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Review

Plant growth promoting rhizobacteria-mediated amelioration of drought in crop plants

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Abstract

Water scarcity is one of the major global issues brought about by climate change. Besides creating socio-economic challenges, drought and osmotic stress generated by these abnormal weather conditions results in decreased agricultural productivity and deterioration of cultivable land resources. Different agronomic practices and strategies such as genetic approaches, and the use of beneficial microbes have been adopted to tackle the effects of these severe conditions. In the rhizosphere, plant-microbe interactions benefit plants through nitrogen fixation, phosphorus solubilization, microbial biofilm association with plant roots, production of antioxidants, siderophores and phytohormones, induced systemic resistance against plant pathogens and 1-aminocyclopropane 1-carboxylic acid (ACC)-deaminase activities. Inoculation of plant growth promoting rhizobacteria (PGPR) is a low cost and environment friendly biotechnology with a high probability of success in the field, and the potential to increase crop (wheat) yield by up to 18%. PGPR has the capability to survive drought and osmotic stress conditions and could be more effective at mitigating the negative impacts of drought on agricultural crops. This review highlights rhizobacteria survival, their interactions with plants under drought stress, and the ability of the PGPR's potential mechanisms to alleviate drought stress impacts by improving physiology, growth and yield of crop plants. However, multi character bacteria, or genetic manipulation used to develop strains of bacteria with multiple characteristics, could be a more effective future approach.

Keywords: Rhizobacteria, drought, crop plants, phytohormones, biofilm, antioxidants

Introduction

Water scarcity and reductions in precipitation are some of the major issues of climate change. Osmotic and drought stresses resulting from these environmental changes are causing loss of crop yields (Verma *et al*. 2016). According to one estimate, the agriculture sector remains a major consumer of global fresh water resources, claiming about 56% of the global withdrawals, thereby creating serious risk of increased water scarcity in future (Alcamo *et al*. 2000). Due to a fall in ground water tables, river and spring flows, and lake water levels, various regions of the world are going to dry out and suffer desertification e.g., levels in the water tables of the North China plain, which supply water for the grain harvest, are starting to decrease at higher rates. In United States, which is third largest grain producer in the world, increased urbanization requires more water for agriculture. For example, the population of California will increase from 26 to 40 million by 2030 (Norton, 2003). In India and Pakistan, water scarcity is creating a food security risk and a reduction in life expectancy (Norton, 2003). In arid to semi-arid climates like Mediterranean dry lands, the production of food legumes (i.e. faba bean, lentil, and chickpea) has been reduced due to terminal drought events. Even in non-dry land countries such as Brazil, where sufficient moisture is available for legume cultivation, water deficiency for few weeks a year leads to significant losses in crop yields (Oya *et al*. 2004). It is predicted that about 38% land is going to be converted into desert due to water shortage (Nunez *et al*. 2010). The situation, therefore, will be highly alarming for the countries situated in arid and semi-arid zones of the world. Failure to fulfill the food, feed, fiber, and fuel demands of the increasing population will result in increasing problematic socio-economic crises; especially in developing countries.

Rainfed agriculture is an important economic activity in developing countries. At world level, rainfed agriculture is responsible for 62% of the production of staple foods (FAOSTAT, 2005; Bhattacharya, 2008). Rainfed agriculture land is affected by the amount and distribution of rainfall in that area (Kadigi *et al*., 2004). Poor rainfall distribution together with drought periods, especially inter-seasonal dry

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spells, cause moisture scarcity (Paavola, 2003; Tilya and Mhita, 2006), which may become life threatening for the people living in semi-arid areas (DFID, 2001). Drought causes severe impacts on crop productivity (Grayson, 2013; Fang *et al*. 2015; Lesk *et al*. 2016). Drought in terms of agriculture is a period of below average precipitation in a given region resulting in prolonged shortage in water supply. Drought is a multidimensional stress which occurs for several reasons (high and low temperature, low rainfall, salinity and high intensity of light) that could cause failure of the crops to grow normally (Mohr and Schopfer, 1995). According to one estimate, global wheat and maize productivity are declining by 5.5 and 3.8%, respectively, due to increasing temperature and decreasing water availability (Lobell *et al*. 2011). In semi-arid and arid regions of the world, irrigation requirements will be increased by 10% for every 1°C rise in temperature (Grover *et al*. 2011). At the same time, a decrease in moisture availability and increase in drought stress will create a serious threat and constrain plant growth for about 50% of the world's arable land by the year of 2050 (Vinocur and Altman, 2005; Ngumbi and Kloepper, 2016). Global cereal production is thus projected to decline from 1.9 to 0.9% between 2007 and 2050 due to the reduction in irrigation water supplies (Alexandratos and Bruinsma, 2012).

Global fresh water shortages demand that serious efforts be made to improve crop production in dry, arid and drought prone areas by adopting novel agronomic and biotechnological approaches. Various approaches and strategies adopted to overcome drought stress on plants have included agronomic practices, genetic engineering and use of beneficial microbes. The interaction of PGPR with plant roots, and its consequent positive impacts on plant growth under stressed and non-stressed conditions, have been very well explored and understood. Bacterial inoculation technology could help plants withstand and overcome the problem of drought stress. Besides providing an account of various physiological, biochemical, agronomic and morphological impacts of drought stress on plants, this review examines strategies that have been adopted to overcome the problem and discusses the types of interactions between plants and bacteria under water-deficit condition. Depending on above mentioned perspectives, useful collection of the research work regarding the different rhizobacterial mechanisms to improve growth and/ or yield of crops (legumes and non-legumes/ cereals) under drought stress is presented in Table 2 and 3.

Crop experiences under drought stress

Water stress decreases crop yields by affecting the physiological, morphological, and agronomic characteristics of crop plants. Physiological impacts of water deficit stress include (i) reduced uptake-efficiency of photosynthetically active radiation (PAR) (ii) decreased canopy-absorption of PAR and (iii) lower harvest index (Earl and Davis, 2003). Drought stress causes leaf senescence (biological aging) and stomata closure by decreasing the cell turgor pressure (Alcazar *et al*. 2011). Drought conditions lead to the production of reactive oxygen-species (ROS) like hydrogen peroxide, singlet oxygen and super oxide dismutase (Tallapragada *et al*. 2016) which damage plants severely through enzyme inactivation, membrane decomposition, oxidation of DNA, membrane lipids and proteins denaturation, and alteration in normal gene expression (Fang *et al*. 2015; Jajic *et al*. 2015). Chlorophyll contents are reduced during drought conditions because of chlorophyll-peroxidation. Moreover, leaf senescence also disturbs the photosynthesis and chlorophyll properties (Ma *et al*. 2012; Kaushal and Wani, 2016). Under prolonged drought, ethylene, produced at an increased level, hampers root growth, which ultimately affects plant growth (Sharp and Le Noble, 2002; Pierik *et al*. 2007). Water deficit hampers the uptake of inorganic ions and nutrients through reduced transpiration and unloading mechanisms (Garg, 2003; McWilliams, 2003; Ullah *et al*., 2016; Egamberdieva *et al*. 2017). From a morphological and agronomical point of view, water-deficit stress affects seed yield, plant height, dry weight and stem diameter of the crops (Ghaffari *et al*. 2012; Egamberdieva *et al*. 2017). During water deficit stress, seed-germination and seedling-stand is severely affected (Kaya *et al*. 2006). Drought reduces cereal yield by affecting crop growth and development. For example, in maize, it delays silking and enhances kernel abortion during pollination and inhibits endosperm development, ultimately reducing grain yield (Morgan, 1990; Ober *et al*. 1991).

Under drought conditions, plants may adopt variety of morphological, bio-chemical and physiological mechanisms and / or strategies to cope with a sessile life style. For example, the accumulation of compatible solutes, stomata closure by increasing the concentration of abscisic acid (ABA), and expression of aquaporins for the adjustment of cell turgidity (Bartels and Sunkat, 2005; Marasco *et al*. 2013; Fang *et al*. 2015). In constitutive tolerance against drought, a plant goes through genetic adaptations which are the response of physiological and morphological adaptations. For example, xerophytes reduce their transpiration rate through sunken stomata and thick cuticle, and C4 plants have high water use efficiency. These characteristics allow xerophytic plants to flourish well under dry conditions, where other plants would fail to grow. Many mosses, lichens and some flowering plants can decrease their water content by up to 90% and enter into dormancy or a metabolic-resting state without any injury, while more than 30% water loss causes the death of mesophytes. An

average mesophyte shows wilting symptoms with 15-20% of water loss, furthermore, -15 bars of soil water-potential (ψ_{soil}) leads to the continuous wilting of plant leaves, and plants fail to rescue their growth, which is referred to as the permanent wilting point.

Abscisic acid (ABA), which is a stress hormone, plays vital role in the induction of drought tolerance in mesophytes. Under drought, ABA is synthesized endogenously in roots and translocated towards shoots, where it regulates water balance and growth of the plant. In osmotic adaptation, drought stress increases the cell water-potential (ψ_{cell}) through active accumulation of osmotic compounds, including organic species (amino acids, sugars) and inorganic species such as NO_3^-, Cl^-, K^+ in cytoplasm and cell sap, ultimately avoiding damage to cytoplasmic components under dehydration. Hence, the potential-gradient between soil and plant is developed which stimulates water uptake by the roots (Mohr and Schopfer, 1995). During water deficit stress, plants can show two different behaviors; isohydric or anisohydric. Isohydric plants keep their leaf water potential constant under both normal and drought conditions, through lowering their stomatal conductance, whereas anisohydric plants have variable leaf water potential, more stomatal opening and a higher rate of photosynthesis for longer periods, even under reduced leaf water potential. Thereby, anisohydric plants are considered to be more water deficit tolerant than isohydric plants (Sade *et al*. 2012). Plant adaptation is very rapid and is reversed when a sufficient amount of water becomes accessible. This type of resistance against water deficit occurs during long periods of drought stress. This hardening process impairs many plant functions such as triggering ABA synthesis to close stomata and cell wall extensibility of growing plants. This demonstrates that during stress conditions these type of plants use different physiological and biochemical response mechanisms to adapt and survive.

Microbial inoculation to combat drought stress

Rhizobacterial inoculation to ameliorate water deficit stress in plants is a growing field of interest. PGPR are beneficial soil bacteria which improve plant growth and development and colonize the narrow zone of plant roots (rhizosphere). PGPR are a heterogeneous group of bacteria that must be able to (i) colonize the plant roots, (ii) compete with other microbes that have similar potential, and (iii) augment plant growth using different promoting/protecting mechanisms (Kloepper, 1994; Rahmoune *et al*. 2016). Their

Table 1: Bacterial mechanisms to survive under low water contents

Bacterial sp.	Survival mechanism	Reference
Rhizobium trifolii T 19C	Enhanced CAT activity	Goyal *et al*. (1986)
Rhizobium meliloti strain 31	Modification in cell morphology	Busse and Bottomley (1989)
Rhizobium meliloti 102F34	Osmolyte accumulation (trehalose, glutamate)	Smith and Smith (1989)
E. coli K-12	EPS production	Ophir and Gutnick (1994)
Bradyrhizobium japonicum 3.2	Modulation / improvement in fatty acid composition of membrane-phospholipids	Boumahdi *et al*. (2001)
Salmonella enterica strain ATCC 14028	Biosynthesis of cellulose and/ or fimbriae	White *et al*. (2006)
Pseudomonas putida strain mt-2	EPS and Biofilm formation	Chang *et al*. (2007)
Salmonella enteric *serovar Typhimurium SJW1103*	Expression of lipopolysaccharide	Garmiri *et al*. (2008)
Rhizobium etli strain Ox	Overexpression of trehalose-6-phosphatase synthase gene	Suarez *et al*. (2008)
Rhizobium leguminosarum bv. *Viciae* 3841	Up regulation of ABC-transporter triggered biofilm (EPS) formation	Vanderlinde *et al*. (2010)
Azospirillum lipoferum AZ9	SID production	Arzanesh *et al*. (2011)
Rhizobium leguminosarum LR-30	EPS, CAT	Hussain *et al*. (2014)
Rhizobium legumniosarum SRL5, *Mesorhizobium cicrae* SRC8	CAT, EPS	Ullah *et al*. (2017)
Ochrobactrum pseudogrignonense strain RJ12, *Pseudomonas* sp. RJ15, *Bacillus subtilis* RJ46	IAA, HCN, SID, P.S, N-fixation efficiency	Saikia *et al*. (2018)

EPS: Exopolysaccharides, HCN: Hydrogen cyanide, SID: Siderophores production, ACCD: 1-aminocyclopropane-1-carboxylate deaminase, P.S: Phosphate solubilization, IAA: Indol acetic acid, CAT: Catalase.

plant-growth-promoting and protecting activities include the production of phytohoromones (e.g., IAA, gibberellins, ethylene, abscisic acid), ACC-deaminase, volatile organic compounds, nutrient acquisition, exopolysaccharides (EPS), biofilm formation and induced systemic resistance (ISR). These mechanisms could be very beneficial to aid plant growth under normal, as well as in stressful, environmental conditions (Conrath *et al*. 2006; Dimkpa *et al*. 2009; Yang *et al*. 2009; Verma *et al*. 2016; Kaushal and Wani, 2016; Singh and Trivedi, 2017; Saikia *et al*. 2018). Literature has confirmed a number of identified strains of PGPR which play a significant role in improving growth and yield of agricultural crop plants such as *Rhizobium*, *Serratia*, *Bacillus*, *Arthrobactor*, *Azospirillum*, *Burkholderia*, *Azotobactor*, *Enterobactor*, *Flavobacterium*, *Beijerinckia*, *Erwinia*, *Acinetobacter*, *Pseudomonas* and *Alcaligenses* (Burd *et al*. 2000; Chaiharn *et al*. 2008; Yang *et al*. 2009; Bharti *et al*. 2013; Jamil *et al*. 2018; Chandra *et al*. 2018). Harmful impacts of drought stress (agronomic and physiological) on plant growth and development, and their amelioration by PGPR is presented in Figure 1.

Survival of bacteria under drought stress

Different environmental factors influence the composition and diversity of rhizobacterial population and the rhizobacterial interactions with the plants. Bacteria can probably survive under drought conditions because of their abilities to produce and accumulate stress proteins such as heat shock proteins, EPS, dehydrin, volatile organic compounds, antioxidants, siderophores, alginate or cell envelop and organic osmolytes (Van de Mortel and Halverson, 2004; Abolhasani *et al*. 2010; Vanderlinde *et al*. 2010; Arzanesh *et al*. 2011; Naylor and Coleman-Derr, 2018), Table 1. Osmolytes include different organic compounds such as glycine betaine, glutamine, proline, ectoine and trehalose which maintain the cell turgor potential, and protect against the oxidation of macromolecules under stress (Welsh, 2000; Bouskill *et al*. 2016). Bacteria carry out the process of sporulation under water scare conditions and become dormant until favorable conditions available (Acosta-Martinez *et al*. 2014). Thickening of the cell wall layer or / and peptidoglycan layering play a vital role in survival during drought periods (Schimel *et al*. 2007). Exopolysaccharides perform various vital functions of stress protection like surface attachment, microbial aggregation or biofilm formation, bioremediation and stimulation interactions with plants (Manca de Nadra *et al*. 1985). Under desiccation or nutrient limitation, bacteria like *Azospirillum* bring some morphological changes in their cells i.e., enlargement of cells cyst-like forms accompanied by the release of poly-β-hydroxy-butyrate and the formation of an outer covering of polysaccharide units. In addition to protection, poly-β-hydroxybutyrate and polysaccharides might be used as a source of energy and carbon under unfavorable stressed conditions (Sadasivan and Neyra, 1985; Tal and Okon, 1985; Sadasivan and Neyra, 1987). Hussain *et al*. (2014) investigated whether the production of EPS and catalase enzyme enhanced the survival of rhizobial isolates (*R. leguminosarum* LR-30, *R. phaseoli* MR-2, *M. ciceri* CR-30) under drought stress (-2.18 MPa) imposed by PEG-6000, Table 1. Marulanda *et al*. (2009) said PGPR like *B. megaterium* and *P. putida* produce growth regulators and proline which help bacteria to tolerate drought conditions.

Rhizobacteria-plant interactions under drought stress

A thorough understanding of rhizospheric-interactions is very important to increase the resilience of the agro-ecosystem against climate change and to maximize crop productivity under harsh conditions (drought, salinity, heavy metal pollution, and temperature stress). In the rhizosphere, diverse types of soil organisms (earthworms, centipedes, millipedes, arthropods, bacteria, algae, fungi) are present and may come into contact with plants to interact and play a significant role in sustainable crop production (Dubey *et al*. 2016). Rhizospheric bacterial interactions with plants may be harmful, beneficial, or neutral. However, beneficial interactions in which bacteria act as plant growth promoters may be disturbed under drought stress. A well-known interaction like symbiosis may also become ineffective under drought.

Endophytic interaction

Endophytic beneficial bacteria promote plant growth while residing within the plant body where they get a protective and suitable environment for better growth compared to bacteria which interact with those plants epiphytically. Endophytes colonize internal plant tissues instead of external surfaces (as in rhizobacteria) and promote plant growth and development in the same way as rhizobacteria through direct (i.e. nutrient availability) and indirect mechanisms (i.e. resistance against diseases) (Cindy *et al*. 2002). It is well documented that these endophytic bacteria are able to enhance plant growth under drought stress. For example, the inoculation of endophytic beneficial bacterial strains (*Enterobacter* sp. FD17 and *Burkholderia phytofirmans* PsJN) efficiently induced drought resilience in maize by colonizing internal portions of root, shoot and leaves (Naveed *et al*. 2014a).

Symbiotic interaction

In this interaction, bacteria form specialized structures with the roots, stems or leaves of the plants. Rhizobia, for example, are well known for atmospheric N_2-fixation in legume plants through a symbiotic relationship, but rhizobia also enhance the growth of non-legumes through root colonization under normal as well as stress conditions (Alami *et al*. 2000). Bacteria can fix nitrogen in either free or symbiotic relationships in which they entrap atmospheric nitrogen into NH_3 to be utilized by the plants. This process is carried out by an enzyme called nitrogenase which is sensitive to oxygen (Bhattacharjee *et al*. 2008). Naturally, various rhizobia form symbiotic relationships with legume plants and are present in the plant body as endophytes such as *Azorhizobium*, *Rhizobium*, *Allorhizobium Mesorhizobium* and *Bradyrhizobium* (Bhattacharjee *et al*. 2008). Polania *et al*. (2016) observed the symbiotic nitrogen fixation (SNF) by *Rhizobium* sp. in common bean using the N^{15} technique. Water deficit reduces SNF by affecting oxygen availability, the feedback of oxygen accumulation and carbon supply between Rhizobial sp. and the host plant (Serraj *et al*. 1999). Thereby, in addition to the application of drought resistant rhizobacterial sp., the selection of a drought resistant crop variety would be a better approach for dry land agriculture.

Asymbiotic and associative interaction

Free living or associative PGPR are bacteria which have the ability to augment plant growth by colonizing plant roots. Free living bacteria release certain proteins (glycoproteins) and have special organs (pili) which help them to attach to plant roots (colonization) (Steenhoudt and Vanderleyden, 2000). Free living bacteria show positive chemo-taxis and are attracted towards root-exudates (Heinrich and Hess, 1985), aromatic compounds (Lopez-de-Victoria and Lovell, 1993), amino acids, organic acids, and sugars (Barak *et al*. 1983; Reinhold *et al*. 1985) moving with the help of flagella (Moens *et al*. 1995) which may benefit rhizobium and PGPR colonization on plant roots. Bacterial interaction with plant roots has been shown to induce plant adaptation in harsh environments. Drought stress tolerance induction by PGPR was first investigated by Timmusk and Wagner (1999). They inoculated *Arabidopsis*

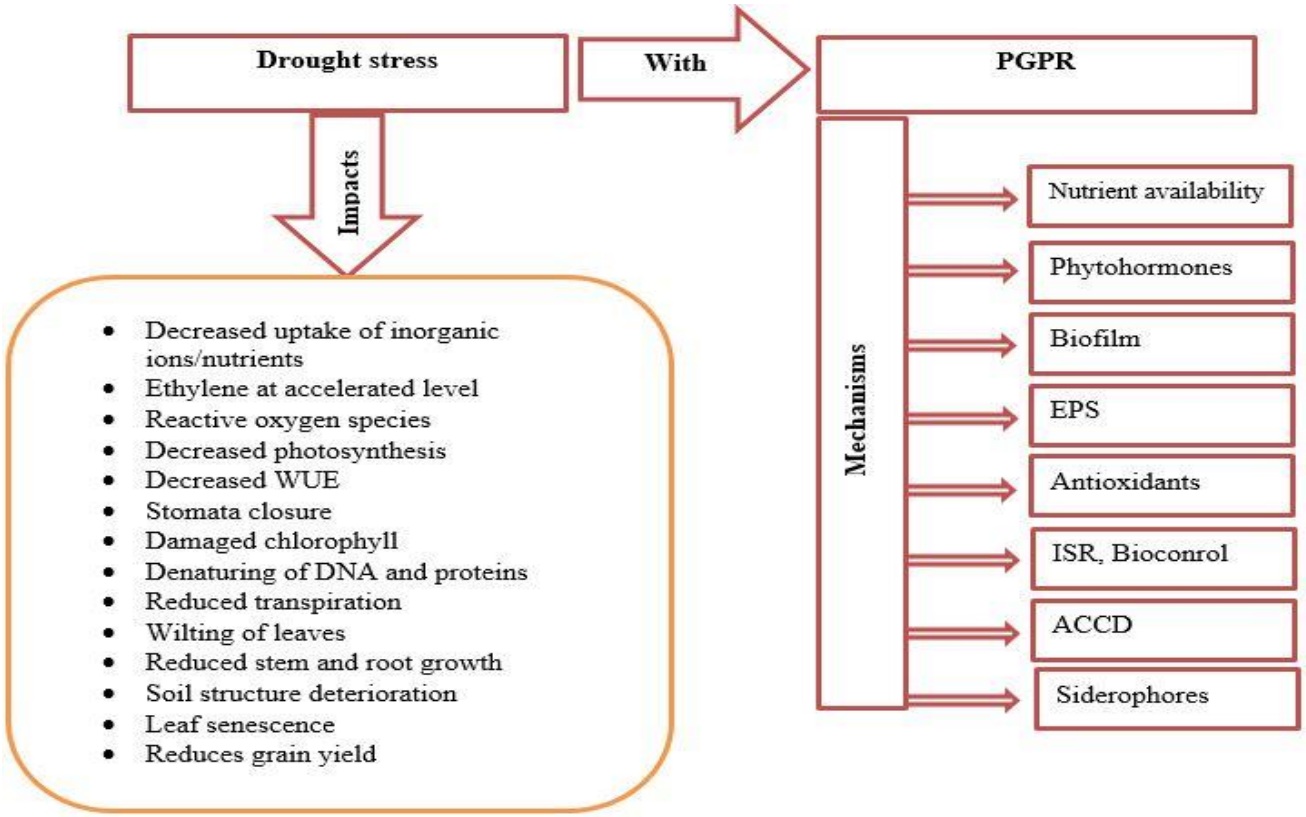

Figure 1. Harmful impacts of drought stress (agronomic and physiological) on plant growth and development, and amelioration of stress impacts through various mechanisms of PGPR

thaliana with a PGPR *Paenibacillus polymyxa* in gnobiotic conditions and found a changed/increased expression of drought stress responsive gene ERD15, showing that inoculated plants were more resistant than un-inoculated control. Moreover, rhizobia work as PGPR for non-legumes or cereals under stress conditions. Ample reports in literature are available which evidenced substantial amelioration of drought stress through asymbiotic/ associative interactions between PGPR and crop plants such as wheat (Alvarez *et al*. 1996; Khalid *et al*. 2004; Afzal and Bano, 2008; Asghar *et al*., 2015), maize (Vardharajul *et al*. 2011), sugarcane (Vargas *et al*. 2014), barley (Cakmakci *et al*. 2007), sunflower (Alami *et al*. 2000; Sandhya *et al*. 2009), common bean (Figueiredo *et al*. 2008), *Pisum sativum* (Andrey *et al*. 2009), Black gram (Saikia *et al*. 2018), *B. juncia* (Asghar *et al*. 2002), *Lactuca sativa* (Kohler *et al*. 2008), cucumber (Wei *et al*. 1995; Wang *et al*. 2012), Arabidopsis (Bresson *et al*. 2013), tomato and pepper (Tallapragada *et al*. 2016; Ibort *et al*. 2018).

Bacterial species involved in above mentioned interactions (endophytic, symbiotic, asymbiotic and associative) act as PGPR to enhance plant growth and development.

Rhizobacterial mechanisms to enhance plant growth under drought stress

It is evident from the above arguments that rhizobacteria possessing growth promoting potential could ameliorate abiotic stress impacts ultimately enhancing plant growth and development through several mechanisms which are discussed in the following section.

Nutrient availability

Plants require essential nutrient elements for their normal growth and production. These are divided into groups as per their plant requirement; those required in large quantities, macro, (C, H, O, N, P, K, Ca, Mg, S) and those required in smaller amounts, micro, (Fe, Zn, Cu, Mn, Mo, Cl, B). Among these essential nutrients H, C, N, and O are easily available from air and water at optimum level. Although soil contains diverse types of reserves of these essential elements, more than 90% are not available to plants due to inaccessibility and being bound within insoluble compounds. However, these nutrients can be made available by using a mineral fertilizer source (organic, biological, or chemical). Microbial inocula as biofertilizers reduce the need for chemical fertilizers by improving the soil fertility status through different soil processes i.e. mineralization, decomposition, and the release/storage of essential nutrients, with no negative influence on the environment (Roy *et al*. 2006). PGPR perform the process of associative N_2-fixation in different non-legume crops such as maize, sugar beet, wheat, rice and sugar cane (Sahin *et al*. 2004; Jha and Saraf, 2015). Alami *et al*. (2000) inoculated the seeds of a non-legume (sunflower) with EPS-generating *Rhizobium* sp. to check their efficiency of the associative N_2-fixation by using ^{15}N-nitrate under normal, as well as water deficit stress conditions. Results showed that EPS production improved N-assimilation (12%) under water deficit due to the increased bacterial population on roots, modified soil structure / improved porosity, and good diffusion rate of nitrate toward roots. Alami *et al*. (2000) confirmed improved N_2-fixation through associative interaction between *Rhizobium* sp. and sunflower under drought stress.

Soil can be rich in phosphorus from organic and inorganic material reserves, but it may not be available to plants due to fixation with Mg, Ca in alkaline soil and Fe, Al in acidic soils. P-solubilizing microbes like bacteria can enhance P availability by lowering the pH through release of organic acids (citric, oxalic, lactic, tartaric, malic and gulonic acid) or H^+ (Illmer and Schinner, 1995; Jha and Saraf, 2015). Rodriguez *et al*. (2004) investigated P-solubilization by *Azospirillum* sp. (*A. lipoferum* JA4 and *A. brasilense* 8-I) via the production of gluconic acid and proton release (which reduced the pH) from sparingly soluble P-source (Ca-phosphate) amended with bacterial food (glucose). Except for *Azospiriullum*, other species which are able to solubilize the inorganic and insoluble phosphate compounds include *Pseudomonas, Aereobacter, Rhizobium, Erwinia, Achromobacter, Agrobacterium, Bacillus, Burkholderia, Microccocus and Flavobacterium*.

K-solubilizing bacteria release organic acids which make the K available through exchange reactions, acidolysis or a decrease in pH and complexolysis, increasing its accessibility for plants from minerals such as muscovite, biotite, feldspar and mica (Sheng and Huang, 2002; Sheng and He, 2006; Uroz *et al*. 2009). Positive effects of rhizobacteria on nutrient availability were related to root adhering soil (RAS), and root morphology such as the length of lateral roots, root hairs, and root hair numbers (Tien *et al*. 1979). Rhizobacteria release siderophores and solubilize inorganic phosphate stimulating the phosphatase-activity of the root system thereby enhancing nutrient availability under stress conditions (Kohler *et al*. 2008; Wang *et al*. 2012). Ortiz *et al*. (2015) confirmed the enhanced uptake of both macro and micro nutrients including P, K, Ca, Mg, Zn and B in *Trifolium repens* through bacterial inoculation in soil that was facing water deficit stress (Table 2). Furthermore, Armada et el. (2014) investigated rhizobacterial (*Bacillus thuringiensis*) potential to increase nutrient availability (Ca, Mg, K, Cu, Zn, and Mn) in *Lavandula dentate* under arid conditions. Nutrients made available due to rhizobacterial-enzymes (nitrogenase, phosphatase) and organic acids. Sharma and Johri (2003) demonstrated siderophores production by *P. Chlororaphis*

ATCC 9446 and *Pseudomonas* sp. PRS9 under iron-limited condition, moreover, seed bacterization of these strains resulted in substantial improvement in growth of maize plants. Plant nutrition can be further improved by genetic manipulation of PGPR for colonizing plant roots under drought stress.

Table 2: Influence of rhizobacterial inoculations on non-legumes and cereals

Crop	Rhizobacterial sp.	Inoculation method, experiment type	Improvement (%) in crop parameters over control	Mechanism of action	References
Capsicum annum L.	*Klebsiella* strains R01ACCd, R05ACCd and R15ACCd), *Achromobacter strain* R10ACCd, *Acinetobacter* strain R04ACCd, *Citrobacter* Strain R16ACCd	Root, Phytotron	Root fresh weight (60) Biomass production (40) Photosynthesis (40)	In vitro PGP activities (ACCD) with drought resistant potential, improved photosynthetic activity and biomass	Marasco *et al*. (2012)
	Bacillus licheniformis K11	Root, Greenhouse	Plant survival (80) Dry weight (up to 80) Root length (up to 13) Shoot length (up to 18)	Activation of drought responsive protein genes (VA, CaPR-10, Cadhn, sHSP) with ACCD potential	Lim and Kim (2013)
Arabidopsis thaliana (L.) Heynh	*Paenibacillus polymyxa* strain B2	Root, Gnotobiotic system	Induction of systemic resistance	Expression of drought responsive gene ERD15	Timmusk and Wagner (1999)
Cucumis sativus L.	*Serratia* sp. XY21, *Bacillus cereus* AR156 and *Bacillus subtilis* M21	Soil, Greenhouse	Chlorophyll a (25) Chlorophyll b (31) Chlorophyll a+b (27) MDA reduction (38) Relative EC (14)	Down regulate the expression of genes rbcl, cAPX and rbcs (ascorbate peroxidase and rubisco) reduced MDA levels, triggered ISR and enhanced chlorophyll contents	Wang *et al*. (2012)
Vitis vinifera L.	*Acineto bacter* sp. S2	Root, Greenhouse	Shoot biomass (81.2) Plant length (57)	Drought tolerance and PGP (EPS, IAA, SID, P.S) potential enhanced plant growth and biomass	Rolli *et al*. (2014)
Platycla dusrientalis (L.)	*Bacillus subtilis* KC428746	Growth medium (Perlite, Peat, vermiculite, fertilizer), Phytotron	CYT (10.22) Shoot dry weight (19.23) Total sugars (85) Organic acid (33.12) Amino acid (18.29) LWP (11.46) RWC (7.18)	CYT potential promoted growth and physiology	Liu *et al*. (2013)
Lavandula dentate L.	*Bacillus thuringiensis* (*Bt*)	Soil, Field	Shoot dry weight (67.69) Root dry weight (41.66)	Increased K-contents decreased GR and APX activity, controlled proline accumulation, lower down the stomatal conductance and oxidative damage	Armada *et al*. (2014)

Triticum aestivum L.	*B. amyloliquefaciens* S-134 *B. muralis* D-5 *E. aerogenes* S-10	Seed, Greenhouse	Shoot length (35) Spike length (34) Seed weight (100)	IAA production efficiency enhanced shoot length of stressed plants	Raheem *et al.* (2017)
	Rhizobium legumniosarum SRL5, *Mesorhizobium cicrae* SRC8	Seed, Greenhouse	Tillers (166) Straw yield (32) Grain yield (48) WUE (36) RWC (32) PR (106) TR (52) Chl 'a' (168) Chl 'b' (126)	Various PGP activities (SID, IAA, P.S, EPS, CAT) augmented physiology and growth of stressed plants	Ullah *et al.* (2017)
	Dietzia natronolimnaea (STR1), *Arthrobacter protophormiae* (SA3),	Roots, C.T room	IAA (80) Shoot length (≈18) Shoot dry weight (≈25)	Modulation of IAA and ethylene level through expression of genes (*TaCTR1/TaDREB2*)	Barnawal *et al.* (2017)
	Burkholderia phytofirmans (strain *PsJN*)	Seed, Field	Grain yield (18) 100 grain weight (16) Straw yield (23) Proteins (11-16) GR activity (77) CAT activity (78) Electrolyte leakage reduction (7-8)	Improved antioxidant and physiological activity of wheat plants	Naveed *et al.* (2014b)
	Rhizobium leguminosarum (LR-30)	Seed, Phytotron	Shoot length (100) Root length (79) Shoot fresh weight (>100) Root fresh weight (>100)	Proposed different PGP traits (EPS, CAT, IAA, Sid, good microbial cell-aggregation) augmented growth of droughted plants	Hussain *et al.* (2014)
	Azospirillum brasilense Sp245	Root, Phytotron	Xylem-vessels area (10^{-2} mm^2) Coleoptiles basal segments (≈31) Coleoptiles apical segments (≈21)	Inoculation resulted wider xylem-vessels which improved the hydraulic conductance of coleoptiles of water-stressed seedlings	Pereyra *et al.* (2012)
	Pantoea agglomerans (strain NAS206)	Seed, C.T room	RAS macro porosity (pore diameter up to 30 μm)	EPS	Amellal *et al.* (1998)
Helianthus annus L	*Rhizobium* sp. (strain YAS34)	Seed, Phytotron	Shoot dry mass (13.19) Root dry mass (10.13) RAS (79)	EPS-producing ability gave more root-adhering-soil (RAS) and growth	Alami *et al.* (2000)

	Pseudomonas putida strain GAP-P45	Seed, Phytotron	Root dry biomass (45.1) Total dry biomass (64.6) RWC (26.35) RAS/RT (49.8)	Rhizobacteria with PGP activities (HCN, EPS, biofilm, Ammonia, Sid, P.S, GIB, IAA,) counteracted the negative impact of drought stress by improving RAS/RT ratio ultimately plant growth	Sandhya *et al*. (2009)
Solanum lycopersicum L.	*Achromobacter piechaudii* ARV8	Root, Phytotron	Fresh weight (≈95) Dry weight (≈100) RWC (≈6)	ACCD efficiency decreased the ethylene	Mayak *et al*. (2004)
Lactuca sativa L	*Bacillus* sp. (strain IB-22)	Sand, C.T-Room	Root dry weight (25) Shoot dry weight (50) Shoot CYT (30)	Inocula gave adaptive drought resilience to lettuce plants due to decreased conc. of CYT in root/shoot ratio leads to stomatal closure and more carbon allocation to roots eventually enhancing plant growth under transient water stress	Arkhipova *et al*. (2007)
Zea mays L	*Enterobacter* sp. FD17 *Burkholderia phytofirmans* PsJN	Seed, Greenhouse	No. of leaves (24) Leaf area (20) Plant biomass (up to 66) Root mass (70) Photosynthetic rate (75) Stomatal conductance (87) transpiration rate (84) chlorophyll contents (22) RWC (30) RMPreduction (43)	Inoculation reduced H_2O_2 production in plants	Naveed *et al*. (2014a)
	Pseudomonas entomophila (strain BV-P13) *Pseudomonas stutzeri* (strain GRFHAP-P14) *Pseudomonas putida* (strain GAP-P45) *Pseudomonas syringe* (strain GRFHYTP52) *Pseudomonas monteilli* (strain WAPP53)	Seed, Phytotron	Root length (up to 48.08) Shoot length (up to 44.11) Total dry biomass (up to 60.36) RAS/RT- ratio (up to 56.72) APX activity (57.4) Proline (6.3 fold)	Drought-resistant rhizobacteria capable for producing IAA, P.S, Sid, GIB, and HCN caused higher antioxidant activity and osmolytes (sugar, proline, amino-acids) production, and RAS/RT ratio eventually better growth and biomass	Sandhya *et al*. (2010)

	Bacillus spp. strains HYD-B17, BKB30, RMPB44 and HYTAPB18 and HYDGRFB19	Seed, Phytotron	Root length (45) Shoot length (42) Total dry biomass (59.06) Electrolyte leakage reduction (65) APX activity (60) Leaf area (127) RWC (45)	Osmo-resistant (-0.73 MPa) rhizobacterial efficiency to produce EPS, amino acids, sugars and prolines improved the physiology (reduced electrolyte leakage and antioxidant activity) of stressed plants, thereby, increased plant growth	Vardharajula *et al*. (2011)
Eleusine coracana Gaertn	Pseudomonas sp. strain DPB13, DPB15, DPB16	Seed, Greenhouse	Shoot length (24.1) Root length (29.9) Shoot fresh wt. (48.6) Root fresh wt. (49.8) Total chl. (59.9) Proline (56) MDA reduction (53) SOD (33.8) CAT (36) APX (33) GPX (47)	ACCD, SID, P.S., IAA potential	Chandra *et al*. (2018)

RWC: Relative water contents, LWP: Leaf water potential, EPS: Exopolysaccharides, IAA: Indol acetic acid, SID: Siderophores, ACCD: 1-aminocyclopropane-1-carboxylate deaminase, P.S: Phosphate solubilization, CAT: Catalase, HCN: Hydrogen cyanide, CYT: Cytokinins, GIB: Gibberellins, RAS/RT: Root adhering soil per root tissue, PR: Photosynthetic rate, TR: Transpiration rate, HCN: Hydrogen Cyanide, SOD: Superoxide dismutase, GPX: Guaiacol peroxidase, APX: Ascorbate peroxidase, RMP: Relative membrane permeability, MDA: Malondialdehyde, C.T: Controlled Temperature, WUE: Water Use Efficiency
*Parenthesis show percent improvement or increase over control.

Plant growth regulators-drought stress signaling molecules

Under drought stress, plants produce signaling molecules including enzymes, compatible solutes, and abscisic acid to close their stomata in order to avoid severe water losses. These mechanisms are very helpful in maintaining cell turgidity (Bartels *et al*. 2005). Especially, the phytohormones (auxins, gibberillin, and abscisic acid) play a vital role in the growth and development of crop plants under stress, as well as normal conditions. Auxins (IAA) increase the surface area of roots and root tips thereby helping them to endure water deficiency during osmotic or drought stress conditions (Mantelin and Touraine, 2004). Auxin production was first discovered in hyperplasia-inducing-bacteria suspected of their role in plant development including *Pseudomonas savastanoi*, *Agrobacterium rhizogenes*, *Agrobacterium tumefaciens* and *Erwinia herbicola* (Morris, 1995; Lambrecht *et al*. 2000). Auxins produced by PGPR i.e. *Azospirillum* sp. enhanced the water status of plants under osmotic stress because auxins stimulate shoot growth by improving apical and basal segments of coleoptiles. During seedling development, release of exudates and auxins by roots, as well as by beneficial rhizobacteria, ensure better root growth (Lambrecht *et al*. 2000; Bais *et al*. 2006). Gibberellins play an important role in different developmental and physiological plant processes such as floral induction, seed germination, leaf and stem growth, seedling emergence, and fruit and flower growth (Sponsel, 2002; King and Evans, 2003). Initially Atzorn *et al*. (1988) reported gibberellins (like GA4, GA9) production in *Rhizobium meliloti*. However, Yanni *et al*. (2001) and Probanza *et al*. (2002) demonstrated that *Rhizobium* and other PGPR like *Bacillus* are capable of producing auxins and gibberellins which enhance plant growth and development. Cytokinins are important for cell division, tissue expansion, stomatal opening and promote shoot growth (Weyens *et al*. 2009). The efficacy of cytokinin-generating PGPR *Bacillus subtilis* was investigated to determine the level of improvement in the growth and physiology of *Platycladus rientalis* under water deficit stress. Results demonstrated that inoculation mitigated the hazardous impacts of drought on plants and increased shoot dry matter, relative water content (RWC), leaf water potential (LWP) and organic acids (root exudates) substantially, by 19.23%, 7.18%, 11.46% and 33.12% respectively, as compared to un-inoculated control plants (Liu *et al*. 2013). Abscisic acid (ABA) plays a key role in

opening and closing of stomata especially under stress conditions such as drought. PGPR, which are capable of producing or modulating ABA concentration, can stimulate plant growth by conserving water loss under drought stress (Cohen *et al*. 2009). Vargas *et al*. (2014) also elucidated the mitigation of water deficit stress by the activation of drought-responsive genes through ABA-dependent signaling pathways by using *Gluconacetobacter diazotrophicus* PAL5 inoculation in sugarcane.

Ethylene is a growth regulating phytohormone for plants but, under stressful environments, ethylene is released at an increased level affecting root growth negatively. Potent rhizobacteria also control the level of ethylene and mitigate this effect through the production of ACC-deaminase which breaks the ethylene precursor into an ammonium ion and α-ketobutyrate, eventually improving plant growth and yield under drought stress (Glick *et al*. 1998; Arshad *et al*. 2008). Application of ACC-deaminase-generating rhizobacteria results in longer roots under drought stress, which help the plants to uptake more water from soil (Zahir *et al*. 2008). Lim and Kim (2013) reported that *Bacillus licheniformis* K11, was capable of producing ACC-deaminase, which can mitigate the adverse impacts of drought stress by decreasing the ethylene levels. The influence of *Bacillus licheniformis* K11 was analyzed for its potential to induce drought resilience in pepper plants. It was determined that inoculation resulted in a substantial increase in plant survival; up to 80%, through the induction of stress-protein genes including *CaPR-10*, *sHSP*, *Cadhn* and *VA* as compared to non-inoculated stressed plants which died after 15 days of drought stress. Marasco *et al*. (2012) designed an experiment to elucidate the influence of different PGPR *Bacillus, Pseudomonas,* and *Klebsiella* sp. on pepper plants under desert farming (drought stress). They concluded that, the inoculation with PGPR possessing ACC-deaminase-activity enhanced root fresh weight and photosynthetic activity by 60% and 40%, respectively, as compared to un-inoculated plants under drought stress. Understanding the mechanism of bacterially produced plant growth signaling molecules under stress and their interaction with plant growth/ development could further improve crop productivity under drought stress.

Microbial biofilm-association

Microorganisms have a natural tendency to release extracellular polymeric substances called EPS containing polysaccharides, proteins, lipids, humic compounds and nucleic acids. With respect to biological function, EPS promotes the attachment of bacteria to root surfaces thereby protecting against abiotic stresses via the formation of biofilms. Biofilms are considered as a 'city of microbes', a living place for bacteria that provides resistance against amoebae, bacteriophage, diverse biocides, host immune response, and extreme condition like dehydration and stress (Vu *et al*. 2009). The alginate (polysaccharide) content of biofilms can help to maintain the hydrated condition for plant (Chang *et al*. 2011). EPS-generating PGPR ameliorate drought impacts on crop plants by improving soil properties like water holding capacity, hydraulic conductivity, and soil structure (Zheng *et al*. 2018). Bacterially generated EPS are the active part of organic matter in soil (Gouzou *et al*. 1993). Vardharajula *et al*. (2011) confirmed the release of EPS, as well as other compounds (amino acids, soluble sugars, proline), which induced drought tolerance in maize crop. The root inoculation of EPS-producing biofilm bacteria of wheat resulted in an increase in root adhering soil, root proliferation, and restricted the uptake of Na-cations under salt stressed conditions (Ashraf *et al*. 2004). The uptake of water by an increased root area, and the microbial biopolymers with positive water potential, were responsible for decreasing the impact of osmotic effect due to salt stress on the growth of crop plants (Ashraf *et al*. 2006). However, future research to predict the mechanism and characterization of microbial biofilms (formed under extreme drought) at molecular level and their interaction with plant growth is the need of time.

Antioxidants

The reactive oxygen species (ROS) are continuously generated in plants during metabolic processes; however, during stress conditions their accumulation is increased. These ROS not only affect the cell membrane, but also other constituents and processes. Plants adopt antioxidant strategies to mitigate the negative effects of ROS. Antioxidants as ROS-scavengers include enzymatic (ascorbate peroxidase, glutathione reductase, catalase, superoxide dismutase), non-enzymatic compounds (ascorbate, carotenoids, anthocyanin, glutathione), amphiphilic molecules (tocopherol), osmolytes and protein compounds (peroxiredoxin) (Bowler *et al*. 1992; Noctor and Foyer, 1998). Under drought stress, ROS or free oxygen radicals, including singlet oxygen, superoxide, hydrogen peroxide, and hydroxyl ions are produced, which damage the plant cell membrane. In defense mechanisms i.e. where superoxide dismutase (SOD) converts superoxide (O_2^-) into H_2O_2 (Wang *et al*. 2012). Rhizobacteria stop peroxidation of plasma-lemma and water loss from cells (by maintaining osmotic potential) through reduction in reactive species like melanaldehyde (MDA) contents, and by enhancing proline concentration respectively, under drought stress (Wang *et al*. 2012). Wang *et al*. (2012) demonstrated that the inoculation of cucumber seedlings with combinations of different PGPR (*Serratia* sp. XY21, *Bacillus cereus* AR156

and *Bacillus subtilisb* M21) ameliorated the negative effects of drought stress by reducing mono-dehydroascorbate concentration and relative electrical conductivity by 27%, 38% and 14%, respectively, in comparison to untreated control plants (Table 2). Beneficial rhizobacteria avoid damage to plants by enhancing the activities of ROS-scavenging enzymes under water deficit conditions. For example, Vardharajula *et al*. (2011) inoculated maize seeds with five different drought-resistant strains of *Bacillus* sp. which were confirmed as *Bacillus subtilis*, *Bacillus amyloliquefaciens*, *Paenibacillus favisporus*, *Bacillus thuringiensis* and *Bacillus licheniformis*. These strains possessed the potential for different plant growth stimulating traits such as growth substances (IAA, GA, cytokinins), EPS, ammonia and siderophores. Inoculation of these strains increased drought resilience of maize crop by increasing APX activity (60%) while lowering the electrolyte leakage (65%) as compared to untreated control plants (Table 3).

Table 3: Influence of rhizobacterial inoculations on legumes

Crop	Rhizobacterial sp.	Inoculation method, experiment type	Improvement (%) in crop parameters over control	Mechanism of action	References
Medicago truncatula L.	*Sinorhizobium meliloti* 2011, *Sinorhizobium medicae* WSM419	Roots, Greenhouse	Protein, Sugars, Starch	Modulation in carbon allocation to starch, sugars and osmolytes	Staudinger *et al*. (2016)
Trifolium repens L.	*Bacillus megaterium* (*Bm*) *Pseudomonas putida* (*PsP*), *Bacillus thuringiensis* (*Bt*), *Rhizophagus intraradices* (*Ri*)	Soil, Green-house	P (89) K (217) Ca (131) Mg (79) Zn (62)	Combined application of autochthonous rhizobacteria and fungi enhanced nutrient contents of stressed plants	Ortiz *et al*. (2015)
Phaseolus vulgaris L.	*Rhizobium tropici* strain CIAT899, *Paenibacillus polymyxa* strain DSM36	Seed, Greenhouse	Plant height (45)	Modulate the hormonal balance	Figueiredo *et al*. (2008)
	Rhizobium etli strain Ox	Roots,Greenhouse	Yield (38)	Overexpression of trehalose-6-phosphatase synthase modulate N and C metabolism	Suarez *et al*. (2008)
Pisum sativum L.	*Pseudomonas fluorescens* biotype G (ACC-5)	Seed, Axenic condition and Pot study	Fresh weight (45) Dry weight (150) Root length (92) Shoot length (45) Number of leaves (140) WUE on fresh weight basis (46) WUE on dry weight basis (147)	ACCD efficiency decreased the ethylene level	Zahir *et al*. (2008)

*Parenthesis show percent improvement or increase over control.

Induced systemic resistance (ISR)

Naturally, plants possess an efficient, complex, and multifaceted system to deal with abiotic stresses (drought, salinity, high temperature, cold, and heavy metal), insect pests, herbivores, and phytopathogens (bacteria, fungi, viruses) present in their environment. Some non-pathogenic

'rhizobacteria' and fungi have a natural tendency to mediate and enhance this natural systemic resistance against a broad range of pathogens called 'Induced Systemic Resistance'. ISR is involved in the activation of defense-related proteins, and the activation of ethylene (ET) and jasmonic acid (JA) while independent of salicylic acid (SA). The signaling pathway is regulated by non-expresser pathogenesis-related protein1 (involved in regulating the plant disease resistance) which acts as the master regulator for the activation of pathogenesis-related and defense-related proteins (Jain *et al*. 2016). Beneficial rhizobacteria trigger ISR in a variety of plants such as cucumber, tobacco, tomato, radish, and Arabidopsis (Van Loon *et al*. 1998). Rhizobacterial-elicited ISR could be very beneficial to aid plant growth under unfavorable conditions (drought and salinity), i.e. ISR can be responsible for nutrient uptake by chemical and physical changes in plants (improved root growth) through controlled release of specific rhizobacterial-determinants including phytohormones (IAA, ABA, cytokinins, ethylene), ACC-deaminase, volatile organic compounds and antioxidants (Yang *et al*. 2009). Recently, Kumari *et al*. (2016) described that the inoculation of mung bean seeds with *P. simiae* strain AU having the potential to produce ACC-deaminase (98 nmol/mg/h), IAA (69.35 µg mL^{-1}) and phosphate solubility-index (8.17), enhanced ISR against water deficit stress by decreasing stomatal-aperture size and net photosynthesis. Chemical and biochemical characterization of microbial defensive molecule (ethylene, jasmonic acid, salicylic acid) at molecular level is necessary to improve plant health under extreme environment.

Siderophores

Siderophore is a combination of two Greek words *Sideros*, meaning iron, and *Phores*, meaning bearer. Siderophores are low molecular weight organic substances released by fungi and bacteria to scavenge/chelate ferric ions (Fe^{+3}) during reduced availability of iron (Fe) because microbes require Fe for heme formation, ATP synthesis, ribotide reduction and other important purposes. Bacterially generated siderophores are gaining significant importance in agriculture due to their functionality in nitrogenase enzyme complex, detoxification of heavy-metal-contaminated samples, iron supply to plants, and control of all noxious microbes (Neilands, 1995; Saha *et al*. 2016). Siderophores are made of different structure types. Depending on the coordination of oxygen-ligand with Fe^{+3} siderophores are categorized in to three main groups: carboxylates, catecholates and hydroxymate siderophores. Hydroxymates are the most common types of siderophores. They contain a C (=O) N-(OH) R group (where R is either an amino acid or its derivative). The two O_2-molecules from the hydroxymate group interact with Fe^{+3} to form a bidentate ligand. In catecholate siderophores, the two oxygen atoms coordinate Fe^{+3} forming a hexadentate-octahedrol chelating complex. Carboxylate siderophores bind ferric ion through hydroxyl or carboxyl groups (Saha *et al*. 2016). All these types of siderophores are produced by different types of bacteria such as *Rhizobium* generates carboxyl siderophores (Dave and Dube, 2000). *Escherichia* sp. generated siderophores are catecholate type and are known as enterobactin (Earhart, 1996), while *Pseudomonas* produce catecholate as well as hydroxymate siderophores (Leong and Neilands, 1982). Under abiotic stresses (drought, salinity, heavy metal) iron supply to plants is greatly affected (Tripathi *et al*. 2018). Bacterial siderophores are the potential source for Fe^{+3} supply to plant under iron limited condition or abiotic stresses (Sharma and Johri, 2003; Grobelak and Hiller, 2017). A drought resistant bacterial strain (*Bacillus* spp. strains HYD-B17) with siderophores potential improved the growth of maize under drought stress (Vardharajula *et al*. 2011). Moreover, biochemical characterization of bacterially produced siderophores under water limited/ drought condition could give new insights to improve/ control the Fe^{+3} nutrition to plants.

Conclusions

Drought stress is one of the biggest issues facing the world today. It leads to decrease in crop yields and loss in the amount of arable lands. About 38% land is currently classified as susceptible to drought stress, and this percentage is expected to increase due to climate change. Various approaches have been established to ameliorate drought impacts on crop plants. But due to the disadvantages associated with these strategies like high cost and potential negative environmental side effects, the success of these strategies is uncertain. Using low cost, environment friendly microbial inoculation could be a useful approach to overcome the negative impacts of drought and lead to improved crop yield under drought stress. Mechanism of drought tolerance in rhizobacteria and genes responsible for these mechanisms could be further research prospects. Plant-microbe interaction to mitigate drought tolerance at genetic, molecular and biochemical level are vibrant issues to be addressed in future studies.

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