antibiotics, siderophores, VOCs, exopolysaccharides (EPS), and induced systemic resistance (ISR) in response to a plant pathogen (Gupta et al. 2015). The occurrence of abiotic and biotic stresses drastically affects crop productivity over the globe. So, there is a need to explore unique PGP characteristics of soil microbiome under extreme environmental conditions, their relations with crop plants, genetic diversity, and successful application methods for increased agriculture production (Grover et al. 2011).

2.4.1 Abiotic Stress

External conditions of either physical or biological nature that unfavorably disturb plant growth are known as stresses. Physical stresses, viz., salinity, drought, waterlogging, heat, cold and heavy metal contamination, etc., are termed as abiotic stresses (Brown et al. 2017), while biological agents like microbial and insect and pest attacks are known as biotic stresses (Flynn 2003). According to an estimate, between 2003 and 2013, 78 types of natural disasters caused 140 billion dollars worth of losses in developing countries (FAO 2015). Abiotic stresses impose their hazardous effects on plant growth by altering the metabolic, biochemical, and physiological attributes of plant growth (Suzuki et al. 2014; Sapre et al. 2021). Abiotic stresses initiate plant responses in terms of cellular metabolism, changes in growth and yield attributes, modulation in metabolites and biochemical attributes, and alteration in gene expression (Singh 2015; Sofy et al. 2021).

Abiotic stresses impair photosynthetic machinery in plants such as photosystem I and II, stomatal conductance, carbon (C) fixation, electron transport, and ATP-generating system (Nouri et al. 2015; Chatterjee et al. 2020; Sharma et al. 2020). These may modify the structure of chloroplasts and thylakoid complexes, cause changes in metabolites concentration, and generate ROS (Gan et al. 2019). For example, salinity stress causes loss of photosynthetic pigments and stomatal closure due to reduced nutrient uptake (Stepien and Kłbus 2006). It also reduces the carbon dioxide (CO_2) availability and carbon (C) fixation that generate ROS, thus causing cellular damage through oxidation of lipids, proteins, and nucleic acids (Lopez-Raez 2016). Abiotic stresses adversely affect plant growth by decreasing water availability that causes an imbalance between enzymatic and non-enzymatic reactions taking place in chloroplasts, mitochondria, and electron transport reactions (Koyro et al. 2012; Adak et al. 2020). Various crop plants differ in their ability to withstand most of the abiotic stresses. The plant tolerates abiotic stresses through genetic and physiological adaptive mechanisms and interacts symbiotically with endophytic and rhizospheric bacteria. Many studies have demonstrated genetic adaptation to abiotic stresses including molecular mechanism, identification of overexpressed genes, and development of stress-tolerant transgenic plants (Zang et al. 2017; Datir et al. 2019; Woo et al. 2020). Several studies have also reported plant-microbe interactions in abiotic stress tolerance. Pre-treatment of plant seed or seedlings with PGPR can improve plant survival during abiotic stresses which are being discussed in subsequent sections for each abiotic stress.

2.4.1.1 Salt Stress

Agriculture is moving into regions with lower rainfall and saline soil that occupy 6% of the world's land area due to the increased need for food production (Munns 2005). High salinity is one of the major abiotic factors that adversely affect crop growth, development, and productivity (Mumtaz et al. 2018). It converts fertile fields to marginal lands and causes desertification. Soil salinization is the buildup of dissolved salts in agricultural soils over a prolonged time. It may arise due to weathering of rocks and minerals, precipitation, wind-borne salts, the influx of seawater, and cultivation operations, viz. unnecessary irrigation, land clearing, and insufficient drainage. The dryland salinity originated due to salt deposition in the topsoil through water evaporation (Rengasamy 2002, 2010; Pitman and Läuchli 2002; Shrivastava and Kumar 2015). Salinity effects are more harmful under the raised groundwater table, arid, and coastal areas, and only salt-tolerant plants called halophytes can grow (Rengasamy 2002; Flowers and Colmer 2008). The salinity-sensitive plants called glycophytes eventually die as their physiological and biochemical attributes are susceptible to salt-induced stress (Hajiboland et al. 2018).

Salinity stress hinders crop production by causing various physiological and metabolic changes. It suppresses plant growth through osmotic stress and ion toxicity (Rozema and Flowers 2008; Rahnama et al. 2010). Osmotic stress due to higher salt buildup in soil and plants causes a reduction in water absorption ability, accelerated water loss from leaves, and various physiological changes, viz. nutrient imbalance, membrane interruption, inability to reduce ROS, and alteration in antioxidant enzymes (Munns and Tester 2008; Rahnama et al. 2010; Sagar et al. 2020). Salinity causes accumulation of sodium (Na^+) and chloride (Cl^-) ions in plant tissues that cause severe ion imbalance and physiological disorders. Accumulation of higher Na^+ contents retard the uptake of potassium ions (K^+) that is necessary for plant growth and development and may cause plant death (James et al. 2011). Due to salt stress, oxidative stress elevates the production of ROS which leads to oxidative damages in proteins, lipids, and DNA and interrupts vital cellular functions of plants (Xie et al. 2014; Kusale et al. 2021).

Plants tolerate high salt stress by developing various physiological adaptations *viz.* ion homeostasis, transport, and compartmentalization, synthesis of osmoprotectants, compatible solutes, polyamines, nitric oxide, and activation of antioxidant enzymes and hormone modulation (Gupta and Huang 2014; Dubey and Verma 2019; Sofy et al. 2021). There is a need to apply an attenuated approach to remediate the effects of salt stress on crops. Due to reduced agricultural production under salinity stress, the production of salinity-resistant crops is a desirable scientific achievement. For successful saline soil reclamation, effective soil management practices are needed (Munns and Tester 2008). The sustainable management practices to facilitate future agriculture production provide more support regarding crop production. Various plant growth-promoting microorganisms (PGPM) play a beneficial role to promote agricultural productivity in an ecofriendly manner (Rodriguez and Redman 2008). Such PGPM associated with the stressed plant augment to adapt their microenvironments (Paul and Lade 2014). Various crops under salinity-stressed conditions respond to PGPM that improves plant growth. Such biotechnology can help to develop salinity-tolerant technologies for growing crops. Augmented PGPR colonizes plant's rhizospheric soil and alleviates stress in crops. This remediation strategy could be successful due to a wide range of salinity-tolerant microbes, their associated interactions with plants, potential PGP metabolites, and prospective application methods.

The PGPR have been investigated under salt-induced stress for their role in improving the efficiency of photosynthesis, ion homeostasis, and plant-water relations regulated by a signaling network that mitigates the stress (Wang et al. 2016; Mahadik and Kumudini 2020; Taj and Challabathula 2021). They optimize water uptake and stomatal opening by improving the transpiration rate and hydraulic conductivity. Marulanda et al. (2010) reported that inoculation with *Bacillus megaterium* improved root hydraulic conductivity in maize under 2.59 dS m^{-1} salt stress that correlated with increased ZmPIP expression. *Arabidopsis thaliana* treated with *Bacillus subtilis* encourages proline production with the expression of proBA genes that conferred salt tolerance to withstand the initial osmotic shocks (Chen et al. 2007). In another study, *Bacillus amyloliquefaciens* strain SN13 inoculated in rice augmented salt stress of 200 mM NaCl through upregulation of stress-related genes (Nautiyal et al. 2013). Upadhyay and Singh (2015) reported that inoculation with *Bacillus aquimaris* promoted total sugar contents in wheat that related to increased NPK and biomass accumulation and reduction of Na^+ in leaves. del Amor and Cuadra-Crespo (2012) reported that pepper plants inoculated with *Azospirillum brasilense* and *Pantoea dispersa* improved salinity resistance in pepper and recorded higher plant dry matter correlated with enhanced stomatal conductance and photosynthetic rate. The PGPR induces accumulation of osmoprotectants and compatible solutes, viz., glycine, proline, and trehalose having more potency than their linked host plants under salt stress (Arif and Ghoul 2018; Taj and Challabathula 2021). These compatible solutes are absorbed by plant roots that maintain osmotic balance. The bean crop overexpressed trehalose-6-phosphate gene when co-inoculated by *Paenibacillus polymyxa* and *Rhizobium tropici* that promoted nodulation and N accumulation. The upregulation of stress tolerance genes through *R. tropici* and *P. polymyxa* induced salinity tolerance in beans (Figueiredo et al. 2008).

The PGPR trap cations in their EPS matrix and limit salt uptake by plants that improve their root structure and regulate ion affinity transporter's expression. They relieve nutrient imbalance by reducing Na^+ and Cl^- influx and increased exchange of macronutrients and micronutrients through mineralizing the nutrients, lowering rhizospheric pH, and producing siderophores (Nadeem et al. 2016; Etesami and Alikhani 2019; Ji et al. 2020). They maintain ion homeostasis by boosting activity of K^+ transporters, improving K^+:Na^+ ratios, decreasing Na^+ and Cl^- buildup, and increasing Na^+ exclusion. Maize inoculation with IAA-producing *Azotobacter* strains C5 and C9 showed improved Na^+ exclusion and K^+ uptake (Rojas-Tapias et al. 2012). Under 200 mM NaCl stress, *Puccinellia tenuiflora* inoculated with *B. subtilis* strain GB03 exhibited reduced Na^+ buildup (Niu et al. 2016). PGPR produce exogenous phytohormones and enzymes that may help ameliorate salt stress. During salinity stress, plants also synthesize phytohormones in the response of plant-microbe relations (Dodd et al. 2010; Kusale et al. 2021).

Several PGPR can produce phytohormones, viz., IAA, CK, GA, and ABA, proliferate roots hairs, and enhance uptake of water and nutrients under salt stress. Salinity stress reduces the endogenous IAA and ABA levels in plants which can be maintained at their normal level through PGPR inoculation. For example, *B. amyloliquefaciens* strain SQR9 stimulated ABA production of inoculated plants under salinity stress (Chen et al. 2016). Similarly, Kim et al. (2014) inoculated *Enterobacter* sp. strain EJ01 in *Arabidopsis thaliana* under salt stress and reported increased expression of salt stress-responsive genes. They also reported that strain EJ01-inoculated plant showed increase in ROS scavenging activities through production of ascorbate peroxidase (APX) under salinity stress. PGPR produce CK under salt stress; however their role in salt stress tolerance is still under question (Arkhipova et al. 2005). Egamberdieva (2009) inoculated wheat with CK-producing *Pseudomonas* strains TSAU22, TSAU6, and TSAU20 that enhanced wheat growth under salt stress. PGPR modulate ABA biosynthesis under salinity stress and support plant growth. In another study, *Dietzia natronolimnaea* strain STR1 induced salt-tolerance in wheat by modulating ABA signaling cascade and upregulation of salt stress-induced gene. These strains contributed to antioxidant enzymes and proline content gene expression that enhanced salt tolerance (Bharti et al. 2016). Cucumber inoculation with strains of *Burkholderia*, *Promicromonospora*, and *Acinetobacter* showed a significant increase in biomass, water potential, and decreased electrolyte leakage at 120 mM NaCl stress. These strains showed downregulation of ABA and increased levels of salicylic acid and GA contents in inoculated plant (Kang et al. 2014). Similarly, improvement in maize growth has also been reported on compacted saline-sodic soil through seed inoculation with *Pseudomonas syringae* and *Pseudomonas fluorescens* (Zafar-ul-Hye et al. 2018).

Under salinity stress, ethylene levels increase, which causes inhibition in auxin transcription and constrain plant growth. PGPR produce ACC-deaminase that inhibit the biosynthesis of ethylene in plants. Soil bacteria produce ACC-deaminase enzyme that converts ACC to ammonia and a-ketobutyrate and enhance salt tolerance and promote plant growth (Glick et al. 2007). Tomato seedlings inoculated with *Pseudomonas putida* strain UW4 grown under 90 mM NaCl stress showed increased shoot growth due to the expression of upregulated Toc GTPase that import stress response proteins (Yan et al. 2014). Okra inoculation with *Enterobacter* sp. strain UPMR18 ameliorated salt stress due to escalating antioxidant activities (Habib et al. 2016). Nadeem et al. (2009) reported salt tolerance in maize due to co-inoculation of ACC-deaminase-producing *Pseudomonas* and *Enterobacter* spp. The ACC-deaminase- and IAA-producing PGPR can ameliorate the negative effects of salt stress effectively. The accumulation of IAA stimulates the ACC synthase genes, resulting in a higher ACC amount that leads to ethylene production. The ACC-deaminase-producing PGPR break down the excess ACC and lower the toxic level of ethylene, and simultaneously IAA production promotes plant growth (Glick 2012; Ahmad et al. 2013b). In another study, the combined use of ACC-deaminase-containing PGPR strains *Agrobacterium fabrum* and *B. amyloliquefaciens* along with biochar improved wheat productivity under drought-stressed conditions (Danish and Zafar-ul-Hye 2019; Zafar-ul-Hye et al. 2019).

The IAA- and ACC-deaminase-producing *Arthrobacter* sp. and *Bacillus* sp. inoculation promoted proline contents under osmotic stress and revealed downregulation of stress-inducible genes in sweet pepper (Sziderics et al. 2007). In another study, Panwar et al. (2016) inoculated IAA- and ACC-deaminase-producing *P. dispersa* strain PSB3 in chickpea under 150 mM NaCl stress and reported significant improvement in plant biomass and grain yield attributes due to reduced Na^+ uptake, electrolyte leakage, and enhanced K^+ uptake. The extracellular secretions from PGPR could also manipulate signaling pathways and alleviate salt stress (Bhattacharyya et al. 2015; Zhou et al. 2016; Kumawat et al. 2020). PGPR produce EPS responsible for bacterial attachment to soil particles. EPS improves soil structure and water-holding capacity by binding soil particles (Upadhyay et al. 2011). Qurashi and Sabri (2012) inoculated chickpea with *Halomonas variabilis* strain HT1 and *Planococcus rifietoensis* strain RT4 and reported salt tolerance by improving plant growth and soil aggregation. *P. polymyxa* ANM59 and *Paenibacillus* sp. ANM76 have also been reported as potential bioinoculants to improve abiotic stress tolerance of crop plants (Ahmad et al. 2019a). The mechanisms of action adopted by PGPR to mitigate salt stress are summarised in Fig. 2.1 and Table 2.1.

2.4.1.2 Drought Stress

Drought is a condition of an uncommon drop in soil moisture content due to a prolonged period of low rainfall. It is the utmost devastating abiotic stress that restricts crop growth and productivity worldwide. The arable lands affected by drought have doubled during the period from 1970 to 2000 and is expected to increase further by 2050, posing serious threat to crop productivity (Vinocur and Altman 2005). In the last four decades, drought caused reduction in cereal yield by up to 10% and is estimated to affect crop production in over 50% of cultivated land by 2050 (Lesk et al. 2016). Drought may be of moderate, short, extremely severe, and prolonged duration (Bottner et al. 1995). It causes a reduction in plant growth by altering physiological traits of a plant (Rahdari and Hoseini 2012; Mumtaz et al. 2020). Growth reduction due to drought stress has been described in cereal crops such as barley (Hellal et al. 2018), maize (Avramova et al. 2015), rice (Mumtaz et al. 2020), wheat (Kosová et al. 2016), etc. Among growth attributes, drought commonly causes a reduction in water content and fresh weight of plants (Jaleel et al. 2009; Meenakshi et al. 2019). Due to limited water availability, drought causes a reduction in nutrient availability and transportation (Selvakumar et al. 2012). Free radicals induced under drought stress cause oxidative stress that affects antioxidant defense and ROS production. The ROS generation damages lipid peroxidation and degradation of membrane, protein, and lipids in plants (Hendry 2005; Chiappero et al. 2019). Drought stress causes a reduction in chlorophyll content,

Fig. 2.1 Proposed salt-tolerance mechanisms mediated by PGPR. Rhizobacteria colonize the root surface and produce extracellular polysaccharides to ameliorate salinity stress. They manipulate phytohormones level and improve nutritional balance and photosynthetic activity through various physiological and biochemical processes

Table 2.1 The use of PGPR to mitigate abiotic stresses in plants

PGPR	Plants	Findings	References
Salt stress			
Klebsiella variicola (SURYA6)	*Triticum aestivum*	This strain showed a potential to ameliorate salinity stress by producing various metabolites including phytase, organic acid, P solubilization, siderophore, IAA, ACC-deaminase, SOD, CAT, and GPX	Kusale et al. (2021)
Pseudomonas azotoformans (CHB 1107)	*Solanum lycopersicum*	This strain possesses ACC-deaminase gene and showed a potential to ameliorate saline stress by increasing shoot and root dry weights and K^+/Na^+ ratio and reducing Na^+ uptake in tomato plants	Liu et al. (2021)
Acinetobacter bereziniae (IG 2), *Enterobacter ludwigii* (IG 10), *Alcaligenes faecalis* (IG 27)	*Pisum sativum*	Application of these strains ameliorated salt stress by modulated chlorophyll and proline contents, total soluble sugars, electrolyte leakage, antioxidant enzymatic activities, and reduced electrolyte leakage and H_2O_2 content	Sapre et al. (2021)
Bacillus subtilis, *Pseudomonas fluorescens*	*P. sativum*	These endophytic bacteria promoted salt stress tolerance in pea through increasing SOD, CAT, POD, glutathione reductase, proline contents, IAA, GA, MSI, photosynthetic pigments, K^+ uptake and expressing antioxidant enzyme genes and reducing Na^+ accumulation	Sofy et al. (2021)
Staphylococcus sciuri (*ET101*)	*Lens esculentum*, *Oryza sativa*	Strain ET101 increased transpiration rate, stomatal conductance, intracellular CO_2, RWC, proline, and glycine betaine in rice and tomato to ameliorate the salinity stress	Taj and Challabathula (2021)
Glutamicibacter sp. (YD01)	*O. sativa*	Strain YD01 was tolerant to 10% salt stress and possessed ACC-deaminase	Ji et al. (2020)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
		activity and IAA production. Upon inoculation in rice, it enhanced salt tolerance by regulating ethylene production, ACC-oxidase, and K^+ uptake and reducing Na^+ accumulation and electrolyte leakage	
Rhizobium sp. (LSMR-32), *Enterococcus mundtii* (LSMRS-3)	*Vigna radiata*	These strains were positive for IAA, EPS, siderophores production, P-solubilization, biofilm formation, and salt tolerance. Their co-inoculation reported an increase in nodulation, leghemoglobin, phosphatase, dehydrogenase, proline, SOD, CAT, POD, K+ uptake, and K^+/Na^+ ratio and reduced Na^+ accumulation	Kumawat et al. (2020)
Pseudomonas sp. (SPF-33, SPF-37)	*Eleusine coracana*	The IAA, ACC-deaminase, siderophore-producing, and biofilm-forming strains promoted antioxidant enzymatic activity, proline, phenolics, flavonoids, protein contents, seed germination, vigor index, and plant height and reduced lipid peroxidation and H_2O_2 production in finger millet under salt stress	Mahadik and Kumudini (2020)
B. subtilis (NBRI 28B, NBRI 33 N), *Bacillus safensis* (NBRI 12 M)	*Zea mays*	Salt-tolerant strains produced metabolites such as ACC-oxidase and ACC-synthase that ameliorated salinity stress in maize through promoting defense enzymes, chlorophyll, proline, and soluble sugar contents	Misra and Chauhan (2020)
Pseudomonas argentinensis (HMM57),	*Brassica juncea*	These strains showed their ability to produce IAA, aminolevulinic acid	Phour and Sindhu (2020)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
Pseudomonas azotoformans (JMM15)		synthase, and ACC utilization activity and reported increase in seed germination and growth of Indian mustard seedlings up to 12 dS m^{-1} salt stress	
Enterobacter sp. (PR14)	*O. sativa*, *Panicum miliaceum*	Strain PR14 having multiple PGP traits including IAA, ACC-deaminase, P solubilization, SOD, CAT, and GPX promoted alkaline and saline stress tolerance in rice and millets through promoting seed germination, seedling vigor, and shoot length	Sagar et al. (2020)
Bacillus siamensis (PM13), *Bacillus* sp. (PM15), *Bacillus methylotrophicus* (PM19)	*T. aestivum*	Salt-tolerant *Bacillus* strains showed IAA, ACC-deaminase, and EPS production. Their inoculation in wheat seedling enhanced seed germination, plant growth, and chlorophyll contents under high salt stress conditions	Amna et al. (2019)
Jeotgalicoccus huakuii (NBRI 13E)	*Z. mays*	Maize plant treated with abiotic stress-tolerant strain NBRI 13E showed salt stress tolerance through modulating defense enzymes, chlorophyll, proline, and soluble sugar contents and improving yield parameters	Misra et al. (2019)
Bacillus megaterium (A12)	*S. lycopersicum*	Inoculated plants showed higher shoot length, dry biomass, and yield under salt stress. This strain showed a reduction in ethylene production and promoted the production of APX, CAT, and SOD and WUE in plants to ameliorate salt stress	Aslam et al. (2018)
Zhihengliuella flava (F-9), *S. jettensis* (F-11), *B.*	*Z. mays*	These strains were positive for IAA, ACC-deaminase, P solubilization, and	Aslam and Ali (2018)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
megaterium (F-58), *S. arlettae* (F-71)		biofilm formation. Inoculation of these strains in maize seedling mitigated salinity stress and promoted shoot and root length	
Glutamicibacter halophytocola (KLBMP 5180)	*Limonium sinense*	Halotolerant PGP strain KLBMP 5180 significantly promoted chlorophyll, proline, flavonoids, K^+, Ca^{2+} contents, and antioxidative enzymes and reduced Na^+ and MDA concentration	Qin et al. (2018)
Klebsiella sp. (IG 3)	*Avena sativa*	Plant inoculated with strain IG 3 reported higher shoot and root length, dry weight, relative water content, proline content, electrolyte leakage, MDA, and other antioxidant enzymatic activities	Sapre et al. (2018)
Klebsiella sp. (SBP-8)	*T. aestivum*	Strain SBP-8 promoted proline content, total soluble sugars and protein contents, SOD, CAT, and POX and reduces MDA in wheat under salt stress	Singh and Jha (2017)
Drought stress			
P. azotoformans FAP5	*T. aestivum*	This strain was capable to produce EPS, IAA, and P solubilization and possessed ACC-deaminase and biofilm-forming genes under water stress conditions. The inoculated wheat plants showed increased plant growth, photosynthetic pigment, physiological attributes, and antioxidative enzymatic activities under drought stress	Ansari et al. (2021)
Azotobacter chroococcum (Ac), *Azotobacter brasilense* (Ab)	*Mentha pulegium*	These strains reduced the adverse effects of water stress on physiological and biochemical attributes and secondary metabolites in plants	Asghari et al. (2020)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
Bacillus licheniformis, *P. fluorescens*, *A. brasilense*	*Chenopodium quinoa*	Seed-based inoculation of PGPR mitigated drought stress by improving crop growth, net assimilation rate, WUE, chlorophyll and phenolic contents, grain yield, protein, and P and K contents in grains	Aslam et al. (2020)
B. subtilis, *Azospirillum brasilense*	*T. aestivum*	These strains showed the production of EPS, osmolytes, and stress-induced phytohormones, viz., IAA, GA, CK, and ABA. They promoted seed germination, seedling vigor, shoot, and root length, leaf area, chlorophyll, carotenoid, proline, amino acid, sugar, and protein contents, SOD, CAT, and POD activities under drought stress	Ilyas et al. (2020)
B. licheniformis, *Bacillus haynesii*, *Bacillus paralicheniformis*	*O. sativa*	PGPR inoculation alleviated drought stress in rice by increasing biomass accumulation and grain yield and reducing SOD, CAT, guaiacol peroxidase, and enzymatic activities	Joshi et al. (2020)
A. calcoaceticus (EU-LRNA-72)	*Setaria italica*	This P-solubilizing strain effectively mitigated the negative effects of drought on foxtail millet by increasing glycine, betaine, proline, and sugar accumulation and decreasing lipid peroxidation	Kour et al. (2020)
B. subtilis (GOT9)	*A. thaliana*	It enhanced drought and salt tolerance in *Arabidopsis* through increasing transcripts of various drought stress- and salt stress-inducible genes	Woo et al. (2020)
Pseudomonas moraviensis	*T. aestivum*	This strain along with biogas slurry improved stomatal and sub-stomatal conductance, transpiration, photosynthetic rates, RWC, CAT, APX, plant	Yaseen et al. (2020)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
		height, and grain yield under drought stress	
P. putida (KT2440, *P. fluorescens* (Pf1)	*Z. mays*	They promoted root length, protein, chlorophyll content, and plant biomass through downregulating drought stress-responsive gene, viz., cold-related dehydrin 410 gene, lipoxygenase genes, and OPR7 genes under drought stress	Ahmad et al. (2019b)
P. fluorescens (WCS417), *B. amyloliquefaciens* (GB03)	*Mentha piperita*	Their inoculation mitigated drought stress by increasing phenolic content, enzymatic activities, and reduced membrane lipid peroxidation under drought conditions	Chiappero et al. (2019)
B. amyloliquefaciens	*T. aestivum*	ACC-deaminase-producing strain along with biochar improved chlorophyll contents, photosynthetic and transpiration rate, grain yield, and macronutrient concentrations in grains under drought stress	Danish and Zafar-ul-Hye (2019)
Bacillus sp. (12D6), *Enterobacter* sp. (16i)	*T. aestivum*, *Z. mays*	These phytohormones, IAA, and salicylic acid-profiling PGPR strains significantly promoted root branching, root length, diameter, and surface area in wheat and maize	Jochum et al. (2019)
B. subtilis, *Bacillus thuringiensis*, *B. megaterium*	*Cicer arietinum*	A consortium of these strains and plant growth regulator significantly enhanced the metabolic activities including chlorophyll, protein, sugar, proline, lipid peroxidation, accumulation of riboflavin, L-asparagine, aspartate, glycerol, nicotinamide, 3-hydroxy-3-methylglutarate, nicotinamide, 4-hydroxy-	Khan et al. (2019)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
		methylglycine, and arginine and decreased the activities of CAT, APOX, POD, and SOD under drought stress	
Paenibacillus beijingensis (BJ-18), *Bacillus* sp. (L-56)	*T. aestivum*, *Cucumis sativus*	These strains along with super absorbent polymer promoted seed germination, plant growth, urease, sucrose, dehydrogenase activities, and downregulated expression of genes involved in ROS scavenging, ethylene biosynthesis, stress response, salicylic acid, and transcription activation in plants under drought stress	Li et al. (2019)
Ochrobactrum pseudogrignonense (RJ12), *Pseudomonas* sp. (RJ15), *B. subtilis* (RJ46)	*Vigna mungo*, *P. sativum*	These strains were capable of N fixation, P solubilization, production of IAA, HCN, siderophores, and ACC-deaminase activity, and their consortium offered drought stress tolerance through promoting seed germination, root and shoot length, dry weight, ROS scavenging enzymes, cellular osmolytes, RWC, and chlorophyll contents	Meenakshi et al. (2019)
P. moraviensis	*T. aestivum*	This strain inoculation along with biogas slurry promoted grain and biological yield and N, P, and K contents in straw and grains of wheat under water drought stress	Yaseen et al. (2019)
Genus of *Bacillus*, *Enterobacter*, *Moraxella*, *Pseudomonas*	*T. aestivum*	IAA-producing PGPR significantly improved shoot and spike length, seed weight, number of tillers, and spikelets under drought stress	Raheem et al. (2018)
Azospirillum sp. (AZ39)	*Z. mays*	This strain was capable to produce siderophore, N	García et al. (2017)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
		fixation, ACC-deaminase activity, IAA, tolerant to osmotic, and salt stress and responded against water deficit condition	
P. putida (GAP-P45)	*Arabidopsis thaliana*	Inoculated plants showed delayed and prolonged upregulation of proline biosynthesis genes, viz., OAT, P5CS1, and P5CR, as well as proline catabolism genes, viz., PDH1 and P5CDH, were positively correlated with better growth and physiology of plants under drought stress	Ghosh et al. (2017)
Flooding stress			
Microbacterium sp. (AR-ACC2)	*O. sativa*	The ACC-deaminase utilizing strain significantly increased seed germination, seedling vigor index, growth attributes, and reduced ethylene production under submerged condition	Bal and Adhya (2021)
Pseudomonas veronii (KJ)	*Sesamum indicum*	This acdS gene-coded strain mitigated waterlogging stress by increasing chlorophyll content, shoot length, root length, and biomass of plant	Ali et al. (2018)
P. veronii (KJ)	*A. thaliana*	Waterlogging stress and salt stress were ameliorated in mutant *A. thaliana* by inoculation of acdS coding strain KJ	Jung et al. (2018)
K. variicola (AY13)	*Glycine max*	IAA-producing strain AY13 initiated adventitious root and promoted plant growth and chlorophyll contents under flooding stress	Kim et al. (2017)
P. putida (WT)	*Rumex palustris*	ACC-deaminase-producing strain ameliorated the waterlogging stress by altering plant hormonal balance	Ravanbakhsh et al. (2017)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
Rhizobium sp. (IRBG74)	*O. sativa*, *Sesbania cannabina*	Strain IRBG74 possessed β-glucuronidase and green fluorescent protein altered the synthesis of the rhamnose-containing O-antigen in nodulation and symbiotic N fixation in *S. cannabina* as well as involved in rice plant growth promotion under flooded stress	Mitra et al. (2016)
P. fluorescens (REN1)	*O. sativa*	ACC-deaminase- and IAA-producing strains REN1 promoted root elongation and endophytic root colonization in rice under flooded stress conditions	Etesami et al. (2014)
Serratia odorifera (CC7), *Aerococcus viridans* (CK3)	*T. aestivum*	These ameliorated the negative effects of waterlogging stress through increasing root and shoot length and dry root and shoot weight of wheat	Bangash et al. (2013)
Pseudomonas sp. UW4	*Cucumis sativus*	This strain ameliorated the waterlogged stress by regulating responsive proteins and metabolism pathways	Li et al. (2013)
Achromobacter xylosoxidans (d2), *S. ureilytica* (Bac5), *Herbaspirillum seropedicae* (Oci9), *Ochrobactrum rhizosphaerae* (Oci13)	*Ocimum sanctum*	ACC-deaminase-producing PGPR showed a potential to protect plant from flooding-induced negative stresses including increasing production of ethylene, lipid peroxidation, reduction in chlorophyll content, and nutrient uptake	Barnawal et al. (2012)
A. chroococcum, *Azospirillum* spp., *Pseudomonas* spp., *B. subtilis*	*Brassica napus*	Seed inoculation and foliar application of biofertilizers alleviated waterlogging stress on canola by improving SOD, CAT, and POX activities and reducing lipid peroxidation and ethylene production	Habibzadeh et al. (2012)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
Mesorhizobium cicero (LMS-1)	*Cicer arietinum*	This mutant strain with an exogenous ACC-deaminase gene showed increased nodulation and plant growth of chickpea	Nascimento et al. (2012)
Heat stress			
B. safensis	*T. aestivum*	Seed primed with this strain showed heat tolerance by improved production of defensive cell organelles, mitigation of ROS by regulating redox enzymes and antioxidants, expression of HSP, and modulation of putrescine biosynthetic genes	Sarkar et al. (2021)
B. cereus (TCR17), *Providencia rettgeri* (TCR21), *Myroides odoratimimus* (TCR22)	*Sorghum bicolor*	The chromium-reducing thermotolerant strains were capable to produce siderophores, IAA, and P-solubilization and induced heat tolerance in sorghum by reducing oxidative stress, improving antioxidant status, and reducing proline and malondialdehyde contents	Bruno et al. (2020)
Brevibacterium linens (RS16)	*Eucalyptus grandis*	Foliar application of ACC-deaminase producing strain RS16 reduced the immediate reduction in photosystem II, net assimilation rate, and stomatal conductance caused reduction in isoprene emissions, and induced expression of DnaK genes under short time heat stress	Chatterjee et al. (2020)
B. cereus (SA1)	*G. max*	Strain SA1 was able to produce IAA, GA, and organic acids and showed amelioration of heat stress in soybean by improving biomass, chlorophyll, salicylic acid, ascorbic acid, SOD, POD, glutathione, and reducing ABA	Khan et al. (2020a)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
B. cereus (SA1)	*S. lycopersicum*	Combined application of strain SA1 and exogenous humic acid improved plant biomass and chlorophyll contents, salicylic acids, APX, SOD, glutathione, and nutrient uptake, and reduced ABA under heat stress	Khan et al. (2020b)
B. cereus	*S. lycopersicum*	ACC-deaminase and EPS producing strains significantly reduced heat stress effects by promoting shoot and root length, fresh and dry weight, and leaf surface area	Mukhtar et al. (2020)
B. tequilensis (SSB07)	*S. max*	The strain counteracted heat stress on soybean by increasing shoot length, biomass, photosynthetic pigment, jasmonic acid, salicylic acid, and down-regulation of stress-responsive ABA	Kang et al. (2019)
Paraburkholderia phytofirmans (PsJN)	*L. esculentum*	This strain alleviated the harmful effect of high temperature by improving plant growth and physiological attributes of tomatoes	Issa et al. (2018)
B. safensis, *Ochrobactrum pseudogrignonense*	*T. aestivum*	Seed priming with these strains improved cell viability, chlorophyll contents, antioxidative response, redox enzymes, osmolytes, and reduced photosynthetic damage, ROS production, and membrane damage due to heat stress	Sarkar et al. (2018)
B. amyloliquefaciens (UCMB5113), *A. brasilense* (NO40)	*T. aestivum*	Seed inoculation with these strains improved heat tolerance in wheat by reducing ROS generation, alteration in the metabolome, and activating heat shock transcription factors.	Abd El-Daim et al. (2014)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
Cold stress			
Pseudomonas sp. (TmR5a), *Curtobacterium* sp. (BmP22c)	*S. lycopersicum*	The consortia application of psychrotolerant strains possessing ACC-deaminase gene, and nitrogenase reductase gene, biocontrol activities, IAA, P-solubilization promoted tomato plant growth under cold stress conditions	Vega-Celedón et al. (2021)
Genus of *Pseudomonas*, *Serratia*, *Staphylococcus*	*Deschampsia antarctica*, *Colobanthus quitensis*	Cold tolerant ACC-degrading bacteria were isolated from the rhizosphere, phyllosphere, and endosphere of Antarctic vascular plants and could ameliorate cold stress in plants	Araya et al. (2020)
Pseudomonas spp.	*S. lycopersicum*	Psychrotolerant PGP strain reported increasing tomato germination and plantlets under low-temperature stress	Tapia-Vázquez et al. (2020)
P. fragi, *P. chlororaphis*, *P. fluorescens*, *P. proteolytica*, *B. frigoritolerans*	*Phaseolus vulgaris*	Psychrotolerant bacterial strains capable to produce ACC-deaminase activity, production of extracellular proteins, stimulation of SOD, CAT, POD, and glutathione reductase improved the cold resistance in bean seedlings through decreasing freezing injury, ice nucleation, lipid peroxidation, and reduction in ROS level	Tiryaki et al. (2019)
Bacillus spp. (CJCL2, RJGP41)	*T. aestivum*	The genetic screening of psychrophilic strain revealed the presence of genes responsible for cold stress tolerance, membrane transport, signal transduction, and osmotic regulation under cold stress. Wheat plants inoculated with this strain responded to cold stress by regulating ABA, lipid peroxidation, and proline accumulation	Zubair et al. (2019)

(continued)

Table 2.1 (continued)

PGPR	Plants	Findings	References
Genus of *Bacillus*, *Paenarthrobacter*, *Pseudomonas*, *Paenibacillus*, *Cupriavidus*	*Lepidium meyenii*	Psychrotrophic PGPR strains were positive for IAA production, P-solubilization, tolerant to varying concentrations of Cd and Pb, and promoted seed germination exposed to low temperature and heavy metal toxicity	Ortiz-Ojeda et al. (2017)
Arthrobacter agilis (L77)	–	Hydrolytic enzymes producing PGP strain L77 genome under cold stress revealed diverse genes involved in metabolism and cold shock variations and diverse polysaccharides biosynthesis	Singh et al. (2016)
Genus of *Arthrobacter*, *Flavimonas*, *Flavobacterium*, *Massilia*, *Pedobacter*, *Pseudomonas*	*S. lycopersicum*	Psychrotolerant bacteria caused an increase in seed germination, plant growth, decrease in membrane damage, induced antioxidant enzymes, and proline synthesis in tomato under chilling stress	Subramanian et al. (2016)
Genus of *Streptomyces*, *Arthrobacter*, *Paenibacillus*	*Thylacospermum ceaspitosum*	Bacterial community and structure of cold desert revealed that actinobacteria dominated cultivable parts of a community. A more diverse bacterial community was associated with finer soil derived from easily weathering and cushion plants in a xeric environment	Řeháková et al. (2015)
Pseudomonas spp.	*T. aestivum*	Inoculation of wheat with *Pseudomonas* strains ameliorated cold stress by increasing chlorophyll, anthocyanin, proline, amino acids, phenolics, RWC, and starch contents and reducing electrolyte leakage and Na^+/K^+ ratio	Mishra et al. (2011)

photosynthetic and transpirational rates, and stomatal conductance in various crops (Ohashi et al. 2006; Mumtaz et al. 2020).

Drought as multi-dimensional stress affects various subcellular compartments, cell organs, and whole plant levels (Horn and Chapman 2012). Drought destructively upsets the quantity and quality of plants. Drought stress alleviation is important to fulfill food demand. To address this global challenge, there is a dire need to develop improved crop germplasm and technologies to increase water use efficiency (WUE) (Passioura 2007). Recently, the application of beneficial microorganisms has got attention for the mitigation of drought by improving WUE (Marulanda et al. 2009; Ngumbi and Kloepper 2016). Under drought stress, the plant-associated bacterial community in the rhizosphere alleviates drought stress and improves plant health by improving the resistance in plants against stressors (Cherif et al. 2015; Aslam et al. 2020; Kour et al. 2020). The PGPR in the water-limited rhizosphere with repeated dry periods is more stress-tolerant and increases plant growth as compared to PGPR population of the well-irrigated rhizosphere (Mayak et al. 2004). Drought tolerance mediated by PGPR could be through the production of phytohormones, viz., IAA, ABA, and GA, production of ACC-deaminase to reduce ethylene production, and induced drought tolerance through the production of metabolites, viz., siderophore and EPS (Timmusk and Nevo 2011; Meenakshi et al. 2019; Ansari et al. 2021).

Plants produce phytohormones such as IAA, ABA, GA, and CK which play important role in drought stress alleviation (Egamberdieva 2013; Fahad et al. 2015; Kumar et al. 2019a). PGPR are reported to produce these phytohormones under drought stress that can improve plant growth (Khan et al. 2020c). The IAA-producing PGPR alleviate drought stress by improving lateral root development and water uptake (Mantelin and Touraine 2004). For example, Dimkpa et al. (2009) reported that *Azospirillum* (IAA producing) promoted drought stress tolerance in plants. Nitric oxide (NO, signaling molecule) produced by *A. brasilense* inoculation in tomato showed induction of IAA pathway and development of adventitious roots. Its inoculation in maize grown under drought stress also improved water content in comparison to uninoculated control plants (Molina-Favero et al. 2008). Wheat treated with *A. brasilense* strain Sp245 improved drought stress tolerance through increased grain yield; Mg, K, and Ca concentration; water content; and lowering volumetric cell wall elasticity (Creus et al. 2004). The IAA-producing *Bacillus thuringiensis* inoculation in *Lavandula dentata* showed drought stress amelioration and improved plant metabolic activities, nutrition, and physiology (Armada et al. 2014). GA- and ABA-producing PGPR also help plants withstand drought stress. Soybean inoculation with *P. putida* strain H-2-3 (GA producing) showed an increase in plant growth under drought stress (Sang-Mo et al. 2014). Similarly, inoculation of maize with *Azospirillum lipoferum* ameliorated drought stress in plants (García et al. 2017). The ABA is a stress hormone, and its biosynthesis is induced during cellular dehydration under water deficit conditions. The inoculation of CK-producing *B. subtilis* in *Platycladus orientalis* improved drought stress alleviation by increasing ABA levels (Egamberdieva et al. 2017).

Drought stress enhances the production of ethylene that causes retarded plant growth (Hardoim et al. 2008). The ACC-deaminase-producing bacteria sequester and degrade plant ACC and improve plant growth, supply N and energy, and reduce the deleterious effect of ethylene in plants (Glick 2005; Nadeem et al. 2017; Danish and Zafar-ul-Hye 2019). Mayak et al. (2004) inoculated ACC-deaminase-producing *Achromobacter piechaudii* in tomato and pepper and reported increase in plant growth under drought stress by reducing ethylene production. The ACC-deaminase-containing PGPR enhance grain yield and N accumulation in grains and repair depressed nodulation in plants (Dodd et al. 2004; Danish et al. 2020). Inoculation with ACC-deaminase-producing *P. fluorescens* in *Pisum sativum* under drought stress showed longer roots due to increased water uptake (Zahir et al. 2008). *Variovorax paradoxus* strain 5C-2 improved pea productivity through increase in WUE due to ABA production in drought stress (Belimov et al. 2009). PGPR promoted wheat growth due to better water and nutrient acquisition over uninoculated control (Shakir et al. 2012; Ansari et al. 2021). Sharma et al. (2013) reported that co-inoculation of *Bacillus*, *Pseudomonas*, and *Mesorhizobium* strains (ACC-deaminase producing) in *Cicer arietinum* under drought conditions promoted seed germination and seedling biomass over uninoculated control (Hui and Kim 2013).

2.4.1.3 Flooding Stress

Waterlogging and submergence are abiotic stresses, collectively called flooding stresses. Flooding stress is a global issue that influences plant composition and productivity (Phukan et al. 2016). Under flooding conditions, soil becomes completely saturated with water and develops an anaerobic environment. Plant roots become hypoxic which impairs the growth and development of the plants (Nishiuchi et al. 2012; Glick 2014). According to an estimate, flooding affected nearly 13% of the country's land and nearly 10% of agricultural lands globally (Cramer et al. 2011). Flooding stress causes yield loss up to 15–80% in various crops (Patel et al. 2014).

Under flooding conditions, poorly adapted plant species are severely affected by excess water that results in 10^4-fold slower oxygen diffusion as compared to air (Armstrong and Drew 2002). Oxygen-deficient conditions lead to higher production of plant hormone "ethylene" that increases ROS production, destruction of macromolecules, and inhibition of photochemical and ultimately causes plant death (Grichko and Glick 2001a; Glick 2005; Ahmed et al. 2006). Under flooding conditions, plants exhibit symptoms of chlorosis, necrosis, and low productivity (Paul et al. 2016). Various wetland plant species are highly effective due to a combination of various physiological adaptations to withstand flooding stress conditions (Ravanbakhsh et al. 2017). Such plants acclimatize flooding stress through a physical method including escape from submerged conditions, prevention of oxygen deficiency via internal aeration, anoxia tolerance, and avoiding oxidative damage (Armstrong et al. 1994; Gibbs and Greenway 2003; Voesenek et al. 2003). Under flooding stress, plant roots produce a larger amount of ethylene that modifies phytohormone cascade of ABA, GA, and IAA to encourage the emergence of adventitious rooting in plants (Vidoz et al. 2010; Dawood et al. 2016; Ali et al. 2020). Root development also requires ethylene that persuades the development of ROS in epidermal cells leading to cell death by dropping antioxidant activity (Steffens and Sauter 2009; Yamauchi et al. 2011).

Under flooding stress, ACC-deaminase-producing bacteria play a key role in reducing excess ethylene production by catabolizing ACC to ammonia and α-ketobutyric acid (Ali and Kim 2018; Sasidharan et al. 2018; Bal and Adhya 2021). Limited literature is available to describe PGPR's role in flooding stress mainly through their ability to produce ACC-deaminase. Transgenic tomato developed through ACC-deaminase expressing transcriptional control of *rolD* promoter from *Agrobacterium rhizogenes* and 35*S* constitutive expression was evaluated under flooding stress (Grichko and Glick 2001b). Development of transgenic plants with the insertion of *rolD* promoter showed ACC-deaminase expression and increased flooding tolerance by improving seedling biomass, epinasty, leaf chlorophyll, and protein content and reducing the ethylene production (Grichko and Glick 2001b). Under flooding stress, ACC synthase is produced in a higher amount in the plant tissues that induces the production of ACC-deaminase by bacteria. Symbiotic bacteria can reduce ethylene stress up to 60–90% by producing ACC-deaminase enzyme (Saleem et al. 2007; Jung et al. 2018; Ali et al. 2018). Grichko and Glick (2001a) inoculated tomato with *Enterobacter cloacae* (strains UW4 and CAL2) and *P. putida* (strains pRKACC) and reported that the expression of ACC-deaminase genes in these strains promoted substantial flooding stress tolerance by improving plant growth and physiological attributes (Grichko and Glick 2001a).

Farwell et al. (2007) inoculated ACC-deaminase-producing *P. putida* strain UW4 in ACC-deaminase-producing transgenic canola and non-transformed canola under flooding and nickel (Ni) stress. They reported that transgenic canola inoculated with strain UW4 showed better shoot biomass as compared to non-transformed canola under flooding conditions (Farwell et al. 2007). Barnawal et al. (2012) investigated the effect of *Achromobacter xylosoxidans* strain Fd2, *Herbaspirillum seropedicae* strain Oci9, *Ochrobactrum rhizosphaerae* strain Oci13, and *Serratia ureilytica* strain Bac5 on *Ocimum sanctum*. They reported that bacterial treatment alleviated waterlogging stress and reduced ethylene production, lipid peroxidation, proline contents, and improved chlorophyll content and nutrient uptake. Strain Fd2 exhibited maximum waterlogging tolerance with 46.5% higher growth and herb yield and a 53% reduction in ACC concentration over uninoculated waterlogged plants (Barnawal et al. 2012). Habibzadeh et al. (2012) treated canola plants with biofertilizers through foliar and seed application and reported their effect on physiological and morphological attributes of canola under flooding conditions. The biofertilizers were AAP (strains of *Azotobacter*, *Azospirillum*, and *Pseudomonas*) and APB (strains of *Azospirillum*, *Pseudomonas*, *Bacillus*). Both foliar and seed treatment with these biofertilizers significantly alleviated flooding stress by improving superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD) activities and by reducing ethylene and lipid peroxidation (Habibzadeh et al. 2012).

Etesami et al. (2014) reported that rice inoculation with endophytic ACC-deaminase-producing *P. fluorescens* strain REN1 promoted root growth under flooding stress. The *Streptomyces* sp. strain GMKU inoculation in mung bean alleviated flooding stress by improving shoot and root growth and chlorophyll content and reducing ethylene formation (Jaemsaeng et al. 2018). Similarly, Ali et al. (2018) reported that *Sesamum indicum* inoculation with *Pseudomonas veronii* strain KJ showed flooding stress mitigation by improving plant growth and physiological attributes. Production of IAA by PGPR induces adventitious root growth that also helps plant maintain their growth and ameliorate flooding stress. Rice seedling inoculation with IAA-producing strain REN1 also showed better root development under flooding conditions (Etesami et al. 2014). Similarly, Kim et al. (2017) inoculated *Klebsiella variicola* strain AY-13 in soybean under waterlogged conditions and reported its potential to induce adventitious root growth, improved plant growth, and flooding tolerance (in soybean). Strain AY-13 was able to produce IAA up to 84.27±3.55 μg mL^{-1} as analyzed through gas chromatography-mass spectrometry selected ion monitoring (GC-MS/SIM) as reported by Kim et al. (2017).

2.4.1.4 Heat Stress

Temperature is a primary factor affecting plant growth and development (Hatfield and Prueger 2015). Each plant species requires a certain temperature regime characterized as a minimum, maximum, and optimal temperature range for its growth and productivity (Hatfield et al. 2011). Global warming is becoming a major issue worldwide due to elevated carbon dioxide that is causing economic losses. It is predicted that greenhouse gas emission is causing a steady increase in average temperature worldwide. The increase in average temperature linked with climate changes usually aggravates the heat stress in agriculture (Carbonell-Bojollo et al. 2019; Zhang et al. 2019). Heat stress negatively affects plant growth and development by causing changes in plant morphology and physiology (Prasad et al. 2008). Repeated extremely high-temperature events have caused phenological disturbances in different plant species (Li et al. 2017). In the early crop growth stages, heat stress inhibits seed germination and seedling's emergence (Wahid et al. 2008). It can damage photosynthetic pigments, carbon metabolism, and organic solute transport (Hasanuzzaman et al. 2013; Balal et al. 2016). El-Daim et al. (2014) reported that temperature at 45 °C caused mortality of wheat seedlings up to 80–95%. The impact of heat stress on the reproductive phase of crops generally leads to variation in mineral nutrition, deactivation of the immune system, and the successive generation of ROS (Zhang et al. 2016; Lanza and dos Reis 2021). Heat stress elevation disrupts the rate of photosynthesis, stomatal conductance, and transpiration (Fahad et al. 2016). The activity of photosystem II (PSII) was inhibited due to heat stress that ultimately reduced photosynthetic rate which is the major cause of the inhibition of chlorophyll production (Chen et al. 2007; Killi et al. 2020).

Plants tolerate heat stress by altering osmotic pressure, antioxidants, plant hormone level, and regulation of HSPs. Plant regulates the production of certain plant hormones, such as ABA, GA, JA, and IAA, to improve heat resistance (Abdelrahman et al. 2017; Khan et al. 2020c). Among these phytohormones, IAA and GA improve plant development processes, while JA and ABA can alleviate the heat stress (Ahammed et al. 2016). Hydrogen sulfide production also improves resistance to heat stress in plants (Chen et al. 2016). The HSPs protect the natural protein and improve protein stability, which in turn improve the thermal tolerance in the plant (Wei et al. 2021). The accumulation of HSP in terms of ZmHSP17.2 in corn and OsHSP26 in rice showed a strong correlation in heat stress tolerance (Lee et al. 2007; Liu et al. 2013; Sarkar et al. 2021). Maize leaves under heat stress expressed sHSP17.2, sHSP17.4, and sHSP26, while these proteins were also regulated by ABA (Hu et al. 2010). HSFA1 is a major regulator of signal perception, transduction, and control of the expression of stress-sensitive genes in tomato plants. The expression of HSP26, HSP17.4, and HSP17.2 also played an important role in heat tolerance in corn (Asada 2006). A multifunctional cytoplasmic protein known as eukaryotic elongation factor 1α (eEF1A) is responsible for the heat resistance in tomatoes (Momčilović et al. 2016). Plants also increase the activity of antioxidant enzymes, including alpha-tocopherol; glutathione; ascorbic acid; CAT, SOD, APX, and POD; and glutathione reductase, to repair the oxidative damage caused by heat stress (Asada 2006; Khan et al. 2020a, b).

Plant inoculation with PGPR improves heat tolerance by enhancing the photosynthetic rate, water use efficiency, antioxidant enzymatic activity, and uptake of water and nutrients (Zhu et al. 2012; Maya and Matsubara 2013; Kang et al. 2019; Sarkar et al. 2021). The literature on the mechanism of heat stress tolerance due to bacterial inoculation is very limited; however, studies are available to support that bacterial augmentation can ameliorate heat stress by producing ACC-deaminase, EPS, and phytohormones which are involved in the expression of HSP. Application of ACC-deaminase-producing PGPR under heat stress could ease unfavorable conditions. Production of ACC-deaminase by PGPR reduces the inhibitory effect of stress hormone “ethylene” generated under heat stress through degrading ACC into ammonia and α-ketobutyrate (Barnawal et al. 2012). The detailed mechanism of conversion of ACC into ammonia and α-ketobutyrate by the action of ACC-deaminase produced by PGPR has already been reported in the above abiotic stress sections of this chapter. The PGPR uses a similar mechanism of action in all abiotic stress to reduce the lethal concentration of ethylene. Recently, Mukhtar et al. (2020) inoculated PGP *Bacillus cereus* having the ability to produce ACC-deaminase up to 0.76 to C0.9 μM/mg protein/h in tomato under heat stress. They reported a significant improvement in growth and physiological and biochemical attributes of tomato plants due to inoculation with EPS-producing, ACC-deaminase-containing *B. cereus*. Wu and Yang (2019) reported that ethylene-mediated signaling under heat stress was involved in the reduction of oxidative damage, maintenance of chlorophyll content, and enhancement of thermo-tolerance in rice seedlings. They also reported that HSP and ethylene-signaling-related genes were involved in complex network regulation that conferred thermo-tolerance to rice seedlings.

Srivastava et al. (2008) reported that high-temperature (40 °C up to 5 days) tolerant *P. putida* strain NBRI0987 isolated from chickpea rhizosphere was affected with drought stress. Strain NBRI0987 was able to tolerate heat stress due to its ability of biofilm formation and overexpression of sigma factor genes. Ali et al. (2009)

inoculated sorghum with thermo-tolerant *Pseudomonas* sp. strain AKM-P6 under elevated temperatures (47–50 °C for day and 30–33 °C for a night). They reported that inoculation with strain AKM-P6 ameliorated the elevated temperature stress through well-established growth on the root surface and promoted root biomass, shoot biomass, amino acids, sugar, proline, chlorophyll, and induced synthesis of protein (Ali et al. 2009). El-Daim et al. (2014) reported the heat tolerance in wheat through inoculation with *B. amyloliquefaciens* strain UCMB5113 and *A. brasilense* strain NO40. They reported that inoculation with these strains improved heat tolerance through activating ascorbate-glutathione redox cycle, reducing generation of ROS and cell damage (El-Daim et al. 2014).

Ali et al. (2011) investigated heat tolerance in wheat through inoculation with thermo-tolerant PGPR *P. putida* strain AKMP7. They reported that strain AKMP7 promoted growth of wheat in terms of root length, shoot length, biomass, tiller, and spikelet number and promoted grain formation through reducing membrane injury and improving the activity of SOD, APX, and CAT and various metabolites like chlorophyll, proline, protein, and carbohydrates (Ali et al. 2011). The heat shock protein could be a key factor in maintaining the functional conformation of the protein under heat (Wang et al. 2004). Among HSP, HSP17.8 is highly upregulated in wheat seedlings under heat stress; however, the response to bacterial treatment may vary between different cultivars and the bacterial strains. Interestingly, the expression of HsfA3 was downregulated in *Bacillus*-treated wheat seedlings compared to untreated heat-loaded seedlings (Suzuki et al. 2008). In *Arabidopsis*, HsfA3 improved the production of several HSPs (Ikeda and Ohme-Takagi 2009) and regulated two independent pathways, suggesting that they play an integrated role in stress management (Liu and Charng 2013). El-Daim et al. (2014) reported that inoculation of wheat with these strains *B. amyloliquefaciens* strain UCMB5113 and *A. brasilense* strain NO40 improved heat tolerance through the transcript level of a stress-related gene. They reported that the preactivation of heat shock transcription factors had an important role in heat stress tolerance (El-Daim et al. 2014).

2.4.1.5 Cold Stress

Low temperature is one of the most important abiotic stresses also known as cold or chilling stress. It limits crop productivity by damaging various physiological and biochemical cell functioning with visible symptoms (Ruelland and Zachowski 2010). Cold stress slows down the plant metabolism by damaging cellular macromolecules and membrane function, clotting of the cell membrane, and alteration in lipid composition and induces synthesis of compatible solutes, proteins, and carbohydrate metabolism (Welti et al. 2002; Baek and Skinner 2003). Chilling stress forms extracellular ice crystals leading to frozen dehydration and concentration of cellular juice and causes several other mechanical effects (Mishra et al. 2012).

Adaptation to cold stress tolerance encompasses a range of biochemical, molecular, and metabolic processes (Zhu et al. 2007; Ritonga and Chen 2020). Plants in the first attempt try to resist changes in cellular metabolism due to lower temperatures. Further, plant regulatory mechanisms are activated and restore levels and normal flow of metabolites (Fernie et al. 2005). They maintain homeostasis to gain tolerance to freezing and implying gene expression (Cook et al. 2004). The cold stress adaptation process involves changes in gene expression, membrane lipids, protein content, soluble proteins, sugar, proline, total phenols, deoxygenase, low leakage of ions from the cell membrane; changes in the accumulation of anthocyanins; and production of metabolites, including osmotic protective agents, and allows osmosis (Kasuga et al. 2004; Barka et al. 2006; Tiryaki et al. 2019). Plant cells sense cold stress by cold-responsive membrane hardening induced by genes that contribute to cold acclimation of alfalfa and *Brasicca napus* (Sangwan et al. 2001).

A major portion of the earth is covered with a low-temperature environment that acts as a reservoir of cold-tolerant (psychrophilic) bacteria having a low metabolic activity (Kumar et al. 2019b). Various psychrophilic bacterial strains including *Acinetobacter rhizosphaerae*, *Arthrobacter nicotianae*, *Bacillus* sp., *Bordetella* sp., *Brevundimonas terrae*, *Exiguobacterium acetylicum*, *Mesorhizobium* sp., *Pseudomonas cedrina*, *P. fluorescens*, *P. putida*, *Providencia* sp., *Pseudomonas corrugata*, *Pseudomonas fragi*, *Rhizobium leguminosarum*, *Serratia marcescens*, *Sinorhizobium meliloti*, *Stenotrophomonas*, etc. having the ability to increase P and iron (Fe) availability under cold stress by producing siderophore and solubilizing P were reported previously (Prevost et al. 1999, 2003; Pandey et al. 2002, 2006; Katiyar and Goel 2004; Negi et al. 2005; Trivedi and Sa 2008; Gulati et al. 2009; Selvakumar et al. 2008, 2009; Verma et al. 2015; Yadav et al. 2015; Zubair et al. 2019; Araya et al. 2020; Tapia-Vázquez et al. 2020; Vega-Celedón et al. 2021). Recently, Awasthi et al. (2019), Gautam et al. (2019b), Kumar et al. (2019b), and Tiryaki et al. (2019) also reported cold-tolerant bacteria including *Arthrobacter humicola*, *Brevibacillus invocatus*, *Brevibacterium frigoritolerans*, *Pseudomonas chlororaphis*, *P. fluorescens*, *Pseudomonas fragi*, *Pseudomonas proteolytica*, *Pseudomonas helmanticensis*, *Pseudomonas koreensis*, *Pseudomonas mandelii*, and *Viridibacillus arenosi* isolated from various cold regions.

The psychrophilic bacteria alleviate cold injury in plants using various mechanisms. Such bacteria could be efficient enough to synthesize antifreeze proteins and have a strong affinity for the promotion of root growth (Sun et al. 1995). Cold-tolerant *Bradyrhizobium japonicum* was reported for its ability to promote nodule formation and nitrogen fixation in soybean under cold stress (Mishra et al. 2009). Barka et al. (2006) reported improvement in cold tolerance in grapevine seedlings due to inoculation with *Burkholderia phytofirmans* that reduce electrolyte leakage. Inoculation with endophytic *B. phytofirmans* strain PsJN improved cold stress tolerance through the process of antioxidant scavenging, modulation in carbohydrate metabolism, and trehalose metabolism in grapevine (Fernandez et al. 2012; Theocharis et al. 2012). Mishra et al. (2011) and Barka et al. (2006) reported that psychrophilic bacterial inoculation also improved sugar metabolism pathway, photosynthetic activity, total phenolic contents, and activation of genes related to C-repeat binding factor. Inoculation with strains of *Azospirillum*, *Bacillus*, and *Raoultella* spp. improved cold tolerance in wheat and barley by reducing freezing injury and sustaining antioxidant enzyme activity (Turan et al. 2013). Tomato inoculated with *Pseudomonas frederiksbergensis* strain OS261 and *Pseudomonas vancouverensis* strain OB155 showed improved cold tolerance due to enhanced cold-acclimatized gene expression, antioxidant activity, proline synthesis, and reduction in membrane damage (Subramanian et al. 2015, 2016). Production of phytohormones by *Serratia nematodiphila* improved cold tolerance in pepper seedling (Kang et al. 2015). Inoculation with strains of *Bacillus* and *Pseudomonas* spp. in *Phaseolus vulgaris* has been reported to improve cold tolerance in plants by regulating freezing injury, ice-nucleating activity, lipid peroxidation, and activities of SOD, CAT, and POD (Tiryaki et al. 2019). So, it is concluded that plant interaction with cold-tolerant bacteria under cold stress environment can sustainably engineer cold stress (Kushwaha et al. 2020).

2.4.2 Biotic Stress

The PGPR help in improving the plant growth by suppressing the growth of phytopathogens, and weeds thus acting as a biocontrol and bioherbicide agents (Adetunji et al. 2019; Khan et al. 2020c). They use the indirect mechanisms of action to promote plant growth through alleviating biotic stresses due to growth of deleterious organisms (Arya et al. 2018). PGPR as biocontrol agents are environment-friendly supplements to treat plant diseases and to reduce the use of chemicals in agriculture (Gerhardson 2002). They control pathogens through pathogen exclusion based on bacterial capacity to colonize faster and effectively and by reducing the nutrient availability to harmful pathogens (Table 2.2). PGPR, for example, limit Fe availability to pathogenic microbes by production of siderophores that chelate Fe, making it unavailable for use by pathogens (Singh et al. 2011). They also produce a heterogeneous group of organic compounds called antibiotics which are lethal to various microorganisms even at low concentrations (Haas and Defago 2005). They reduce the pathogen attack by provoking a defense response in plants known as induced systemic resistance (ISR) involving synthesis of various defense metabolites that modify physical and biochemical properties of host without causing disease (Bent 2006; Bukhat et al. 2020).

PGPR produce antibiotics that are bioactive metabolites having the ability to inhibit growth of disease-causing agents. Under stress, PGPR secrete antibiotics having varying degrees of specificity and mode of action (Pathak et al. 2017). *Pseudomonas* sp., for example, can produce antibiotics including 2,4-diacetylphloroglucinol, amphisin, phenazine, phenzine, pyoluteorin, pyrrolnitrin, tensin, and tropolone (Compant et al. 2005; Showkat 2012). Many *Pseudomonas* strains produce pyrrolnitrin antibiotic which is a broad-spectrum antifungal compound. Similarly, in another study, Perneel et al. (2008) reported that *Pseudomonas aeruginosa* and *P. chlororaphis* can produce phenazine, which is a heterocyclic, broad-spectrum antibiotic used in biocontrol against phytopathogens. Two broad-spectrum antibiotics called kanosamine and zwittermicin are produced by *B. cereus* that act against damping-off of the alfalfa seedlings (Lozano et al. 2016). Iturins with β-amino fatty acid produced by strains of *Bacillus* sp. exhibit strong antifungal activity and rely predominantly on the ability to augment membrane permeability due to strong interaction with the phospholipids and sterols

Table 2.2 Use of PGPR to mitigate biotic stresses in plants

Biocontrol agent	Plant	Phytopathogen	Findings	References
P. peoriae (RP20, RP51, RP62, RP51), *Paenibacillus* sp. (RP31)	*R. pseudoacacia*, *D. triangulare*, *O. semicastrata*, *C. arietinum*, *A. crassicarpa*, *A. implexa*	*F. graminearum*, *M. oryzae*, *R. solani*, *S. sclerotiorum*, *B. cinerea*	These nodule-inhabiting strains showed an antagonistic effect against phytopathogenic fungi by producing multiple hydrolytic enzymes, siderophores, and lipopeptide fusaricidins	Ali et al. (2021)
Bacillus sp. (BS-Z15)	Cotton	*V. dahliae*	BS-Z15 possessed various genes coding for antagonism or synthesizing mycosubtilin, chitinases, glycoside hydrolases, antibiosis, and biofilm production	Chen et al. (2021)
P. polymyxa (N179)	Pear, Turnip cabbage	*E. amylovora*, *X. campestris*	Strain N179 suppressed phytopathogen in pear fruit and turnip cabbage	Fallahzadeh-Mamaghani et al. (2021)
S. fulvissimus (A12), *S. venezuelae* (A30), *S. anulatus* (A34), *P. donghuensis* (P17), *Pseudomonas* sp. (P3)	Onion	*P. penetrans*, *F. oxysporum* (C1-1), *Ilyonectria* spp. (C2-1), *I. macrodidyma* (C1-1),	Results revealed that application of PGPR caused a reduction in the growth of phytopathogen through delaying production of nematicidal lytic enzymes, viz., chitinases and proteases and form biofilms	Marin-Bruzos et al. (2021)
Bacillus sp., *T. harzianum*	Rice	*M. oryzae* (MG01)	Metagenome sequencing explored the antagonistic diversity, distribution, and abundance of microflora to phytopathogen strain MG01	Prasannakumar et al. (2021)

(continued)

Table 2.2 (continued)

Biocontrol agent	Plant	Phytopathogen	Findings	References
B. velezensis EB14	*Populus* sp.	*S. musiva*	Strain EB14 possessed several gene clusters coding for the biosynthesis of antimicrobial compounds	Sachin et al. (2021)
B. halotolerans (JZ7)	Chinese jujube	*F. oxysporum*	This strain showed antagonistic activity by producing acetoin, 2,3-butanediol, and fenretinide	Wang et al. (2021)
B. amyloliquefaciens (PMB04, PMB05)	Strawberry	*C. gloeosporioides* (SC01)	These strains intensified plant immunity through the generation of ROS and callose deposition against conidia and reduced the occurrence of anthracnose on strawberries	Wu et al. (2021)
B. velezensis (8-4)	Potato scab	*P. foveat*, *R. solani*, *F. avenaceum*, *C. coccodes*	This strain showed antagonistic activity against potato pathogen	Cui et al. (2020)
C. muytjensii (JZ38)		*P. infestans*	Strain JZ38 revealed its ability to grow under a range of abiotic stresses due to the presence of genes coding for phytohormone	Eida et al. (2020)
B. subtilis (RH5)	Rice	*R. solani*	This strain produced defense-related enzymes, siderophores, hydrolytic enzymes, viz., chitinase, protease, cellulase, xylanase activity, and antimicrobial peptide biosynthetic genes (bacylisin, surfactin, and fengycin) in rice plants against *R. solani*	Jamali et al. (2020)
S. plymuthica (A294), *E. amnigenus* (A167), *R. aquatilis* (H145), *S. rubidaea* (H440), *S. rubidaea* (H469)	Potato tubers	*Pectobacterium* spp., *Dickeya* spp.	Consortium powder formulation of these strains reduced the severity and incidence of soft rot disease	Maciag et al. (2020)

Bacillus, *Pseudomonas*, *Sphingomonas* spp.	*D. officinale*	*S. rolfsii*	These strains produced antibiotic-encoding genes, viz., surfactin, phenazine, and iturin A	Shen et al. (2020)
B. xiamenensis (PM14)	*S. officinarum*	*C. falcatum*, *F. moniliforme*, *F. oxysporum*, *P. splendens*, *R. solani*, *M. phaseolina*	The results revealed the production of antioxidative enzymes and proline by strain PM14 involved in biocontrol activity	Xia et al. (2020)
B. velezensis	Maize	*T. funiculosus*, *P. oxalicum*, *F. verticillioides*	It showed biological control by producing lipopeptide antibiotic genes (bioA, bmyB, ituC, fenD, srfAA, srfAB, yngG, and yndJ)	Yang et al. (2020)
B. velezensis (D747, QST713)	Olive trees	*X. fastidiosa* (ST53)	Strains D747 and QST713 were registered as a biocontrol agent to control olive quick decline syndrome	Zicca et al. (2020)
K. oxytoca (D1/3), *E. indicum* (D1/8), *B. cereus* (D1/17, D1/18),	Tomato	*P. aphanidermatum*	These strains were capable of controlling the damping-off of tomato	Al-Hussini et al. (2019)
L. plantarum (CC100, PM411, TC92)	Kiwifruit, Prunes, Strawberry	*P. syringae*, *X. arboricola*, *X. fragariae*	These strains showed biocontrol against phytopathogen due to chitosan, acibenzolar-S-methyl, kasugamycin, and production of lactic acid	Daranas et al. (2019)
B. amyloliquefaciens (KU_2S1, $R_2S_{(1)}$, $RG1_{(3)}$, $AG1_{(7)}$)	Tomato	*C. michiganensis*	These strains showed antagonistic activity against the bacterial canker of tomato	Gautam et al. (2019a)

(continued)

Table 2.2 (continued)

Biocontrol agent	Plant	Phytopathogen	Findings	References
P. parafulva (JBCS1880)	Soybean	*X. axonopodis*, *B. glumae*	Strain JBCS1880 showed a potential for antagonism by producing novel lipopeptide	Kakembo and Lee (2019)
B. amyloliquefaciens (SW-34)	Ginseng plants	*B. cinerea*	This strain produced broad-spectrum antibiotics	Sun et al. (2019)
Streptomyces sp. (N2)	Rice	*R. solani*	This bacterium produces novel antifungalmycin N2	Wu et al. (2019)

(Alvarez et al. 2012). Microbial HCN is involved in biocontrol as well as sequestration of metal ions and consequently increases the availability of nutrients which is beneficial both for the rhizobacteria and plant host (Rijavec and Lapanje 2016; Meena et al. 2020).

Microbial production of siderophores has a central role in the development of a plant (Beneduzi et al. 2012). Siderophores are one of the strongest carriers of Fe^{3+} in combination with enterobactin (Saharan and Nehra 2011). The production of siderophores is affected by the type of iron ion; pH; enough availability of N, C, and P; and other trace elements (Compant et al. 2005). Pseudobactin or pyoverdine have been reported to be produced by *P. fluorescens*, which have a high affinity for sequestration of Fe^{2+}. The ferripyoverdins (a complex of pyoverdine with Fe^{3+}) are reported to be combined with the receptors of the outer membrane and transported to the cytoplasm and ultimately get reduced to Fe^{2+} (Haas and Defago 2005). The plant growth is directly increased by production of the siderophore as they make Fe available for plants. It has been reported that PGPR also consumes Fe for effective rhizospheric colonization. PGPR produce lytic enzymes to degrade cells of the pathogens (Compant et al. 2005). The synergistic effects of PGPR metabolites such as antibiotics and lytic enzymes are responsible for the degradation of cell walls of microbial pathogen and weeds (Dunne et al. 1998).

In response to phytopathogens, PGPR help plants stimulate a defense mechanism having a hypersensitive reaction called ISR (Compant et al. 2005). Numerous *Bacillus* sp. trigger ISR in biotic stress that improves plant growth through ultrastructural changes and cytochemical alteration in plants (Kloepper et al. 2004). The bacteriocins produced by PGPR are different from narrow-spectrum antibiotics that can kill closely related bacterial strains (Beneduzi et al. 2012). The bio-surfactants are considered to be effective for the biocontrol of phytium species (Perneel et al. 2008). For example, *P. fluorescens* is capable of protecting plants from disease-causing pathogenic fungi. It secretes a varying degree of exoproducts through antibiosis, phytohormone activities, lytic activities, and antimicrobial compounds to be considered as a primary mechanism to suppress disease in root area (Péchy-Tarr et al. 2008). Such PGPR play a major role in biocontrol by producing a wide range of secondary metabolites including the production of volatile compounds, antibiotics, siderophores, HCN, and other disease-suppressing compounds (Showkat 2012).

Numerous microorganisms have been reported as potential bioherbicides. PGPR are the most suitable biocontrol agents as compared to other microorganisms due to their rapid growth and genetic variation via mutagenesis (Johnson et al. 1996; Li et al. 2003). Various strains of *P. fluorescens* have shown their benefits as well as inhibitory effects on plants (Banowetz et al. 2008). Their suppressive effects were reported due to production of extracellular metabolites that suppress plant germination (Banowetz et al. 2008). Growth inhibition of various grassy weeds including downy brome was observed through inoculation with *P. fluorescens* strain D7 (Kennedy et al. 2001). These strains showed plant growth inhibition due to combined production of extracellular peptides and lipopolysaccharides (Gurusiddaiah et al. 1994). However, their mechanism for weed growth suppression has not yet been described. *P. fluorescens* strain WH6 showed growth inhibition of 21 monocot and 8 dicot plant species; however it was unable to affect the germination of hybrid corn (Banowetz et al. 2008). Its ability to suppress weed germination was reported due to production of germination arrest factor (GAF) composed of 4-formylaminooxy-L-vinylglycine and oxyvinylglycines due to synthesis of their regulatory genes (Banowetz et al. 2008; McPhail et al. 2010; Halgren et al. 2013; Okrent et al. 2014). The strain BRG100 showed suppression of *Setaria viridis* due to the production of extracellular metabolites (pseudophomin A and B) having phytotoxic effects (Caldwell et al. 2012).

Pseudomonas strains produced phytotoxins including phenazine-1-carboxylic acid, 2-aminophenoxazone, and 2-aminophenol that have allelopathic effects against plant growth (Adetunji et al. 2019). The strains of *Xanthomonas campestris* were also reported as a potential weed control agent. Its strain JT-P482 showed specific control against grasses *Poa annua* and *Poa attenuate* (Imaizumi et al. 1997). The strain LVA-987 also showed weed control against horseweed (Boyette and Hoagland 2015). No information on phytotoxic compounds produced by these strains is available in support of its application as a bioherbicide. Such strains spread in their host plant through colonizing plant xylem. They interact with host plant through their receptor proteins that can recognize pathogen-associated molecular patterns that activates plant defense responses in terms of production of ROS and programmed cell death (Guy et al. 2013; Dugé de Bernonville et al. 2014). Such allelopathic bacteria may also produce enzymes and broad-spectrum antibiotics that have inhibitory effects on plant growth (Abbas et al. 2017). Production of elevated IAA levels by PGPR also possesses allelopathic effects (Sarwar and Kremer 1995). The HCN production by rhizobacteria is a major suppressor of weed growth (Kremer and Souissi 2001).

Recent developments in bioherbicides support the potential use of HCN-producing bacterial strains along with multiple PGP traits for improving crop growth by suppression of weeds. In a recent study, Dar et al. (2020) reported *Pseudomonas* strains with potential *Pseudomonas* for both potential to control *Phalaris minor* and *Avena fatua* in wheat. They reported four *Pseudomonas* strains having HCN-producing ability along with multiple PGP traits such as P solubilization, ACC-deaminase activity, siderophores production, and oxidase activity during in vitro studies. In the bioassay, they reported these strains as strong phytotoxic for lettuce seedling having a mortality rate of up to 73.3%. Consortia of these strains were more effective than sole inoculation in the biocontrol of *Pectoralis minor* and *Avena fatua* seedlings. In addition to biocontrol of weeds, these strains were also effective in improving wheat growth. They argued that the use of these strains as bioherbicide may improve human and environmental health. So, inoculation with allelopathic bacteria could support the existing herbicides that not only control weeds but also alleviate the allelopathic effects of weeds. The mechanisms of biotic stress amelioration by PGPR have been summarized in Fig. 2.2.

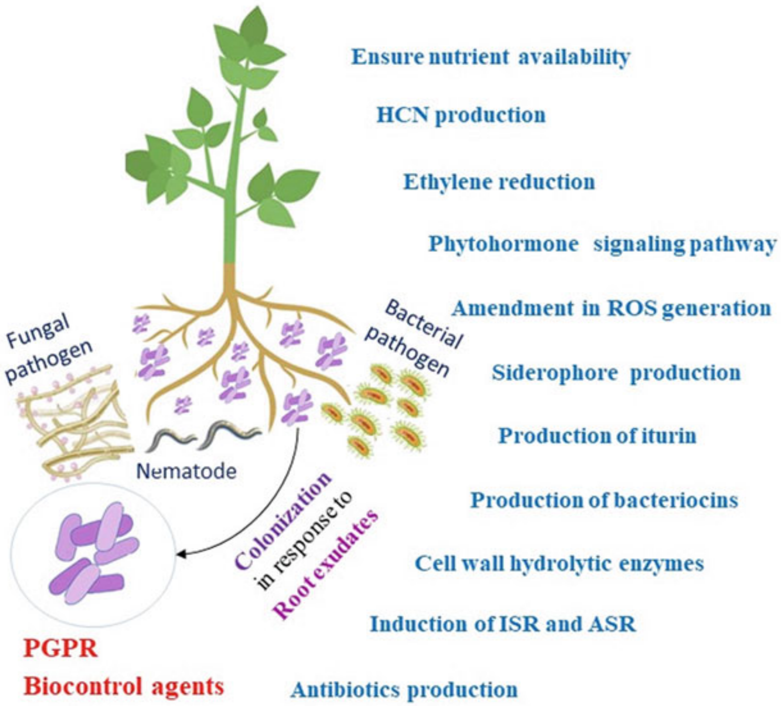

Fig. 2.2 Mechanisms of biocontrol by plant growth-promoting rhizobacteria

2.4.3 Integrated Stress Amelioration

Abiotic and biotic stresses due to climate change are a major cause of productivity loss in major crops (Anderson et al. 2020). The effects of abiotic and biotic stresses on plant growth and their amelioration by PGPR have already been discussed in the above sections. Under field conditions, crops face multiple stresses which drastically decline crop productivity (Pandey et al. 2017; Hussain et al. 2018). Managing abiotic and biotic stresses with competent and cost-effective approaches is a major challenge. Such approaches including the development of stress-tolerant varieties and application of chemical fertilizers and pesticides are cost-intensive. Recently, the application of PGPR to ameliorate various environmental and biotic stresses has been revealed as a cost-effective and efficient approach in integrated stress management (Grover et al. 2011). We have proposed a possible mechanism of action in the amelioration of integrated stresses (Fig. 2.3).

As described in the above sections, the PGPR having the ability to produce ACC-deaminase, phytohormones, antioxidant enzymes, siderophores, EPS, VOCs, and solubilization of nutrients can ameliorate all the abiotic stresses. Similarly, in

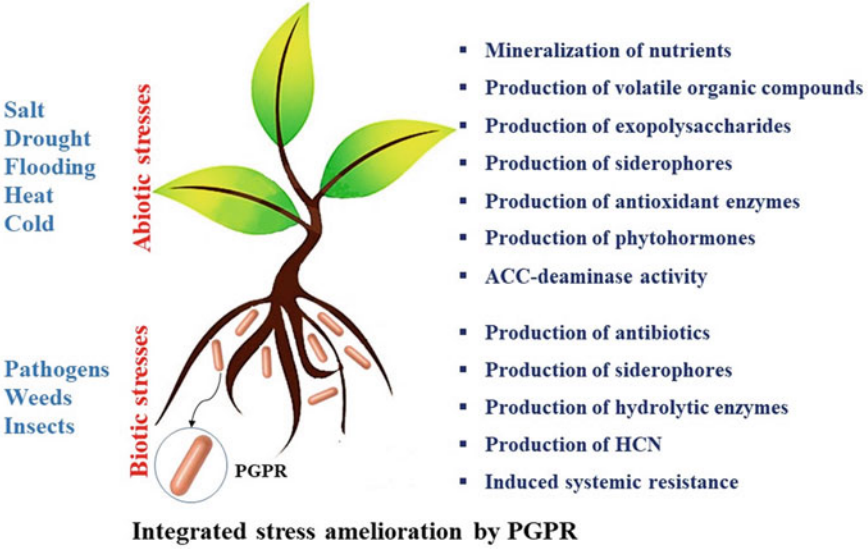

Fig. 2.3 Proposed mechanisms of action for integrated stress amelioration by plant growth-promoting rhizobacteria

biotic stress control, the HCN-producing PGPR along with production of antibiotics, lytic enzymes, siderophores, and ISR are effective (Fig. 2.3).

The PGPR with multiple PGP traits can be effective in integrated stress amelioration (ISA). As a combination of stresses enhance the ethylene production, ACC-deaminase-producing PGPR with multiple PGP traits can be more effective in ISA. For example, recent studies reported the effectiveness of ACC-deaminase-producing PGPR in ISA (Barnawal et al. 2017; Srinivasan et al. 2017; Saikia et al. 2018; Orozco-Mosqueda et al. 2020; Li et al. 2020). Some mechanisms of stress mitigation by PGPR including the production of siderophores, nutrient mineralization, production of VOCs, and EPS are not well understood in all abiotic stresses; however, these metabolic activities have been reported to be effective in various environmental stresses (Talaat and Shawky 2017; Khan and Bano 2019). PGPR release secondary metabolites including antibiotics, siderophores, hydrolytic enzymes, and HCN that mitigate the biotic stresses in terms of infection by pathogens and allelopathic effects of weed as well as help improve crop productivity (Jha 2018). As reported by Dar et al. (2020), HCN-producing rhizobacteria with multiple PGP traits can be strong candidates for integrated stress amelioration.

2.5 Conclusion and Prospects

Under natural field conditions, plants face several abiotic and biotic stresses which negatively affect plant growth. These stresses result in the enhanced biosynthesis of ethylene and damage the plant physiological and biochemical attributes. The application of PGPR is well reported for mitigation of these stresses. These beneficial rhizobacteria directly mitigate integrated stresses by metabolic activities in terms of production of phytohormones, ACC-deaminase, siderophores, and EPS and ensure nutrient availability through improving their solubility. PGPR have an indirect role as well in stress alleviation by producing antibiotics, HCN, and hydrolytic enzymes and induce ISR that help plant tolerate biotic stresses.

Improvement in PGPR population and diversity through rhizosphere engineering or use of microbial inoculants and/or their metabolites should be practiced for better agroecosystem and soil health. There is a need to study interactive effects of various stresses on a plant to know about impacts of combined stresses on crop production. Future research is needed to evaluate the role of PGPR under multiple stress conditions.

Future research should also be focused on understanding the mechanisms involved in PGPR-induced stress tolerance in crop plants. There is also a need to investigate why certain PGPR with specific PGP traits could not induce stress tolerance in crop plants under soil (field) and environmental conditions. Strategies should be developed to study and improve plant-microbe interactions using bioinformatics, modeling tools, and other molecular techniques to enhance crop stress tolerance and for sustainable agroecosystems.

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