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Rhizobacteriome: Promising Candidate for Conferring Drought Tolerance in Crops

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Abstract

Drought is a global water shortage problem which poses challenge to crop productivity. Novel strategies are being tried to find out solution to sustain agriculture under drought conditions. Rhizobacteriome is an exclusive genetic material of bacteria resident to rhizosphere plays critical role to health and yield of plant. The interaction of rhizobacteriome with plant provides basis for protecting plants from various abiotic and biotic stresses. Plant growth promoting rhizobacteria (PGPR) are root-colonizing bacteria which produce array of enzymes and metabolites that assist plants to withstand harsh environmental conditions. Various formulations of rhizobacteria are being applied to enhance the tolerance or endurance to drought in crops which in turn increase crop productivity. This could be a one of the promising methods with wide potentiality to improve the growth and yield of crops under limited water resources and changing climatic conditions to ensure food security of the globe. In this review, we summarize (1) existing knowledge and understanding about the rhizobacteria, (2) their role in imparting tolerance to crops in drought conditions and (3) discuss future line of work in this frontier research area.

Keywords: Rhizobacteriome, bacteria- plant interactions, rhizosphere, drought stress, ACC deaminase, rhizobacteria

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INTRODUCTION

Drought stress has increased tremendously in last few years affecting food security at global level. The drought stress duration is ranged as short, severe, extremely severe and prolonged that adversely affects the agricultural productivity[1]. Drought is the most destructive abiotic stress which may affect crops of 50% of the arable lands by 2050[2]. It is a serious issue in the context of agricultural sector as it reduces crop yield in regions with scanty rainfall in various parts of the world[3]. Presently, various effective practices like efficient water irrigation techniques, conventional and modern plant breeding methods, and production of drought-tolerant transgenic plants through genetic engineering can be adopted to address the problem of sustainable crop production in drought situations. However, such techniques or procedures or methods need sophisticated technical knowhow and are costly and labor intensive as they are arduous to implement. An alternative method for promoting plant growth under drought conditions is to manipulate plant growth promoting rhizobacteria (PGPR) that are found in the rhizosphere and endorhizosphere in plant root systems. PGPR induces plant growth by various direct or indirect mechanisms under normal, biotic or abiotic stress conditions[4]. Rhizosphere is the area where, interaction among soil, plants and microorganisms take place. The microorganisms present in the rhizosphere, compete for their survival. This competition is for the need of nutrients, water and space to develop their association with plant. The plant-microbes interactions lead to the improvement in growth and development of plants[5]. Diverse bacterial genera form the important component of soils facilitating various biotic activities like recycling nutrient of the soil ecosystem which is essential for sustainable crop yield[6,7]. PGPR mobilize different nutritive components in soil, produce plant growth regulators and inhibit phytopathogens[8]. They also improve quality of soil by bioremediation of the pollutants by facilitating uptake of heavy toxic metal and degradation of xenobiotic compounds including pesticides[9,10]. Agronomists and environmentalists adapting various biological methods for integrated plant nutrient management system[11]. Rigorous research has been undertaken globally on exploring rhizobacteria possessing novel characteristics like ability to detoxify heavy metals[12], salinity tolerance[13], biological control of phytopathogens and insects[14] along with the plant growth promoting properties like, phytohormones production[15,16] phosphate solubilization[17],1-aminocyclopropane-1-carboxylate[18], hydrogen cyanide (HCN), and ammonia production[19] nitrogenase activity[20], siderophore[21] production. Hence, diverse groups of symbiotic bacteria like *Bradyrhizobium, Rhizobium, Mesorhizobium* and non-symbiotic like *Bacillus, Klebsiella, Pseudomonas, Azotobacter,Azomonas, Azospirillum* have been used worldwide as biofertilizer for promoting growth and development of plants under abiotic stress[22,7]. Although no single mechanism of rhizobacteria –mediated plant growth promotion is completely understood, however PGPR show significant contribution to the improvement in crop production[23].The potential of inoculated bacteria to survive, multiply to outnumber the native bacteria and other microflora, and colonize the rhizosphere is crucial for its successful application[22] specifically in drought-affected soils. The bacteria that are not adapted to drought conditions will die out under these unfavorable growth conditions[24,25]. But, the drought-tolerant rhizobacteria are capable of thriving in new drought stressed soil in sufficient number to show plant growth promoting manifestations on plants[26,27]. The present review highlights past and current status of role of rhizobacteriome on plant growth promotion under drought conditions. Further, it will also emphasize mechanisms associated with in conferring drought tolerance in crops on application of rhizobacteria.

Rhizosphere and rhizobacteriome

The term "rhizosphere" was first used by Hiltner[27]. Rhizosphere is multidimensional and dynamic region around root where significant plant-microbe interactions occur[28]. The root exudates alter the physicochemical properties of soil, which directly effects the multiplication of soil microorganisms[29]. These root exudates have ability to attract or repel microorganisms and promote symbiotic interactions which help in growth and development of plant[30]. PGPR are characterized by their capability to colonize the plant root surface, multiply, compete and survive to promote plant growth[31]. PGPR are broadly categorized into two classes: 1) ePGPR (extracellular PGPR) which grow in the rhizospheric area or in between cells of root cortex, examples include *Agrobacterium, Azotobacter, Erwinia, Serratia, Bacillus* etc. 2) iPGPR (intracellular PGPR) which grow inside root cells, examples include *Azorhizobium, Mesorhizobium, Allorhizobium etc*[24]. The entire set of genetic material of the root associated bacteria is called "rhizobacteriome".

The rhizosphere is hot spot for number of organisms which represent most complicated and dynamic ecosystems on the Earth[32,33]. Rhizosphere organisms consist of arthropods, archaea, viruses, algae, protozoa, nematodes, oomycetes, fungi and bacteria[34]. The rhizosphere examplifies complicated food web which utilise various nutrients produced by plants. Rhizosphere is identified by presence of exudates, border cells, mucilage called as rhizodeposits. Rhizodeposits represent diverse microbial community and microbial activity on plant roots[35]. However, the organisms of rhizosphere are analysed for their beneficial impact on growth and development of plants including nitrogen fixing bacteria, protozoa, mycoparasitic fungi, biocontrol microorganisms, fungi and plant growth promoting bacteria (PGPR)/ rhizobacteria. Some of organisms present in rhizosphere like nematodes, bacteria, oomycetes and pathogenic fungi, have adverse effects on growth of plants. Some human pathogens are also found in the rhizosphere[36]. Abiotic stresses have various impacts on rhizospheric bacteria. Total bacterial biomass decline under drought situations[37] resource limitation but stable biomass has been observed in certain cases of soil bacteria in drought condition[31] as repeated drought exposures make; bacteria to learn to survive[38].

Drought forces shift microbial composition in drought affected soil[39]. An increased ratio of Gram-positive to Gram-negative bacteria has been observed during water stressed conditions[40]. Drought affected soil decreases members of Gram-negative phyla like Proteobacteria, Verrucomicrobia, and Bacteroidetes and increases members of Gram-positive phyla like Actinobacteria and Firmicutes[41,42]. Also, the total numbers of genes of microbes present in the drought striken rhizosphere are exceeding the numbers of genes in plant in that area. Variation in metatranscriptome and metagenomics profiling of microbial genes related to metabolism, signal transduction and other vital activities of dry and well aerated soil suggests that microbial genes might contribute to plant survival and drought tolerance[43]. Some important

Table 1. Role of bacterial IAA on plant growth under drought stress condition

S.No.	PGPR	Plant	Impact on plant	Reference	Year
1.	*Azospirillum brasilense*	Tomato	Nitric oxide a signaling molecules and IAA pathway for induction of lateral and root hair growth	Molina-Favero *et al.*[52]	2008
2.	*Azospirillum* sp.	Wheat	Enhanced lateral roots, root growth, increased water and nutrient uptake	Arzanesh *et al.*[51]	2011
3.	*Pseudomonas putida, Bacillus megaterium*	*Trifolium repens*	Increased shoot and root mass	Marulanda *et al.*[57]	2009
4.	*B. thuringiensis*	*Lavandula dentate*	Increased levels of K-and proline, decresed glutathione reductase (GR) and ascorbate peroxidase (APX)	Armada *et al.* [55]	2014
5.	*Rhizobium phaseoli* (MR-2) *Mesorhizobium ciceri* (CR-30 and CR-39) and *Rhizobium phaseoli* (MR-2)	Wheat	IAA from consortia improved growth, biomass and drought tolerance index	Hussain *et al.*[56]	2014

members of rhizobacteriome are *Acinetobacter, Achromobacter, Agrobacterium, Alcaligenes, Arthrobacter, Azotobacter, Azospirillum, Bacillus, Bradyrhizobium, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Gluconacetobacter, Herbaspirillum, Klebsiella, Leclercia, Micrococcus, Paenibacillus, Phyllobacterium, Proteus, Pseudomonas, Raoultella, Rhizobium, Rhodococcus, Serratia, Variovorax* and *Xanthomonas*[24]. These rhizospheric bacteria show profound impact on germination of seed, plant growth, seedling vigor, development, diseases, nutrition and productivity[44].

PGPR and their drought tolerance mechanisms

PGPR induce tolerance to drought stress in crops by production of phytohormones, producing volatile compounds, ACC deaminase, osmolyte and exopolysaccharides, and triggering antioxidant activities.

Role of rhizobacterial phytohormones in drought stress tolerance

In drought stress, there is reduced production of phytohormones which inhibit normal plant growth. PGPR are capable for producing phytohormones that help to sustain growth and division of plant cell under abiotic environmental stress[45]. Phytohormones like indole -3-acetic acid (IAA), gibberellin (GA), cytokinin, abscisic acid and ethylene produced by rhizobacteriome become significant for promoting growth and development and helping plants to escape abiotic stress[46,47]. These pose as important targets for engineering metabolic products for conferring drought tolerance to crop plants[48].

Inoculation with various IAA producing bacteria enhanced lateral roots and roots hairs formation along with overall root growth, thus effecting increased water and nutrient uptake in drought conditions[49,50]. For example, IAA produced by *Azospirillum* increased plant ability to tolerate drought stress in maize and wheat[51], and by nitric oxide production in tomato[52]. The simultaneous production of siderophores and auxins by *Streptomyces* increases the plant growth-promoting effects of auxins, which in turn enhances the phytoremediation potential of plants[53]. A. *brasilense* Sp245 applied in wheat (*Triticum aestivum*) improved crop yield, micronutrients content, water content, water potential thus increased drought tolerance in plants[54]. *A.brasilense* also triggers nitric oxide signaling in IAA pathway and thereby improved growth of lateral root and root hair in tomato under drought stress[52]. *B.thuringiensis* improved nutritive value, physiological activities and metabolic activities of *Lavandula dentate* through IAA produced by the bacteria[54,55]. IAA signaling by consortium of *Rhizobium leguminosarum* (LR-30), *Mesorhizobium ciceri* (CR-30 and CR-39), and *Rhizobium phaseoli* (MR-2) inoculated in wheat improved crop[56]. Inoculation of *Pseudomonas putida, Pseudomonas* sp. and *Bacillus megaterium* increased water content and shoot / root biomass in *Trifolium repens* under water stressed conditions[57] (Table 1). *Bacillus subtilis*, *B. cereus, Enterobacter cloacae, Pseudomonas koreensis*, and *P. fluorescens* promoted seed germination by IAA production and phosphate solubilization under drought like condition induced by different concentrations of polyethylene glycol (PEG 6000)[58].

The capability of gibberellin producing bacteria to stimulate plant growth has also been well documented as it plays prominent role in various physiological processes. For example gibberellin produced by bacterial strains *B. macroides* CJ-29, *B. cereus* MJ-1, and *B. pumilus*

Table 2. Role of rhizobacterial gibberellin on plant growth under drought stress condition

S.No.	PGPR	Plant	Impact on plant	Reference	Year
1	*P. putida* H-2-3	Soybean	Improved plant growth using gibberellins	Sang-SM *et al.*[60]	2014b
2.	*Azospirillum lipoferum*	Maize	Gibberellins increased ABA levels and alleviated drought stress	Cohen *et al.*[50]	2009
3.	*B. cereus* MJ-1, *B. macroides* CJ-29, and *B. pumilus* CJ- 69	Pepper	Increased GA	Joo *et al.*[59]	2005

CJ enhanced the growth of red pepper plants[59]. Similarly, gibberrelin producing *P. putida* H-2–3, a increased growth of soybean plants in drought[60] (Table 2). *Azospirillum lipoferum* supported in mitigating activity of stress created by drought in plants of maize via yielding of ABA and gibberellin[50].

Under water deficit situation, biosynthesis of stress hormone i.e. ABA is triggered by dehydration conditions[61]. The involvement of ABA has been observed in regulating water loss through controlling the closing of stomata and transduction pathways of stress signals[62]. *Arabidopsis* plants showed elevated levels of ABA when inoculated with *A. brasilense* sp245[50]. *Phyllobacterium brassicacearum* strain STM196 isolated from the rhizosphere of *Brassica napus*, elevated ABA content leading to decreased leaf transpiration and enhanced osmotic stress tolerance in *Arabidopsis* plants[63]. Cytokinin producing *Bacillus subtilis* enhanced ABA in shoots and increased the stomatal conductance conferring drought stress resistance in *Platycladus orientalis* seedlings[64] (Table 3).

Cytokinin producing bacterial strains like *Pseudomonas* E2, *Bacillus licheniformis* Am2 and *Bacillus subtilis* BC1 reported to enhance cotyledon growth in cucumber[65]. Inoculation of lettuce with cytokinin producing bacteria increased shoot cytokinins and also promoted the accumulation of shoot mass and shortened roots[66]. Cytokinin producing *B. subtilis* strain IB-21 stimulate rhizodeposition for rhizobacterial colonization in the wheat rhizosphere[67,68](Table 4).

ACC deaminase production by rhizobacteria

Ethylene, a ubiquitous hormone in plants, plays role in seed germination, leaf abscission, ripening of fruits, senescence of leaf, initiation and elongation of roots, rhizobia nodule formation etc.[69,70]. In drought stress, synthesis of ethylene increase by conversion of S-adenosylmethionine (SAM) into 1-aminocylcopropene-1-carboxylase (ACC), the precursor of ethylene, in presence of ACC synthase[71]. PGPR act as sink of ACC by controlling ethylene formation using the ACC (1-aminocyclopropane-1-carboxylate) deaminase enzyme. These PGPR hydrolyse the ACC into ammonia and α-ketobutyrate, and thereby stimulate the expulsion of ACC from the roots to the soil[72]. Decreased ACC concentration in root further decreases the formation of endogenous ethylene preventing retardation in plant growth. Reducing ethylene-mediated inhibitory effects on plant growth and facilitate enhanced plant resistance to drought. *Achromobacter picchaudii* ARU8 secretes ACC deaminase that degrades ACC to ammonia for nitrogen and energy supply and thus decreases ethylene production under water deficit condition[73,74]. *Pseudomonas fluorescens, Enterobacter hormaechei*, and *Pseudomonas migulae* are three ACC and EPS producing microbes which when inoculated in foxtail millet could promote seedling germination in drought condition[75]. PGPR possessing ACC deaminase activity reduce toxicity of heavy metals, drought stress and other abiotic stresses like extreme temperature, salinity and soil pH, besides, antagonism against phytopathogens[76]. Dodd *et al.* (2005)[77] studied effect of ACC deaminase producing *Variovorax paradoxus* 5C-2 on pea plant physiological (*Pisum sativum L.*) in water conditions. Consortium of *Ochrobactrum. pseudogrignonense* RJ12, *Pseudomonas* sp. RJ15, and *B. subtilis* RJ46 showed mitigation of drought

Table 3. Role of rhizobacterial bacterial abscisic acid on plant growth under drought stress condition

S.No.	PGPR	Plant	Impact on plant	Reference	Year
1.	*Bacillus subtilis*	*Platycladus orientalis*	Increased shoot ABA levels and increased the stomatal conductance	Liu *et al.*[64]	2013
2.	*Phyllobacterium brassicacearum* STM 196	*Arabidopsis thaliana*	Reduced leaf transpiration due to increase level of ABA	Arzanesh *et al*[51]	2013
3.	*Azospirillum lipoferum*	Maize	Increased gibberellins and ABA levels	Cohen *et al.*[50]	2009

stress in garden pea and black gram plants[73]. *Leclercia adecarboxylata* and *Agrobacterium fabrum, Bacillus amyloliquifaciens* with higher ACC-deaminase and IAA production traits elevated nutrients uptake and high chlorophyll contents[78,79]. *Pseudomonas fluorescens* DR7 having high ACC deaminase- and EPS-producing ability increased moisture content in soil and enhanced the root adhering soil and root growth in foxtail millet[80]. Pot trials experiment showed that inoculation with ACC deaminase-producing bacterial strains of *Pseudomonas* (DPB13, DPB15, and DPB16) conferred vital improvement in growth of wheat plant in drought-stressed conditions[81,82]. Similarly, *Bacillus lecheniformis* K11 protected pepper and *Bacillus, Psuedomonas* and *Mesorhizobium ciceri* protected chickpea in drought stress[83,84,85] (Table 5).

Volatile organic compounds (VOCs) producing rhizobacteria and drought stress tolerance

Under stress condition, plants produce volatiles which act as signal for development of systemic response or for priming within the plant or in neighboring plants. VOCs that are produced by diverse group of bacteria *Pseudomonas, Bacillus, Arthrobacter, Stenotrophomonas*, and *Serratia* increase growth of plants, inhibit fungal and bacterial pathogens and nematodes along with inducing systematic resistance in plants towards phytopathogens[86]. Various VOCs produced by different species of microorganisms in soil include 11-decyldocosane, dotriacontane, 2,6,10-trimethyl, tetradecane, 1-chlorooctadecane, dodecane, benzene(1-methylnonadecyl),1-(N-phenylcarbamyl)-2-morpholinocyclohexene, decane, methyl, benzene, 2-(benzyloxy) ethanamine and cyclohexane[87].

Gram-positive *Bacillus* spp. (GB03 and IN937a) and Gram-negative *E. cloacae* strain JM22 elicited growth promotion of *Arabidopsis* seedlings through VOCs production[88]. Inoculated with *P. chlororaphis* O6 or exposed to 2,3-butanediol increased process of stomata closure and hence reduced loss of water in *Arabidopsis* plants thereby enhanced drought tolerance[89]. High rate of photosynthesis correlated with reduced VOCs production, enhanced survival under drought stress in plants primed with *Bacillus thuringiensis* AZP2. This proved that inoculation with bacterial improved drought stress tolerance[90] (Table 6).

Exopolysaccarides (EPS) producing rhizobacteria and drought tolerance

Many bacteria like *Pseudomonas* are capable of surviving in drought conditions due to development of exopolysaccharides (EPS). *Pseudomonas sp.* P45 produces EPS and protects sunflower plant from stress created by drought condition[91]. EPS consist of high molecular weight polymer of monosaccharide residues and their derivatives. These are biodegradable polymers biosynthesized by various algae, plants and bacteria[91]. Microbes produce EPS in capsular form and release it into the soil, the clay surface absorbs the EPS by Van der Waals force, hydrogen bonding, cation bridges or anionic absorption[92]. This protective capsule provides soil, the capacity of holding water and drying water more slowly under drought condition[93] and nutrients uptake by increasing the water potential around roots. Inoculating with EPS and catalase producing

Table 4. Role of cytokinin producing rhizobacteria on plant growth under drought stress condition

S.No.	PGPR	Plant	Impact on plant	Reference	Year
1.	*Bacillus subtilis* IB-21	Wheat	Stimulate rhizodeposition	Kudoyarova *et al.*[67]	2014
2.	*Micrococcus luteus*	*Zea mays*	Growth promotion	Raza and Faisal[68]	2013
3.	*Bacillus subtilis*	*Platycladus orientalis*	Stomatal conductance	Liu *et al.*[64]	2013
4.	*Bacillus*	*Lettuce*	Increased growth of plant	Arkhipova *et al.*[66]	2007
5.	*Pseudomonas, Bacillus* and *Azospirillum*	Maize	Increased spike length, tiller number and seeds weight	Hussain *et al.*[65]	2011

Mesorhizobium ciceri (CR-30 and CR-39), *Rhizobium leguminosarum* (LR-30), and *Rhizobium phaseoli* (MR-2) increased root length, biomass and drought tolerant index in seedlings of wheat in presence of polyethylene glycol (PEG) 6000 induced drought[94]. Priming of maize seeds with EPS- producing strains like *Alcaligenes faecalis* AF3, *Proteus penneri* Pp1 and *Pseudomonas aeruginosa* Pa2 increased root and shoot length, biomass of plants, and moisture content in soil[94]. Under dehydrated conditions, sunflower showed increase in root tissue when inoculated with EPS-producing bacterial strain YAAF34[95]. EPS play a pivotal role to maintain water potential, make sure obligate connection among rhizobacteria and roots in stress condition created by drought[96]. *Pseudomonas* sp. strain P45 improved soil structure through EPS formation to protect sunflower seedlings from dehydration[97,91]. Ghosh *et al.*, (2019)[98] observed four drought tolerant bacterial strains namely *Pseudomonas aeruginosa* PM389, *P. aeruginosa* ZNP1, *Bacillus endophyticus* J13 and *B. tequilensis* J12 were able to alleviate the deterimental effects of osmotic-stress induced in *Arabidopsis thaliana* by adding 25% PEG in agar medium. *Rhizobium* sp., *Xanthomonas* sp., *Agrobacterium* sp., *Enterobacter cloacae, Bacillus drentensis, Azotobacter vinelandii* and *Rhizobium leguminosarum* play significant function in improving fertility of soil thus sustain agriculture[99] (Table 7).

Role of osmolytes on drought tolerance in plants

Under water deficit condition, plants secrete different forms of osmolytes such as sugar, betaine, proline, polyhydric alcohol or other amino acids or dehydrin (drought stress protein)[100]. PGPR also release osmolytes in drought stress

Table 5. Role of ACC deaminase producing rhizobacteria on plants growth under drought stress condition

S.No.	PGPR	Plant	Impact on plant	Reference	Year
1.	*Agrobacterium fabrum, Bacillus amyloliquifaciens*	Wheat	Increased grain yield and biomass	Zafar *et al.*[79]	2019
2.	*Leclercia decarboxylata* and *A. fabrum*	Wheat	Elevated nutrients uptake and high chlorophyll contents	Danish *et al.*[78]	2019
3.	*O. pseudogrignonens* eRJ12, *Pseudomonas* sp. RJ15, and *B. subtilis* RJ46	Pea	Decreased ACC accumulation	Saika *et al.*[73]	2018
4.	*Pseudomonas fluorescens, Enterobacter hormaechei, Pseudomonas migulae*	Foxtail millet	Improved seed germination and seedling growth	Niu *et al.*[75]	2017
5.	*Psuedomonas flourescens* DPB15 and *P.palleroniana* DPB16	Wheat	Enhanced root and shoot growth	Chandra *et al.*[81]	2018
6.	*Variovorax paradoxus*	Pea	Reduction in ethylene production, increased growth, yield and efficiency of water use	Belimov *et al.*[82]	2009
7.	*Pseudomonas fluorescens*	Pea	Enhanced water uptake and induced longer roots	Zahir *et al.*[83]	2008
8.	Variovorax *paradoxus*	Pea	Increased yield, nitrogen content and number of seed	Dodd *et al.*[77]	2005
9.	*Achromobacter piechaudii*	Tomato and Pepper	Increased fresh and dry weight	Mayak *et al.*[74]	2004
10.	*B. licheniformis*	Pepper	Increased expression of stress genes	Lim and Kim[84]	2013
11.	*Bacillus* and *Pseudomonas* with *Mesorhizobium ciceris*	Chickpea	Increased concentration of proline, improved root and shoot, length, seed germination	Sharma *et al.*[85]	2013

condition (Table 8). These osmolytes interact with those produced by plants and enhance growth of plants[101]. These secreted solutes trap water molecules which help in decreasing the hydric potential of cells. This kind of regulation is known as osmoregulation. These accumulated solutes increase membrane integrity and protein stability to counteract cellular damage. *Bacillus* spp. effects osmoregulation by preventing electrolyte leakage and enhancing proline synthesis, sugars, free amino acids accumulation[102]. The function of the osmolytes is to prevent water molecules loss by reducing the cell water potential during drought period. Also, osmolytes help in protecting cellular damage by maintaining the integrity and stability of membranes and proteins in water scarce condition. PGPR consortia lessened the effect of drought stress in rice crop by accumulation of proline which improved the plant growth[103].

Inoculation of *B. thuringiensis* (Bt) in *L. dentate* showed increased shoot proline content in water shortage conditions[55]. Similarly, phosphate solubilizing bacteria *Bacillus polymyxa* secreted excess proline in tomato plants to induce drought tolerance[104]. Sandhaya *et al.* (2010b)[105] showed that priming cultivars of rice with consortia containing *Pseudomonas jessenii* R62, *Pseudomonas synxantha* R81 and *Arthrobacter nitroguajacolicus* strain YB3 and YB5 increased plant growth in drought area. This consortium enhanced proline accumulation in plants by up regulating its biosynthetic pathway hence preserving cell water potential, stabilizing the cell membrane and protein during drought stress[105]. It has been reported that enhanced concentration of osmolytes like proline, betaine, glutamate, glycine and trehalose stimulated by *Azospirillum* help plants to overcome osmotic stress[106]. Similarly, *A. lipoferum* metabolic activities lead to accumulation of free amino acids and soluble sugars thus improving maize growth in drought[107]. *Pseudomonas putida* GAP-P45 enhance plant biomass, relative water content and leaf water potential by stimulating accumulation of proline in maize plants in drought conditions[97]. *Azospirillium* spp. z19 made maize seedling to tolerate drought stress to a higher level as compared to uninoculated plants due to higher proline levels[108]. Evidences of increased biosynthesis and accumulation of choline, a precursor of gibberellin (GB), showed increased biosynthesis in maize when inoculated with *Klebsiella variicola* F2, P. *fluorescens* YX2 and *Raoultella planticola* YL2.This resulted in upgraded level GB thereby bettering leaf relative water content (RWC) and dry matter weight (DMW)[109,110]. Inoculating plants with PGPR increases existing concentrations of proline in maize plants by *P. fluorescens* under drought stress[111]. *Phaseolus vulgaris* plants inoculated with *Rhizobium* showed improved metabolism of carbon and nitrogen and upregulation of trehalose-6-phosphate synthase gene[112,113]. *Pseudomonas putida* GAP-P45 showed upgraded expression of polyamine biosynthetic genes (*ADC, AIH, CPA, SPDS, SPMS and SAMDC*) and polyamine levels in *Arabidopsis thaliana* during drought stress[114,98].

Role of rhizobacteria on antioxidant defense system for induction of drought tolerance

During normal growth of plant, ROS is produced at low level. Stress condition results into overproduction of ROS which causes oxidative damage. ROS affects signalling, transport, metabolism and biosynthesis of auxin. It also interacts with phytohormones production process, for example, H_2O_2 causes ethylene production. In response to the stress condition, antioxidant

Table 6. Role of rhizobacterial-VOCs on plant growth under drought stress condition

S.No.	PGPR	Plant	Impact on plant	Reference	Year
1.	*Bacillus thuringiensis*	Wheat	Increased rate of photosynthesis and reduction in emission of volatiles	Timmusk *et al.*[90]	2014
2.	*Pseudomonas chlororaphis*	*Arabidopsis thaliana*	Prevent loss of water by stomatal closure	Cho *et al.*[89]	2008
3.	*Bacillus* spp. (GB03) and (IN937a), *Enterobacter cloacae* JM22	*Arabidopsis thaliana*	Phenotypic improvement	Zhang *et al.*[88]	2010

Table 7. Effect of rhizobacterial-EPS on plant growth under drought stress condition

S. No.	PGPR	Plant	Impact on plant	Reference	Year
1.	*Pseudomonas aeruginosa* PM389, *P. aeruginosa* ZNP1, *Bacillus endophyticus* J13 and *B. tequilensis* J12	*Arabidopsis thaliana*	Increased in IAA, cytokinin, gibberellins, and EPS secretion	Ghosh *et al.*[99]	2019
2.	*Proteus perneri, Pseudomonas aeruginosa, Alcaligenes faecalis*	Maize	Enhanced protein, proline, sugar and relative water content	Naseem & Bano[93]	2014
3.	*R. leguminosarum, M. ciceri* and *R. phaseoli*	Wheat	Promoted growth of plant, drought tolerance index and biomass	Hussain *et al.*[56]	2014
4.	*Bacillus thuringienesis*	Wheat	Production of alginate resulted into drought tolerance	Timmusk *et al.*[90]	2014
5.	*Pseudomonas* sp.	Sunflower	Enhanced plant biomass, RAS/RT ratio	Sandhya *et al.*[91]	2009
6.	*P. putida*	Maize	Improved physiological response	Vardharajul *et al.*[96]	2009
7.	*Rhizobium* sp. YAS34	Sunflower	Enhanced ratio of RAS/RT (Root adhering soil per root tissue)	Alami *et al.*[95]	2000

defense system is used by plants, in which plants produce various enzymatic and non-enzymatic antioxidants[115]. It has been observed that enzymatic activities lead to reduction of oxidative damage but at very high level of ROS, it can results into deleterious effects[116]. Thus, it is important to maintain balance between ROS production and annihilation of free radicals produced[117]. This can be done by using PGPR and their inoculation to plants shows higher survival rate by preventing oxidative damage than those which were not inoculated with PGPR.

Pseudomonas sp. is reported to improve catalase activity in drought stress condition in basil plants (*Ocimum basilicum* L.). Similarly, *Pseudomonas* sp., *Bacillus lentus* and *A. brasilense* consortium induce high activity of glutathione peroxidase and ascorbate peroxidase in *Ocimum basilicum* L.[118]. Consortium of PGPR containing *P. jessenii* R62, *P. synxantha* R81 and *A. nitroguajacolicus* strainYB3 and YB5 improved growth of plant along with inducing superoxide dismutase, catalase (CAT), peroxidase (PX), ascorbate peroxidase (APX) and lowering H_2O_2, malondialdehyde (MDA) in Sahbhagi (drought tolerance) and IR-64 (drought sensitive) rice crop[103]. *Pseudomonas* spp. namely *P. entomophila, P. stutzeri, P. putida, P. syringae* and *P. montelli* are responsible for reducing action of antioxidant enzymes significantly in maize under drought stress[97]. *Bacillus* species have also shown protection against drought stress by decreasing antioxidant enzymes APX and glutathione peroxidase (GPX)[96]. *B. thuringiensis* (Bt) improved growth via drought avoidance and reduction of glutathione reductase (GR) and ascorbate peroxidase (APX) activity in *Lavandula dentata* and *Salvia officinalis* in drought conditions[55]. *Streptomyces pactum* Act12 treatment in wheat increased osmoregulation and antioxidant efficiency of plants. *Bacillus pumilus* DH-11 and *B. firmus* 40 induced ROS-scavenging enzymes like ascorbate peroxidase and catalase in tomato plants. A remarkable increase in antioxidant enzymes like APX, SOD, and CAT was evident under drought stress in PGPR treated plants compared with non-treated plants[119,120]. Increased activity of CAT in green gram plants inoculated with *Pseudomonas fluorescens* Pf1 and *Bacillus subtilis* EPB was reported by Saravanakumar *et al.* (2011)[121]. Similarly, increased level of CAT production and drought tolerance has also been correlated in cucumber[122] and maize[96,98,123]. Up-regulation of expression of drought resistance-related genes like EXPA2, EXPA6, P5CS, SAMSI HSP17.8 and SnRK2 and accumulation of abscisic acid mitigated drought stress impact in wheat[124,119]. These experimental evidences proves that PGPR have significant role in increasing plant tolerance towards drought (Table 9).

Table 8. Effect of osmolytes of PGPR on plant growth in drought stress condition

S. No.	PGPR	Plant	Impact on plant	Reference	Year
1.	*Pseudomonas putida* GAP-P45	*Arabidopsis thaliana*	Enhanced polyamine biosynthetic genes	Sen *et al.*[114] Ghosh *et al.*[98]	2018
2.	*Azospirillium* spp AZ39 and ,AZ19)	Maize	Increased proline	Garcia *et al.*[108]	2017
3.	*Bacillus polymyxa*	*Lycopersicon esculentum*	Increased production of proline	Shintu and Jayaram[104]	2015
4.	Consortia of *P. jessenii, P. synxantha* and *A. nitroguajacolicus*	*Oryza sativa*	Improved plant growth because of proline accumulation	Gusain *et al.*[103]	2015
5.	*Klebsiella variicola, P. fluorescens* and *Raoultella planticola*	Maize	Improved RWC in leaf due to gibberellin and choline accumulation	Gou *et al.*[109]	2015
6.	*B. thuringiensis*	*Lavandula dentate*	Enhanced physiological, nutritional and metabolic activities	Armada *et al.*[56]	2014
7.	*Azospirillum lipoferum*	Maize	Free amino acids and soluble sugars accumulation lead to improved growth of plant	Bano *et al.*[107]	2013
8.	*P. fluorescens*	Maize	Improved growth of plant due to increased proline and phytohormones content	Ansary *et al.*[111]	2012
9.	*Pseudomnas putida*	Maize	Improved RWC, leaf water potential	Sandhya *et al.*[105]	2010
10.	*Bacillus subtilis*(GB03)	*Arabidopsis*	Increased glycine, betaine and choline content	Zhang *et al.*[88]	2010
11.	*Azospirillum brasilense*	Maize	Increased synthesis of trehalose	Rodriguez *et al.*[106]	2009
12.	*Rhizobium etli*	*Phaseolus vulgaris*	Increased synthesis of trehalose	Suarez *et al.*[112]	2008

Table 9. Role of antioxidant activity of PGPR in drought tolerance in plants

S. No.	PGPR	Plant	Impact on plant	Reference	Year
1.	*Streptomyces pactum*	Wheat	ABA accumulation upregulation of drought resistant related genes	Li *et al.*[119]	2019
2.	*Pseudomonas* spp.	Wheat	Prevent oxidative damage	Chandra *et al.*[81]	2012
3.	*Pseudomonas putida* MTCC5279 (RA)	Chickpea	Reduced/controlled the expression of stress response gene, increased ROS scavenging (CAT, APX, GST)		2016
4.	*P. jessenii, P. synxantha, A. nitroguajacolicus*	Rice	Enhanced growth of plants, induced SOD, CAT, POD, APX, reduced H_2O_2, MDA level	Gusain *et al.*[103]	2015
5.	*B. thuringiensis*	*Lavandula dentate* and *Salvia officinalis*	Enhanced growth of plant, reduced GR, APX activity	Armada *et al.*[55]	2014
6.	EPS producing bacteria	Maize	Reduced APX, CAT and GPX activity	Naseem and Bano[94]	2014
7.	*Pseudomonas* sp. GGRJ21	Mung beans	Enhanced CAT, POX and SOD activity	Sarma and Saikia[123]	2014
8.	*Bacillus amyloliquefaciens* 5113 and *Azospirillum brasilense* N040	Wheat	Increased fresh and dry weights, Antioxidant enzymes, enhanced of stress response genes APX1, SAMS1, and HSP17.8	Kasim *et al.*[124]	2013
9.	*Serratia* sp., *Bacillus cereus, B. subtilis*	Cucumber	Chlorophyll content increased, increased CAT	Wang *et al.*[122]	2012
10.	*Bacillus* sp.	Maize	Lower APX, GPX activity	Vardharajula *et al.*[96]	2011
11.	*Pseudomonas sp., Bacillus lentus, A. brasilense, Pseudomonas* sp.,	*Ocimum basilicum* L.	Enhanced activity of CAT enzyme, Enhanced GPA and APX activity	Heidari and Golpayegani[118]	2011
12.	*Pseudomonas fluorescens* strain Pf1 *Bacillus subtilis* EPB5, EPB22, and EPB 31	Green gram	Stress-related enzymes Proline content	Saravana kumar *et al.*[121]	2011

Table 10. Stress responsive genes induction by rhizobacteria and molecular techniques involved in their analysis

S. No.	PGPR	Plant	Technique involved	Impact on plant	Reference	Year
1.	*Gluconobacter diazotrophicus*	Sugarcane	Illumina sequencing	Activation of ABA dependent signaling genes	Vargas *et al.*[136]	2014
2.	*P. chlororaphis*	*Arabidopsis thaliana*	Microarray analysis	Up regulation of transcripts of jasmonic acid-marker genes, pdf-1.2 and VSP1, salicylic acid regulated gene (PR-),Ethylene response gene (HEL)	Cho *et al.*[137]	2013
3.	*Bacillus amyloliquefaciens, A. brasilense*	Wheat	Real time PCR	Stress related genes (APX1, HSP 17.8, SAMS1) up regulated	Kasim *et al.*[124]	2013
4.	*B. licheniformis*	Pepper	2D-PAGE, DD-PCR	Enhanced stress response genes (Cadhn, sHSP, CaPR-10 and VA)	Lim and Kim[84]	2013

Molecular mechanism of drought stress tolerance induced by rhizobacteria

In water deficit conditions, gene induction forms two different types of proteins: functional proteins and regulatory proteins. Functional proteins include mRNA binding proteins, LEA proteins, water channel proteins, enzymes for osmolytes biosynthesis, proteases etc[125]. They function directly in abiotic stresses. On the other hand, regulatory proteins include protein kinase, calmodulin binding protein, phosphatase and other transcription factors. These are involved in stress responsive genes expression and signal transduction[126]. Hsps are heat shock proteins which inhibit misfolding of protein and are classified according to their molecular weight [127]. LEA proteins are the proteins which accumulate during late embryonic phase in response to abiotic stress. Plants inoculated with PGPR helps in up regulation of stress tolerance inducing genes. Various molecular strategies have established the mechanism of microbes induced gene expression modulation for abiotic stress tolerance. The differential expression of multiple genes such as *COX1* (regulates energy and carbohydrate metabolism), *ERD15* (*Early response to dehydration 15*), *PKDP* (protein kinase), *AP2-EREBP* (stress responsive pathway), *Hsp20, bZIP1* and *COC1*(chaperones in ABA signalling) in *Pseudomonas fluorescens* treated rice was established. Similarly RAB18 (ABA-responsive gene), *LbKT1, LbSKOR* (encoding potassium channels) in *Lycium barbarum*, jasmonate MYC2 gene in chickpea, *ADC, AIH, CPA, SPDS,SPMS* and *SAMDC* (polyamine biosynthesis), *ACO, ACS* (ethylene biosynthesis), *PR1* (SA regulated gene), pdf1.2 (JA marker genes) and *VSP1* (ethylene-response gene) in *Pseudomonas* treated *Arabidopsis* plants were established for drought tolerance[125,128,129]. Molecular networks of signal transduction genes are also involved in drought stress responses[130,131].

There are different molecular techniques which give huge amount of information about induced genes expressions and pathways during plant and rhizobacteria interactions. The techniques include high throughput whole genome gene expression such as microarrays, proteomics, RNA sequencing, 2D-PAGE, differential display[132,133]. This helps in exploring physiological functions of such genes and tolerance induced by PGPR[134]. Upregulation of *EARLY RESPONSE TO DEHYDRATION 15 (ERD15)* in *Arabidopsis thaliana* was seen when inoculated with *Paenibacillus polymyxa* B2 as investigated at transcriptional level[135]. Pepper plants when inoculated with *Bacillus* showed more than 1.5-folds increase in Cadhn, VA, sHSP and CaPR-1084. Inoculation of *Bacillus amyloliquefaciens* 5113 and *A. brasilense* NO40 alleviating the deleterious impact of drought stress in leaves of wheat by upregulation of stress response genes APX1, SAMS1, and HSP17.8. These upregulated genes enhanced plant ascorbate–glutathione redox cycle help in alleviating drought stress[124]. Bacterial priming of *Gluconacetobacter diazotrophicus* PAL5 stimulated the ABA-dependent signalling genes which confer tolerance to drought in sugarcane cv. SP70-1143 as studied by Illumina sequencing (HiSeq 2000 system)[135,136] (Table 10). In *Pseudomonas chlororaphis* colonized *Arabidopsis thaliana* plants, upregulated but differential expression of jasmonic acid-marker genes, *VSP1* and *pdf-1.2*, salicylic acid regulated gene, PR-1 and the ethylene-response gene, was observed[137].

In the past several decades, researchers have been able develop many resistant varieties of plant species, but they have gained a very little success in development of drought tolerant crops using genetic engineering[138]. Monsanto introduced

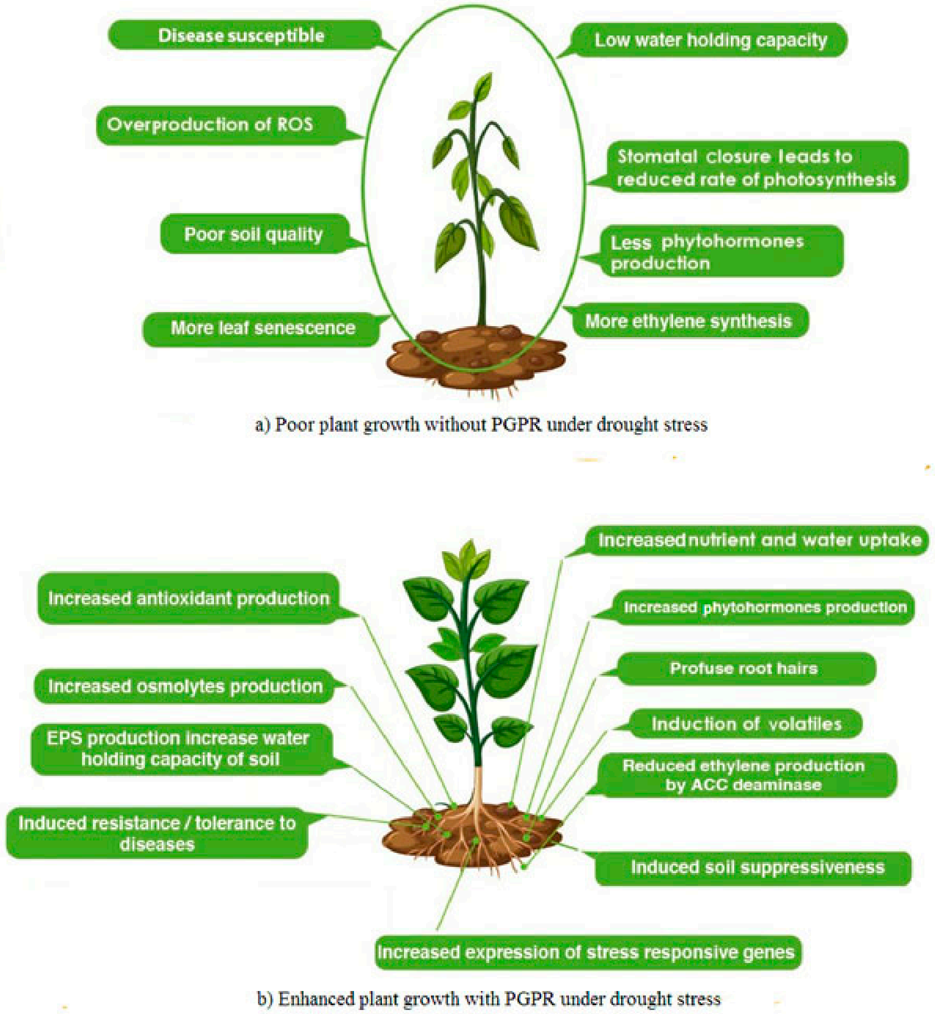

Fig. 1. Strategies used by PGPR to modulate plant growth under stress conditions (a) Poor plant growth without PGPR and (b) Enhanced plant growth with PGPR

GM crop MON 87460, a maize (*Zea mays* L), in 2009 which was drought stress tolerant. This crop increased production 5.5-folds from 50,000 ha in 2013 to 275,000 ha in 2014. Cold shock protein B (CSPB) inserted from *Bacillus subtilis* in MON 87460 expresses to imparted drought tolerance[139,140]. In bacteria, cold shock proteins help in preserving normal cellular functions by stabilizing cellular RNA and enhancing gene expression under abiotic stress[141]. Similarly, the translation of CSPB have been reported to enhance tolerance to abiotic stress in *Arabidopsis* and rice[142]. Another important gene OsNLI-IF overexpressed by cold, heat, salt and drought stresses improved drought tolerance in transgenic tobacco plants[143]. Argentina developed genetically modified soybean contains a gene from a naturally drought-resistant sunflower adapted to drought. Rhizospheric microbes not only support the growth of plants in limited water conditions but also reduce use of chemical fertilisers.

The rhizosphere research field is flooded with metagenomics and metabolomics data, establishing genes identity and their functional taxonomic relationships. Scientists are putting their research efforts on developing consortia of microbes and metabolites of microbial origin in the formulations that best suited for individual crops in stressed environment[144].

CONCLUSION

In this review, we have attempted to highlights the existing knowledge of plant-bacterial interactions in maintaining plant growth under drought stress. To overcome drought conditions, plants adapt various morphological, biochemical and physiological changes. Now, it has been established that members of the rhizospheric bacteria can alleviate abiotic stress of drought in plants. This can be a promising alternative to tedious and costly genetic engineering and plant breeding methods. This review establishes that various PGPR play significant role in inducing tolerance to drought stress in plants employing different mechanisms. The rhizobacterial induced drought stress tolerance in the plant is over and above the drought resistance genes either present or absent in the plant (Fig. 1).

Future Perspectives

Future research should be undertaken to increase crop yield, soil fertility and shelf life of products of PGPRs. Drought stress is a severe environmental factor that limits agricultural productivity. Rhizobacteriome offer plethora of PGPR in imparting adaptation and tolerance to drought stresses and prove to be promising strategy to improve productivity in drought areas. The plant and rhizobacteria interaction changes plant as well as soil properties in drought conditions. Rhizobacterial stimulation of osmotic responses and induction of novel genes expression play a significant role in ensuring plant survival under drought stress conditions. The development of drought tolerant crop varieties through genetic engineering and plant breeding approaches is good option but it is a labor intensive, lengthy and costly affair. Alternately, rhizobacteria inoculation to mitigate drought stresses in plants is environment friendly and safe option for agriculture drought affected areas. Future research must focus on (1) identification and characterization of the novel abiotic stress-tolerant bacteria from unexplored niches, (2) discover novel bacteria with novel molecule or mechanism, (3) better formulation with appropriate delivery system and (4) perform rigorous field trial in order to select potential rhizobacterial candidate to combat drought stress.

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The authors declare that there is no conflict of interest.

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DATA AVAILABILITY

All datasets generated or analyzed during this study are included in the manuscript.

ETHICS STATEMENT

This article does not contain any studies with human participants or animals performed by any of the authors.

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