Chapter 12
Microbe-Mediated Drought Tolerance in Plants: Current Developments and Future Challenges

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Abstract   Drought is a conspicuous stress-causing deleterious effect on plant growth and productivity. In order to compensate the yield loss due to drought, efficient and sustainable strategies are required for its management. Drought stress tolerance is complex trait involving clusters of genes; hence, genetic engineering to generate drought-resistant varieties is a challenging task. In this context, the application of plant growth-promoting microbes (PGPM) to mitigate drought stress is gaining attention as an attractive and cost-effective alternative strategy. PGPM have envisaged a plethora of mechanisms to overcome drought stress in plants which encompasses ACC (1-aminocyclopropane-1-carboxylate) deaminase activity, production of exopolysaccharide (EPS) and volatile organic compounds (VOCs), osmolyte and antioxidant production, enhanced uptake of mineral nutrients, phytohormones production, and modulation. These mechanisms either individually or collectively bestow the PGPRs to combat drought stress in plants. The association of arbuscular mycorrhizal fungi (AMF) with the roots of crop plants can significantly promote water and nutrient uptake by host plants and induce tolerance to drought stress. The inoculation of PGPM in crop plants is also capable of modulating host transcriptome for induced drought tolerance. Further, efforts are needed to develop proficient microbial consortia for enhancing plant growth under drought stress. Thus, the application of PGPM/AMF represents a promising approach to increase nutrient availability and expedite the development of sustainable agriculture.

Keywords Drought · Plant growth-promoting rhizobacteria · Arbuscular mycorrhizal fungi · Sustainable agriculture

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12.1 Introduction

Plants being sessile are subjected to a wide array of environmental stresses such as salinity, drought, heavy metals, waterlogging, chilling, and high temperature. Furthermore, climate change is influencing the austerity of abiotic stresses, particularly high temperature and drought. Intense drought is mostly associated with the global climate change which is having a major impact of crop productivity (Etesami and Maheshwari 2018). It is being projected that drought will affect more than 50% of the arable lands worldwide by the year 2050 (Vurukonda et al. 2016). Among these stresses, drought is a conspicuous stress-causing deleterious effect on plant growth and productivity. This stress adversely affects many physiological and biochemical processes of plants such as phytosynthesis, respiration, transpiration, carbohydrates metabolism and nutrient uptake, translocation, and assimilation (Khan et al. 2018). In order to compensate the yield loss due to drought, efficient and sustainable strategies are required for its management. From past years, mainly two strategies are mostly focused to combat the drought stress in plants such as traditional breeding methods and genetic engineering of crop for drought-resistant (Naveed et al. 2014). The major constraint for application of these techniques is time taking, tedious, and expensive. Furthermore, the acceptance of a transgenic crop is uncertain in the market regarding the consumer response to genetically modified plant products which varies from country to country (Ullah et al. 2019a).

In addition to several ethical issues, genetic engineering of all crops is not feasible (Etesami and Maheshwari 2018). Besides, drought stress tolerance is complex trait involving clusters of genes; hence, genetic engineering to generate drought-resistant varieties is a challenging task (Nautiyal et al. 2013; Saikia et al. 2018). Another sustainable strategy to limit drought stress is soil resource management by application of mulching, crop residues, crop cover, non-crop mulch material (plastic foil, geotextile), etc. These methods tend to reduce runoff and evaporation from soil surfaces. Besides, use of crop residue as mulch can increase the soil organic matter which in turn increases the soil water storage capacity and its availability to crops during drought conditions (Bodner et al. 2015).

In this context, the use of plant growth-promoting microbes (PGPM) to mitigate drought stress is gaining attention as an attractive and cost-effective alternative strategy. There are various studies which suggest the beneficial role of plant growth-promoting rhizobacteria (PGPR), actinomycetes, and mycorrhiza in boosting plant growth and endurance toward drought stress (Gontia-Mishra et al. 2016; Saikia et al. 2018; Zade et al. 2019). This chapter summarizes the present understanding toward drought stress and their physiological and molecular responses in plants. The later section of the chapter highlights the imperative mechanisms of PGPM for mitigation of drought stress in plants. In the present chapter, we have also attempted to comprehend the perceptive use of PGPM to alleviate the drought stress in crop plant by fine-tuning the metabolic, signaling, and molecular pathways, thereby enhancing crop productivity.

12.2   Impact of Drought on Crop Plants

Similar to other abiotic stresses, drought is also multidimensional in its effects and has various deleterious impacts on plant. The plants respond to drought stress at physiological, biochemical, and molecular levels, from seed germination to maturity and senescence (Tiwari et al. 2017). Nonetheless, adaptability of plants to drought is determined by the severity and time of exposure to stress, plant species as well as the developmental stages (Kaur and Asthir 2017). Under water scarcity, plant exhibits various events to acclimatize such as morphological (reduced biomass and altered root structure), physiological (reduced photosynthesis and altered transpiration and stomatal activity), and biochemical changes (accumulation of osmolytes, increased oxidative enzyme activity) (Conesa et al. 2016).

Excessive loss of water in drought condition leads to closed stomata and controlled gas exchange and desiccation which lead to complete metabolism and cellular structure disruption; this gradually ends in interruption in enzymatic reactions (Jaleel et al. 2007). Aboveground parts of plant are more susceptible to drought stress than their counterparts. During water-deficit conditions, plants respond by shrinking leaf area, spiraling, and in some cases by shedding their leaves. Leaf size reduction is an important strategy to drought stress as it can directly influence the rate of transpiration. However, reduction in leaf size leads to marked decline in the photosynthetic activity of plants. Drought stress in plants is noted by declined leaf water potential, stomatal closure, and marked reduction in cell growth (Farooq et al. 2009). The first plant organs to feel and react to water deficiency are the roots. Under moderate drought stress, the root length is increased which is attributed to the plants need to utilize the groundwater (Forni et al. 2017), but severe drought conditions can retard root growth. Characteristics related to root traits like biomass, root length, root density, and depths of roots have been identified as the major drought avoidance traits under drought environment (Kashiwagi et al. 2006). A decrease in growth is the most obvious plant response to water stress, which results from decrease in water uptake by roots.

Plant growth and morphology are proportional to enlargement, division, and differentiation of cell. Drought is also reported to inhibit mitotic division of cells along with elongation and expansion which results in growth retardation of plants (Hussain et al. 2008). Various physiological changes occur in plants to overcome drought stress as the early response of plant to stress can make the plant to survive. The basic mechanism to show drought response is to decrease the osmotic potential of plant cells; as a result, the turgor potential gets maintained for routine metabolic processes (Levitt 1980). Drought stress leads to an imbalance between antioxidant defenses and the amount of Reactive Oxygen Species (ROS) resulting in oxidative stress. ROS are required to trigger the signaling but eventually at high concentration can cause impairment of plant organelles especially chloroplasts (Smirnoff 1993). Later on, ROS can initiate lipid peroxidation and degradation of vital proteins, lipids, and nucleic acids (Kaushal and Wani 2016).

Plants under drought stress starts synthesis of new metabolites for their proper functioning. Plants can accumulate biomolecules such as dehydrins (DHNs), heat shock proteins (HSPs), late embryogenesis abundant (LEA) proteins (Lipiec et al. 2013), osmolytes like proline, trehalose, and sugars (Ilhan et al. 2015), glycine, and betaine (Chen and Murata 2011). Changes in membrane fluidity, fatty acid, and protein composition of membranes help to maintain the cellular integrity of plants under drought stress (Bohnert et al. 1995). The osmolytes like ectoine, glycine, and betaine interplay in protein solubilization, and the uncharged solutes like mannitol, trehalose, and pinitol play an important role as scavengers of ROS (Ashraf and Foolad 2007). Plants have envisaged several enzymatic mechanisms including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR) and non-enzymatic components such as cysteine, glutathione, and ascorbic acid, to aid them fight against the oxidative damage caused by ROS (Kaushal and Wani 2016).

Nitric oxide also protects plants under water-deficit condition from oxidative stress. Most of these processes are regulated through a complex network governed by abscisic acid (ABA), ion transport system, and various transcription factors. Water stress in the root tips results in release of a stress-signaling hormone ABA, which is transported from root zone to the aerial parts of plants. It is directly involved in regulation of stomatal aperture closure. Various reports argued that early interaction of drought signals is mediated by transmembrane protein like histidine kinase which functions like osmosensor (Posas et al. 1996; Urao et al. 1999). Other membrane proteins like aquaporins also involved in regulation of cell volume and turgor homeostasis. In addition, some genes are also identified which regulates the synthesis of osmolytes in the cytoplasm in order to maintain the osmotic potential at water stress condition. Other mechanism involved in sensing of drought stress is changed in the fluidity of membrane lipids (Knight and Knight 2001). Phospholipase C and D along with phosphatidyl-4,5-phosphate 5-kinase are found to be involved in this mechanism which leads to control ion and water channels (Mikami et al. 1998).

12.3   PGPM with Special Context to Drought Stress Management

Almost every parts of the plant are colonized by microbes, but the rhizosphere (soil in the proximity of roots) represents the main source of bacteria with plant-beneficial activities. The microbial community residing in the rhizosphere is comparatively different than its surroundings due to the presence of root exudates (Vejan et al. 2016). These bacteria largely utilize root exudates a source of nutrients for their growth and survival, hence termed as PGPR (Kolepper and Schroth 1978; Verma et al. 2015a, b; Yadav et al. 2015). They interact with the plant roots and influence plant growth and yield as well as enhance soil fertility. Besides PGPR, association of arbuscular mycorrhizal fungi (AMF) with the roots of crop plants can significantly

promote water and nutrient uptake by host plants and induce tolerance to drought stress (Xu et al. 2018; Hashem et al. 2019; Yadav et al. 2019b, c, d). Many researchers have advocated the positive impact of PGPR and AMF to promote plant growth under drought stress; hence, it is an effective developing technology (Compant et al. 2010; Carmen et al. 2016; Wu et al. 2019; Verma et al. 2017; Yadav et al. 2018a, b). Crop plants in association with PGPRs persuade morphological and biochemical adjustments leading to increased tolerance to drought by eliciting induced systemic tolerance (IST) (Naveed et al. 2014).

It is determined that PGPR can intercede the drought stress in host plant by increasing accumulation of osmolytes (compatible solutes like proline, glycine betaine, polyamines, sugars like trehalose and polyols), improved uptake of nutrients and modulating the activities of antioxidant enzymes (Barnawal et al. 2019; Kour et al. 2019c; d). Phytohormones are known to control signaling of many abiotic and biotic stresses in plants. It is an established fact that phytohormone synthesis and signaling have a great significance in response to extreme environmental conditions (Tiwari et al. 2017; Kour et al. 2019b; Yadav et al. 2019a). Interestingly, this approach is adopted by PGPR to induce drought tolerance in host plant by regulating the level of phytohormones, like ABA, salicylic acid (SA), and ethylene, therefore directly affecting plant signaling networks and altering drought-responsive genes (Lu et al. 2018). Similarly, inoculation of AMF in host plants can accelerate plant growth and yield under drought stress by increased water and nutrient uptake, modulating stress-responsive genes and cell membrane fatty acid composition and degree of unsaturation (Xu et al. 2018; Wu et al. 2019). The use of various PGPR and AMF for alleviation of drought stress and their positive impact on host plants is presented in Tables 12.1 and 12.2.

12.4 Ways Out by Which PGPM Handle Drought Stress

PGPM have envisaged a plethora of mechanisms to overcome drought stress in plants which encompasses ACC (1-aminocyclopropane-1-carboxylate) deaminase activity, production of exopolysaccharide (EPS) and volatile organic compounds (VOCs), osmolyte production, uptake of mineral nutrients (N, P, and K), phytohormones production/modulation [auxin/indole acetic acid (IAA), cytokinins, abscisic acid (ABA), salicylic acid (SA) and jasmonic acid (JA)], and eliciting the activity antioxidant enzymes in host plants. These mechanisms either individually or collectively bestow the PGPRs to combat drought stress in plants.

12.4.1 ACC Deaminase Activity

Ethylene is a crucial plant hormone which controls a number of plant processes ranging from seed germination, fruit ripening, abscission of leaves, and plant senescence

Table 12.1 The role of PGPR in mitigating drought stress in plants

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Bacillus spp.	Rhizosphere of *Pennisetum glaucum, Helianthus annuus, Zea mays*	*Z. mays*	EPS and IAA, gibberellins, cytokinin production, and P-solubilization	Inoculated maize seedlings showed improved physiological response to drought	Vardharajula et al. (2011)
Bacillus licheniformis	Field soil	*Capsicum annuum*	ACC deaminase activity	PGPR-inoculated pepper plants tolerate the drought stress and showed differentially expressed stress proteins	Lim and Kim (2013)
Burkholderia phytofirmans	Roots of onion	*Triticum aestivum*	IAA production and ACC deaminase activity	PGPR inoculation improved grain yield and nutrients in grains	Naveed et al. (2014)
Pseudomonas aeruginosa	Rhizosphere of *Vigna radiata*	*V. radiata*	IAA, ACC deaminase, P-solubilization, and endogenous proline and glycine betaine accumulation	Increased the levels of antioxidant enzymes, proline, and subsequently modulated the regulation of stress-responsive genes in PGPR-treated plants under water stress conditions	Sarma and Saikia (2014)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Bacillus thuringiensis and Paenibacillus polymyxa	Pinus ponderosa and Oryza sativa	T. aestivum	ACC deaminase activity and P-solubilization	Greater plant biomass and fivefold higher survivorship under severe drought; reduced emissions of stress volatiles	Timmusk et al. (2014)
Pseudomonas spp., Bacillus cereus, and Arthrobacter sp.	Rhizosphere soil	O. sativa	IAA production	Improved plant growth and antioxidant defense systems and stability of membranes in plant	Gusain et al. (2015)
Bacillus subtilis	Roots of Panicum virgatum	Brachypodium distachyon	Phytohormone production and P-solubilization	Amelioration of phenotypic effect of drought and up-regulation of drought-responsive genes	Gagné-Bourque et al. (2015)
Klebsiella sp, Enterobacter ludwigii, and Flavobacterium sp.	Rhizosphere of T. aestivum	T. aestivum	IAA and siderophore production, ACC deaminase, P and Zn solubilization	Affected various growth parameters, water status, membrane integrity, osmolyte accumulation, and stress-responsive gene expressions, which were positively altered by PGPR inoculation in wheat under drought	Gontia-Mishra et al. (2016)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Pseudomonas putida and *Bacillus amyloliquefaciens*	–	*Cicer arietinum*	ACC deaminase activity, minerals solubilization, biofilm formation	PGPR inoculation improved the biomass and antioxidant enzymes in plants under drought stress	Kumar et al. (2016)
Pseudomonas putida	Desert regions of Rajasthan	*C. arietinum*	IAA production and P-solubilization	Altered various physiological and biochemical parameters as well as regulation of stress-responsive genes	Tiwari et al. (2016)
Bacillus subtilis	Rhizosphere soil of lemongrass	*T. aestivum*	IAA production and ACC deaminase activity	PGPR inoculation improved the physiological parameters such as net CO_2 assimilation, stomatal conductance, and transpiration rate as well as increased the endogenous IAA and ABA content under drought stress	Barnawal et al. (2017)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Azospirillum spp.	Roots of wheat and maize	*Z. mays*	N₂ fixation, IAA and siderophore production, ACC deaminase activity, P-solubilization	Significant biomass gain and better osmotic balance were noted in PGPR-inoculated plants under drought stress	García et al. (2017)
Enterobacter cloacae and *Citrobacter* sp.	Rhizosphere of *T. aestivum*	*T. aestivum*	IAA and siderophore production, ACC deaminase, P, K, and Zn solubilization	Bio-inoculants showed growth enhancement of wheat seedlings under drought stress	Gontia-Mishra et al. (2017)
Bacillus amyloliquefaciens	Alkaline soil	*O. sativa*	IAA production, ACC deaminase activity, P-solubilization, and proline accumulation	PGPR inoculation positively stimulated membrane integrity and osmolyte accumulation as well as modulated the drought-responsive genes under water-deficit condition	Tiwari et al. (2017)
Pseudomonas fluorescens, Enterobacter hormaechei, and *Pseudomonas migulae*	*Setaria italica*	*S. italica*	ACC deaminase activity and EPS production	PGPR inoculation caused a significant increase in dry biomass	Niu et al. (2018)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Bacillus amyloliquefaciens	–	*Arabidopsis thaliana*	EPS and IAA production	Increased the survival rate of plants, biomass, osmolytes, antioxidant enzyme activities, and modulated stress-responsive genes	Lu et al. (2018)
Ochrobactrum pseudogrignonense, Pseudomonas sp, and *Bacillus subtilis*	Rhizosphere soil	*Vigna mungo* and *Pisum sativum*	ACC deaminase activity, IAA production, and P-solubilization	Better plant growth and biomass, increase activity of antioxidant enzymes, down-regulation of ACC-oxidase gene under drought stress	Saikia et al. (2018)
Enterobacter sp. and *Bacillus* sp.	*Mucuna pruriens*	*M. pruriens*	ACC deaminase activity and IAA production	Improved photosynthetic performance and biomass and increased leaf isoprene content	Saleem et al. (2018)
Bacillus licheniformis	Compost	*A. thaliana*	IAA production and P-solubilization	Exposure to PGPR increased the tolerance toward water deficits and positive-modulated stress-responsive genes	Sukkasem et al. (2018)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Bacillus subtilis and *Paenibacillus illinoisensis*	–	*Capsicuum annuum*	Synthesis of nitric oxide and volatile organic compounds	Increase in root length and photosynthetic activity as well as enhanced expression and activity of vacuolar proton pumps	Vigani et al. (2018)
Variovorax paradoxus, *Pseudomonas* spp., *Achromobacter* spp, and *Ochrobactrum anthropi*	*T. aestivum*	*T. aestivum*	ACC deaminase activity	Improved plant growth and foliar nutrient concentrations and significant changes in antioxidant properties in treated with PGPR under drought stress	Chandra et al. (2019)
Pseudomonas spp., *Bacillus* spp.	–	*A. thaliana*	EPS and phytohormone production	Bio-inoculation remarkably increased the biomass and plant water content under drought stress	Ghosh et al. 2019

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Paenibacillus beijingensis and *Bacillus* sp.	–	*T. aestivum* and *Cucumis sativus*	–	Bio-inoculation significantly increased seed germination, whereas decreased free proline and soluble sugar in the plants. The modulation of stress-responsive and ROS scavenging genes in PGPR-treated plants under drought stress was noted	Li et al. (2019b)
Streptomyces pactum		*T. aestivum*	Biocontrol agent against antagonists	Enhanced osmotic adjustment and antioxidant capacity of plants via induction of abscisic acid accumulation and up-regulation of drought resistance-related gene expression	Li et al. (2019c)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Pseudomonas simiae	Rhizosphere of *Glycine max*	*G. max*	ACC deaminase activity	PGPR inoculation increased the accumulation of osmolytes and sugars as well as down-regulated the drought stress-responsive genes	Vaishnav and Choudhary (2019)
Bacillus pumilus	Roots of *Glycyrrhiza uralensis*	*G. uralensis*	–	PGPR inoculation increased the total biomass, oxygen species, and antioxidants in plants. It also enhanced the flavonoids, total polysaccharide, and glycyrrhizic acid contents in plants under drought conditions	Xie et al. (2019)
Streptomyces rimosus and *S. monomycini*	–	*Mentha piperita*	Auxin and siderophore production, biocontrol activity against *Phytophthora drechsleri*	PGPR inoculation increased the biomass and growth and essential oils as well as menthol content under drought stress	Zade et al. (2019)

Table 12.2 The role of AMF in mitigating drought stress in plants

Crop/plant	Effect of AMF inoculation on plant	References
Strawberry	AMF inoculation plants had greater water-use efficiency under the regulated deficit irrigation (RDI) regime in comparison to non-mycorrhizal inoculated plants	Boyer et al. (2015)
Phaseolus vulgaris	AMF inoculation and methyl jasmonate prevented inhibition of root hydraulic conductivity under drought conditions, by causing reduction in root salicylic acid contents	Sanchez-Romera et al. (2016)
Zea mays	AMF symbiosis induced an improvement in physiological parameters in drought-sensitive plants including efficiency of photosystem II, membrane stability, accumulation of soluble sugars and plant biomass production. In addition, the drought-responsive genes were down-regulated by the AMF inoculation	Quiroga et al. (2017)
Sorghum bicolor	AMF inoculation alleviated plant growth retardation and prolonged plant lifespan under drought. The improved biomass and the specific leaf area were noted in inoculated plants under drought stress conditions	Sun et al. (2017)
Poncirus trifoliate	AMF inoculation significantly increased leaf sucrose, glucose, and fructose concentration under drought stress, accompanied with a significant increase of leaf sucrose phosphate synthase, neutral invertase, and net activity of sucrose-metabolized enzymes	Wu et al. (2017)
Damask rose	AMF colonization can enhance growth, flower quality, and adaptation of rose plants under drought stress levels, particularly at high level of drought stress via improving their water relations and photosynthetic status	Abdel-Salam et al. (2018)
Poncirus trifoliate	AMF inoculates seedlings showed significantly higher root density, length, and diameter and root IAA level under stress. Mycorrhization caused the up-regulation in IAA biosynthesis. The inoculation also down-regulated the transcript level of root auxin efflux under drought stress	Liu et al. (2018)
Zea mays	AMF association modifies root hydraulic responses to drought. AMF plants showed increased hydrostatic root hydraulic conductivity and osmotic root hydraulic conductivity	Quiroga et al. (2018)
Sorghum bicolor	AMF inoculation improved their transpiration efficiency and increased the nitrogen and phosphorus content of sorghum, especially under water was limiting conditions	Symanczik et al. (2018)
Glycyrrhiza uralensis	The inoculation of AMF to the plants demonstrated improved growth and physiological status such as stomatal conductance, photosynthesis rate, and water-use efficiency compared with non-AM plants. The AMF association also up-regulated the expression of an aquaporin gene PIP and decreased root abscisic acid concentrations	Xie et al. (2018)
Leymus chinensis and *Hemarthria altissima*	AMF inoculation to plants enhanced plant biomass, photosynthetic rate, stomatal conductance, intrinsic water-use efficiency, and SOD activity of the *L.chinensis* and reduced levels of malondialdehyde. The inoculation also demonstrated increased shoot growth in *H.altissima*	Li et al. (2019a)

(Sapre et al. 2019). It is also produced in plant in response to several environmental stresses including drought stress (Gontia-Mishra et al. 2014). Consequently, the ethylene generated under stressful condition is often termed as "stress ethylene" (Glick 2014). The ethylene produced during stress can subsequently induce the defoliation, retarded root, and stem growth along with the expression of genes leading to plant senescence, leading to inferior crop performance (Vejan et al. 2016). Interestingly, it is noted that ACC works as precursor for ethylene biosynthesis (Shaharoona et al. 2006). Among the different suggested strategies for improvement in plant growth under drought stress, the most plausible one is alteration in the endogenous levels of ethylene caused by the PGPR (Kumar et al. 2019a, b).

Furthermore, many PGPR possessing the enzyme ACC deaminase catalyze the conversion of ACC to ammonia and α-ketobutyrate, which indirectly decrease the ethylene concentration in plants under drought stress (Glick et al. 1998). By facilitating the development of longer roots, these PGPR may enhance the survival of seedlings, which help in combating the effect of stress ethylene. The root elongation plants under drought stress can allow a better access to water and uptake of nutrients. Ethylene is also known to compromise the nodule formation and nitrogen fixation in legume (Sapre et al. 2019). *Rhizobium* with ACC deaminase activity can diminish the deleterious effect of ethylene under drought stress by increasing the nodulation and nitrogen fixation in its symbiotic legume partner (Belimov et al. 2009). In this regard, numerous researchers have documented the application of ACC deaminase-producing PGPR in ameliorating drought stress in crop plant such as chickpea (Tiwari et al. 2016), mung bean (Sarma and Saikia 2014), wheat (Gontia-Mishra et al. 2016; Barnawal et al. 2017), rice (Tiwari et al. 2017), foxtail millet (Niu et al. 2018), and other tropical crop plants (Kumar et al. 2019a, b; Kour et al. 2019a; Yadav et al. 2017a; b; Yadav and Yadav 2018).

12.4.2 EPS Production

PGPR have the unique ability to produce exopolysaccharide (EPS)/extracellular polymeric substances. The biofilm formation and EPS production by PGPR are important mechanisms to tolerate drought stress in the environment. The EPS has multifarious function in bacterial cells ranging from quorum-sensing signals, development, survival, and host colonization (Nocelli et al. 2016). The EPS largely constitutes of high-molecular-weight macromolecules like polysaccharide along with smaller proportions of protein, lipids, and uronic acid (Naseem et al. 2018). The EPS-producing PGPR can better clamp and colonize the root surface under adverse conditions (Ali et al. 2014).

It can protect PGPR and its host plant under drought stress by enhancing water retention than the surrounding environment (Hepper 1975; Vurukonda et al. 2016). The EPS secreted by PGPR into the soil can be absorbed by soil particle due to their different anionic functional groups (e.g., sulfhydryl, carboxyl, hydroxyl, sulfonate, amine, and amide) and increase the water-holding capacity of soil and improve

physicochemical properties of soil under prolong desiccation conditions (Sandhya et al. 2009). Hence, plants inoculated with EPS-producing PGPR can maintain the higher water potential, boost root-adhering soil/root tissue ratio, and accelerate the uptake of nutrients by plant, thereby enhancing plant growth and yield under drought stress (Selvakumar et al. 2012; Rolli et al. 2014; Kaushal 2019). Many researchers have suggested the use of EPS-producing rhizobacteria in alleviating drought stress in important crop plants such as maize (Vardharajula et al. 2011), sunflower (Sandhya et al. 2009), wheat (Timmusk et al. 2014), and foxtail millet (Niu et al. 2018).

12.4.3   Production of VOCs

Unlike plants, soil bacteria produce a range of volatile compounds, which have specific function in their life cycles as well as interplay with other microbes and plants (Sharifi and Ryu 2018). The bacterial VOCs are chemically characterized as alkenes, ketones, and alcohols. PGPR can stimulate plant growth by synthesizing and releasing volatile compounds, which is now known as an essential mechanism of plant–microorganism interactions (Froni et al. 2017). The role of these VOCs is largely associated as activator against plant pathogens, leading to induced systemic resistance in plants (Ruzzi and Aroca 2015). Remarkably, it is noted that besides their role in biotic stress tolerance, these compounds can actively alleviate several abiotic stresses including drought (Timmusk et al. 2014). The VOCs produced by PGPRs can promote plant growth by increasing photosynthesis, carbon assimilation, enhancing mineral uptake, altering root structure, and intensive phytohormone signaling under abiotic stress conditions (Sharifi and Ryu 2018).

It was demonstrated that a PGPR *Pseudomonas chlororaphis* releases characterized as 2R, 3R-butanediol, can induce drought tolerance in *Arabidopsis thaliana* (Cho et al. 2008). Moreover, few studies suggest the role of VOCs (produced by PGPR) in modulation of the transcript levels in plants, resulting in enhanced biosynthesis of choline and glycine betaine which in turn to shielded *A. thaliana* plants from drought stress (Cho et al. 2008; Zhang et al. 2010). It was noted that VOCs produced by soil bacteria such as acetic acid can stimulate the formation of biofilms/EPS, which can indirectly influence drought stress in plants (Chen et al. 2015). Another study of bacterial inoculation with *Bacillus thuringiensis* in wheat seedlings under drought stress markedly decreased the stress-induced volatile compounds emitted by plants and increased plant biomass and photosynthesis (Timmusk et al. 2014). VOCs producing PGPR are potential for application as bio-stimulants to improve plant health under drought stress. The mechanism of PGPR-induced VOCs in ameliorating drought stress in crop plants is limited and requires to be explored extensively.

12.4.4 Phytohormones Production

The production of phytohormones in plants is essential because of their physiological effects on its growth. The phytohormones such as auxins, cytokinins, gibberellins and ethylene, and abscisic acid (ABA) have a particular function in the regulation of plant growth and development (Vurukonda et al. 2016). PGPR have been widely known to produce these phytohormones which can help in promoting plant growth under stressed conditions by stimulating cell growth and division (Kaushal 2019). One of the important aspects of the bacterial–plant interaction that has received worldwide attention is the bacterial production of IAA/auxins. Production of IAA, a plant hormone that does not any apparent function as a hormone in bacterial cells, may have evolved in bacteria because of its significance in the bacterium–plant relationship (Patten and Glick 2002). A positive correlation is noted between the in vitro production of auxins by PGPR strains and their growth promotion effects (Jha et al. 2012). The auxin-producing PGPR can influence root proliferation and formation of lateral and adventitious roots, which results in an increased mineral and water uptake by the plants rotoscoping them against drought stress (Gontia-Mishra et al. 2016). Besides, some of the PGPR have known to modulate the expression of auxin-responsive genes in host–plant roots (Lakshmanan et al. 2013) resulting in stress tolerance in plants. Several authors have suggested the IAA production by PGPR as a mechanism to drought tolerance enhancement in crop plants such as maize, wheat, mung bean, etc. (Naveed et al. 2014; Sarma and Saikia 2014; García et al. 2017).

Gibberellins have a crucial function in plant growth such as stem elongation, germination, flowering, and senescence (Kaushal 2019). In contrast, cytokinins play a vital role in regulation of cell division and nutrient allocation, and maintain photosynthetic activity under drought stress (Ullah et al. 2019b). The application of cytokinin-producing PGPR, *Bacillus subtilis* in *Platycladus orientalis,* conferred drought stress tolerance by increasing shoot growth (Liu et al. 2013). Similarly, maize and soybean plants inoculated with gibberellin-producing PGPRs (*Pseudomonas putida* and *Azospirillum lipoferum*) registered improved plant growth under drought stress (Cohen et al. 2009; Kang et al. 2014). Consequently, there are evidences from many studies which advocate that PGPM have the ability to positively alter phytohormone levels of plant, leading to drought stress tolerance (Saakre et al. 2017; Ali et al. 2018).

12.4.5 Osmolytes Production and Alteration in Antioxidant Enzyme Activities

Water-deficit conditions result in altered osmotic balance in plants; hence, the water-absorbing capacity of plants get reduced and plant tries to change various physiological and biochemical processes for adaptation under stressed environment. Under

these conditions, plants tend to produce a wide range of osmolytes or commonly known as osmoprotectants. Some cellular events like protein and membrane stabilization are supported by osmoprotectants (Nahar et al. 2016). Due to their diverse chemical properties, osmolytes also protect plant cells from oxidative stress by attacking on ROS (Zhu 2002). There are several osmoregulators like proteins, sugars, and free amino acids reported to play a key role in balancing osmotic pressure in plant cells (Hasegawa et al. 2000). It is reported in various studies that microbes residing in soil also produce and secrete osmolytes when encounter to drought stress. These osmolytes function as produced by plants. Maize inoculated with *Pseudomonas fluorescence* growing under drought has potential for accumulating proline and resulted in increased water content and plant biomass (Ansary et al. 2012). Soil microbes also reported to alter the amount of osmoprotectants and antioxidant enzyme in plants (Kaushal 2019).

Plants in response to drought also generate various types of ROS oxidative damage by reacting with importing biomolecules like protein and lipids of cell. To protect from this oxidative damage, cell has developed antioxidant defense system which includes enzymatic as well as non-enzymatic pathway (Miller et al. 2010). Inoculation of plants with beneficial microbes suppresses the activity of antioxidant enzyme activity to alleviate the drought stress. Various species of *Pseudomonas* and *Bacillus* inoculated with maize are reported to reduce the activity of antioxidant enzymes when compared to un-inoculated plants under drought (Sandhya et al. 2010; Vardharajula et al. 2011).

12.4.6   Nutrient Availability

Water deficit can reduce the uptake of nutrients in the soil due to poor soil structure. PGPR and AMF have the capability to increase the accessibility of nutrient in the rhizosphere either by fixing nutrients (N_2) or by solubilizing insoluble minerals such as P, K, and Zn into the soluble form (Vejan et al. 2016). The explanation for enhanced nutrient status in AMF inoculation in plant has increased absorption surface of extraradical hyphae for extensive acquisition of nutrients from soil. The extraradical hyphae of AMF have a deep network into the soil readily absorption of nutrients which in turn is transported to arbuscules in cortical cells and are finally released into the apoplast to ameliorate nutrient deficiency caused by stress (Zhao et al. 2015; Kaushal 2019). Several reports suggest that PGPR inoculation can improve uptake of nutrients especially P under drought stress (Sandhya et al. 2010; Timmusk et al. 2014). In addition, there are evidences of increased mobility of nutrients (P, N, K, Ca, and Zn) in plants inoculated with AMF during drought stress (Gholamhoseini et al. 2013; Zhao et al. 2015; Abdel-Salam et al. 2018).

12.5 Modulation of Host Transcriptome by PGPR Inoculation

The PGPRs have been efficiently utilized in crops to alleviate disease stress. Nevertheless, they can also be used as potential targets for inducing drought tolerance in crop species. Physiological studies in few crop species suggest an efficient application of PGPRs to reduce drought stress (Khan et al. 2018; Niu et al. 2018) (Fig. 12.1). Drought stress is a complex trait which influences various cross-linked signaling between biotic and abiotic stresses. Hence, the beneficial effects of PGPRs in biotic stress can indirectly induce tolerance to drought stress. This mode of genetic improvement comprises understanding the PGPR-induced biochemical differential regulation. These biochemical changes are governed by differential expression of genes involved in induced systemic response (ISR), which are ultimately triggered through salicylic acid (SA)-signaling pathway (Zhang et al. 2002). The PGPR inoculation greatly modifies the transcriptome of the plant species, regulating expression of several genes (Rekha et al. 2018). Microarrays and RNA-seq studies have been employed in certain crop species to understand the molecular mechanism of PGPR-induced drought tolerance.

PGPRs often colonize the root surface and may induce production of several phytochemicals that regulate phytohormone signaling like auxins and ABA (Srivastava
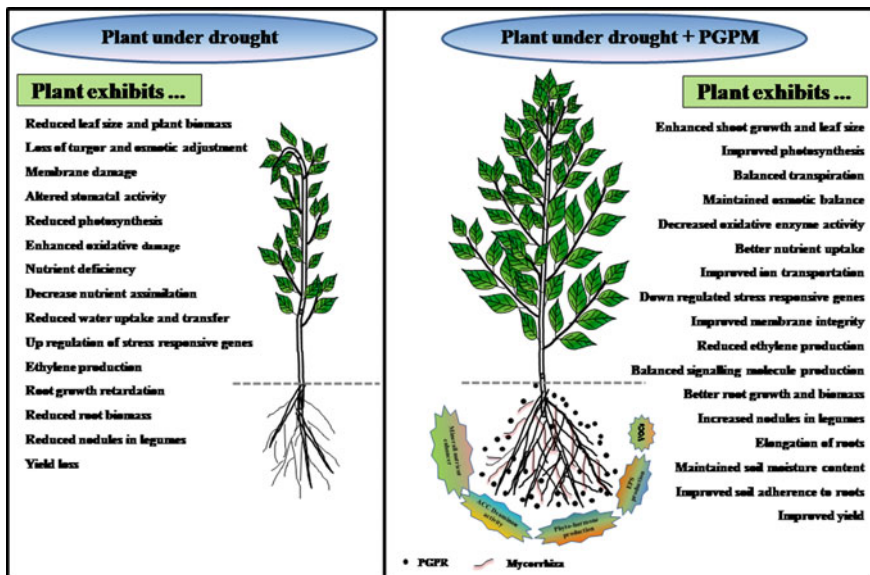

Fig. 12.1 Comparative account of effect of drought stress on plants without PGPM inoculation and with PGPR and AMF inoculation. The PGPR and AMF have envisaged diverse mechanisms for alleviation of drought stress in plants

et al. 2012). Systemic acquired resistance (SAR) is strongly regulated by phytohormones and their *in planta* levels. The inoculation of PGPR *Pseudomonas* sp. in rice plants induced the expression of LEA (late embryogenesis abundant) genes, which encodes IAA amido synthetases resulting in drought stress tolerance (Yasmin et al. 2017). Similarly, the inoculation of *A. thaliana* with PGPR *Paenibacillus polymyxa* induced drought tolerance through enhanced transcription of Early Responsive to Dehydration 15 (ERD15) gene (Timmusk and Wagner 1999). The drought alleviation by PGPR is mediated primarily through differential regulation of ABA-responsive pathway. The ABA-responsive signaling pathway transcription factor genes bZIP1, COC1, and Hsp20 proteins were overexpressed in susceptible rice cultivar upon PGPR *Pseudomonas fluorescens* inoculation, conferring drought tolerance (Saakre et al. 2017).

DHNs are a class of proteins of group 2 LEA proteins and proportionately related to their active accumulation during water stress tolerance. Microarray studies of barley seedlings overexpressing DHNs genes were drought-tolerant (Rodriguez et al. 2005). Plants expressing drought-tolerant CaDHN gene were highly expressed in pepper plant inoculated with PGPR *Bacillus licheniformis* (Lim and Kim 2013). DHN genes are interacting members of the SA-induced SAR response (Jing et al. 2016), commonly observed in PGPR-associated stress alleviation. The inoculation of water-stressed *A. thaliana* roots with *Pseudomonas chlororaphis* O6 induced an overexpression of LEA and dehydrin genes to over 100-folds (Cho et al. 2013). Trehalose is a nonreducing disaccharide, which is actively synthesized in bacteroids of *Rhizobium* sp. (Streeter 1985). It is an osmoprotectant and plays an essential role as a signaling molecule (Paul et al. 2008) during water stress management. The transformed *Rhizobium etli* and *Azospirillum brasilense* mutant with an overexpressing trehalose-6-phosphate synthase gene inoculated to *Phaseolus vulgaris* and maize, respectively, resulted in the enhanced expression of drought tolerance genes (Suárez et al. 2008; Rodríguez-Salazar et al. 2009).

To identify the transcriptional regulation of plants with drought stress in the presence of PGPRs, few transcriptomic studies have been undertaken. The PGPR inoculation improves drought stress tolerance by repressing the enhanced expression of abiotic stress response genes, viz., ABA and ethylene. The transcriptome study of sugarcane plants colonizing *Gluconacetobacter diazotrophicus* identified a reverse regulation of drought stress genes to that of stressed non-inoculated roots. The DREB1A/CBF3, DREB1B/CBF1, and NCED3 homologs were down-regulated in water-stressed plants treated with *G. diazotrophicus*. Although the auxin metabolism and ABA pathway were equally enriched in both the inoculated and non-inoculated plants, cytokinin hormone pathway up-regulation was observed only in the inoculated plants. However, the auxin, ABA, and ethylene-mediated stress-responsive signaling were mainly down-regulated (Vargas et al. 2014). Similar results have been demonstrated through transcriptome analysis of maize plants inoculated with *Pseudomonas putida* strain FBKV2 displayed drought stress alleviation, by Ali et al. (2018).

The expressions of ABA and ethylene signaling pathway genes were down-regulated, including down-regulation of bZIP transcription factor (TFs), and 1-aminocyclopropane-1-carboxylate synthase2 and ethylene-responsive TFs, respectively. The transcriptome of *A. thaliana* treated with PGPR *P. chlororaphis* O6 identified remarkable up-regulation of calmodulin and calcium-binding proteins. These genes play important role in cell-to-cell communication. The stress-responsive down-regulated genes in PGPR inoculation also include class of MYB and AP2 domain transcription factors (Cho et al. 2013). This clearly presents that plant growth-promoting bacteria reduce the drought stress by reducing the expression of stress-induced molecules, keeping optimum environment to plants. It is evident from several studies that PGPRs prime the stress-responsive pathway and following subjection of plants to drought stress reduces the production or biosynthesis of stress molecules.

12.6 Concluding Remarks and Future Prospects

Agricultural productivity is largely dependent on climatic conditions. Climate change is expected to reduce water accessibility for agriculture in coming years. Drought has the noxious effects on growth and development of plant. Hence, it is the need of the hour to search for the effectual solution to overcome the problem of drought stress in plants. Moreover, drought is a complex trait, so developing transgenic plants resistant to drought stress is also a challenging task. Under such stressful conditions, the interaction of plant and beneficial microorganisms is of great importance. The application of drought-tolerant PGPM has gained abundant attention as an alternative and eco-friendly option to mitigate drought stress in crop plants. Another effective option to combat drought stress in plant is the exogenous application of PGPM in combination with either the plant growth regulators (SA, JA, Trinexapacethyl, and ABA), polyamine-like putrescine, biochar (organic carbon), silicon nanoparticles, or seaweed extracts (Ali et al. 2017; Khan et al. 2019; Hashem et al. 2019).

In the current scenario, research must be concentrated to increase the number and diversity of effective and competitive drought-tolerant PGPM from drought-stricken agricultural ecosystems. The drought-tolerant PGPM could be useful to design new bio-inoculants/biofertilizers, especially for arid regions. Additionally, the performance of potential PGPR strains should be essentially assessed under field conditions, as plants usually face cyclic drought conditions rather than continuous drought. Further efforts are needed to develop proficient microbial consortia for enhancing plant growth under drought stress. Regardless of several findings, on the adaptation of plants under drought stress and their association with PGPM for mitigation of stress, substantial efforts are required to explore the underlying molecular mechanisms of interplay between plant and PGPM in soil to hasten the process of stress amelioration in crops. Thus, it could be concluded that the use of PGPM represents a promising approach to increase nutrient availability and expedite the development of sustainable agriculture under drought stress.

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