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Review

Bacterial-mediated drought tolerance: Current and future prospects

Esther Ngumbi*, Joseph Kloepper

Department of Entomology and Plant Pathology, Auburn University, Auburn, AL 36849, United States

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ABSTRACT

With ongoing climate change, the severity, frequency and duration of drought in cotton (*Gossypium hirsutum* L.), soybean (*Glycine max* L.), and corn (*Zea mays* L.) producing areas around the world are predicted to increase. Plants' tolerance to drought stress needs to be improved in order to allow growth of crops that satisfy food demands under limited water resource availability. Plant-associated microbial communities, such as mycorrhizal fungi, nitrogen-fixing bacteria, and plant growth-promoting rhizobacteria (PGPR), enhance crop productivity and provide stress resistance. PGPR represent a wide range of root-colonizing bacteria with excellent root colonizing ability and capacity to produce a wide range of enzymes and metabolites that help plants tolerate both biotic and abiotic stresses. Their roles in the management of abiotic stresses such as drought are only beginning to gain attention. In this review, we synthesize research concerning bacterial-mediated drought tolerance in agricultural crop plants. We summarize in a table and provide details of most relevant and recent studies about the crop system studied, experimental system, means of applying drought stress, and physiological traits measured (such as relative water content, photosynthesis). Furthermore, we highlight the research needed to understand mechanisms behind observed bacterial-mediated drought tolerance and the need to homogenize and develop screening protocols.

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* Corresponding author at: Department of Entomology and Plant Pathology, 301 Funchess Hall, Auburn University, Auburn, AL, 36849, United States.
E-mail address: enn0002@tigermail.auburn.edu (E. Ngumbi).

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1. Introduction

1.1. Definitions and concepts of drought

One of the key obstacles to increasing crop growth and productivity in many parts of the world is drought (Vinocur and Altman, 2005; Naveed et al., 2014). Due to differences in hydrometeorological variables, socioeconomic factors, and the stochastic nature of water demands in different regions of the world, many definitions of drought have been proposed (Yevjevich, 1967; Dracup et al., 1980; Wilhite and Glantz, 1985; American Meteorological Society, 2004). Depending on the variable used to describe drought, drought definitions are classified into four different categories (Wilhite and Glantz, 1985; American Meteorological Society, 2004): (1) meteorological drought, defined as a lack of precipitation for a period of time; (2) hydrological drought, defined as a lack of adequate surface and subsurface water resources for established water uses of a given water resources management system; (3) socio-economic drought, defined as the failure of water resources systems to meet water demands; and (4) agricultural drought, defined as a period with declining soil moisture resulting in crop failure. In this review, we focus on agricultural drought.

Drought is one of the major limitations to food production worldwide and is estimated to have reduced national cereal production by 9–10% (Lesk et al., 2016). Drought is expected to cause serious plant growth problems for crops on more than 50% of the earth's arable lands by 2050 (Vinocur and Altman, 2005). With ongoing global climate change, the severity, frequency and duration of drought in cotton (*Gossypium hirsutum* L.), soybean (*Glycine max* L.), and corn (*Zea mays* L.) in many crop-producing areas around the world are predicted to continue to increase (IPCC, 2007; EEA, 2011). In addition, the world population is expected to reach 9 billion by 2050, necessitating continued increases in crop production to assure food security (Gatehouse et al., 2011; Foley et al., 2011). Therefore, there is a renewed interest in finding solutions to water-related problems such as drought and its impacts on food security (Alexanratos and Bruinsma, 2012). In particular, there is a need to find solutions that increase plants' tolerance to drought stress and allow growth of crops that satisfy food demands under limited water resource availability (Editorial, 2010; Mancosu et al., 2015).

1.2. Concepts of drought adaptations

The ability of plants to sustain growth and survive during periods of drought stress has been termed drought resistance (Levitt, 1980; Chaves et al., 2003). Plants have developed several mechanisms allowing them to cope with drought stress including morphological adaptations, osmotic adjustment, optimization of water resources, antioxidant systems that diminish the harmful effects of reactive oxygen species (ROS) linked to drought, and induction of a variety of stress-responsive genes and proteins (Farooq et al., 2009). These and other adaptations have been detailed in multiple research articles and reviews (e.g. Chaves et al., 2003; Boomsma and Vyn, 2008; Farooq et al., 2009; Lopes et al., 2011; Huang et al., 2014) and are not be included in this review. These adaptations of plants to drought broadly fit into three categories. First is drought escape, in which the plant completes its life cycle before the onset of drought and undergoes dormancy before the onset of the dry season (Levitt, 1980; Turner et al., 2001; Farooq et al., 2009). Second is drought avoidance and phenotypic flexibility, which is the ability of a plant to sustain its normal water status under drought conditions (Blum, 2005). This can be achieved when the plant obtains more water from the soil or minimizes water loss through transpiration. Third is drought tolerance, which occurs when normal plant growth and metabolic activities are maintained even under water stress. These activities include strategies such as osmotic adjustment, maintenance of root viability and membrane stability under dehydration as well as accumulation of proteins and other metabolites that work directly or indirectly in structural stabilization (Nilsen and Orcutt, 1996; Huang et al., 2014).

1.3. How bacteria in soil experience water stress

Soil microorganisms including beneficial soil bacteria experience drought (Schimel et al., 2007; Barnard et al., 2013). Drought stress affects soil bacteria through osmotic stress and resource competition (Schimel et al., 2007; Chodak et al., 2015) and can result in nucleic acids damages (Dose et al., 1991) that may occur via chemical modifications (alkylation or oxidation), cross-linking, or base removal (Potts, 1999). Drought stress results in an accumulation of free radicals due to conformational protein changes, restricted enzyme efficiency, and changes in electron transport chains (Vriezen et al., 2007; Bérard et al., 2015). Accumulation of free radicals induces protein denaturation and lipid peroxidation that ultimately leads to cell lysis (Potts, 1999). Moreover, drought stress can induce protein conformational changes and affect the membrane characteristics of microbes through phospholipid fatty acid composition changes (Russell et al., 1995; Bérard et al., 2015).

Soil microbes are small, in intimate contact with soil water, and have semipermeable membranes (Schimel et al., 2007). As water potentials decline and soils dry due to drought, cells have to accumulate solutes to decrease their internal water potential to avoid dehydration and death (Schimel et al., 2007). To survive drought and protect cell structures and organelles, soil bacteria employ a variety of physiological mechanisms including accumulation of compatible solutes, exopolysaccharide production, and the production of spores (Conlin and Nelson, 2007; Schimel et al., 2007; Allison and Martiny, 2008; Bérard et al., 2015). Accumulation of compatible solutes such as proline, glycine betaine and trehalose increases thermotolerance of enzymes, inhibits proteins thermal denaturation, and helps maintain membrane integrity (Welsh, 2000; Conlin and Nelson, 2007; Schimel et al., 2007; Bérard et al., 2015). Bacteria also synthesize heat shock proteins (HSPs) that recognize and bind to other proteins if they are in non-native conformations (Hecker et al., 1996; Feder and Hofmann, 1999). Alternatively, some bacteria store high quantities of ribosomes, which allow them to respond with rapid protein synthesis when the stress is released (Placella et al., 2012). Other mechanisms that help bacteria to cope up with water stress include increased efficiency of resource use and re-allocation within microbial cells (Tiemann and Billings, 2011) and the production of extracellular polymeric substances (EPS). EPS serve to protect the cell as well as the local environment in which the cell is embedded (Rossi et al., 2012).

The strategies used by soil bacteria to withstand drought stress have also been reported as some of the key adaptation strategies that are employed by plants to survive drought. For example, many of the compatible solutes (proline and glycine betaine) that help bacteria to cope with drought stress also help plants to tolerate drought stress.

1.4. Bacterial-mediated drought tolerance

To date, creation of drought-tolerant cultivars has been the approach used to mitigate the negative effects of drought stress on crops and crop yields (Barrow et al., 2008; Eisenstein, 2013). Conventional plant breeding techniques have allowed the development of high-yielding, drought- tolerant crop varieties. The disadvantages of this approach are that it is time consuming, labor intensive, may lead to the loss of other desirable traits from the host's gene pool, and that breeding confers benefits to a single crop species that are not transferrable to other crop systems (Ashraf, 2010; Eisenstein, 2013; Philippot et al., 2013). Genetic engineering of crops with improved tolerance to drought could, theoretically, be faster, but it would come with its own set of challenges including time and labor (Ashraf, 2010; Eisenstein, 2013). In addition, when transgenic crops reach the market, their success is not guaranteed as consumer response to genetically modified crop products varies among different countries (Fedoroff et al., 2010).

The approaches mentioned above overlook the ecological context of the soil environment in which the crops are grown (Morrissey et al., 2004). In most studies the crops were grown in sterilized potting soils or soilless amendments. For example, Waterer et al. (2010) evaluated the tolerance of genetically modified potatoes (*Solanum tuberosum* L.) to drought stress by using transgenic potatoes that had been grown using a peat: vermiculite mixture (Sunshine Mix #3). Similarly, Witt et al. (2012) evaluated metabolic and phenotypic responses of greenhouse-grown maize hybrids to drought stress using plants that were planted in a 1:1 mix of peat moss and vermiculite. Results generated from such studies may not translate into practical applications as conditions in agricultural soils are different. Furthermore, classical breeding and genetic engineering approaches consider plants as independent organisms that are solely regulated by their genetic code and cellular physiology (Barrow et al., 2008; Coleman-Derr and Tringe, 2014), although plant-associated microbes can influence plants' responses to the environmental conditions, including drought stress (Budak et al., 2013; Cooper et al., 2014). Therefore, there is a need for microbial-based approaches to mitigate drought stress.

Plant-associated microbial communities currently have received increased attention for enhancing crop productivity and providing stress resistance (Mayak et al., 2004; Glick et al., 2007; Marulanda et al., 2009; Yang et al., 2009). The most well studied of these plant associated microbes include the mycorrhizal fungi (Rodriguez and Redman, 2008; Bonfante and Anca 2009; Singh et al., 2011; Aroca and Ruíz-Lozan, 2012; Azcon et al., 2013), nitrogen-fixing bacteria (Lugtenberg and Kamilova, 2009), and plant growth-promoting rhizobacteria (Kloepper et al., 2004; Glick, 2012); the latter represent a wide range of root-colonizing bacteria that have received global attention because of their root colonizing ability and their capacity to produce a wide range of enzymes and metabolites that help plants tolerate biotic and abiotic stresses (Mayak et al., 2004; Glick et al., 2007; Kim et al., 2009; Pineda et al., 2013; Chauhan et al., 2015).

In recent years, efforts have been directed at harnessing these naturally-occurring, beneficial soil microbes to improve crop production under a changing climate (Yang et al., 2009; Nadeem et al., 2014). Although the roles of PGPR in plant growth promotion, nutrient management, and disease control are well known, their roles in the management of abiotic stress such as drought has more recently gained importance (Yang et al., 2009; Dimpka et al., 2009; Grover et al., 2010). The advantages of using PGPR to help plants tolerate stress include their ability to confer drought tolerance to many plant hosts such as monocotyledonous and dicotyledonous row and vegetable crop species (Timmusk and Wagner, 1999; Mayak et al., 2004; Sandhya et al., 2009; Kasim et al., 2013) and their ability to confer more than one type of biotic and/or abiotic stress tolerance (Timmusk et al., 1999; Mayak et al., 2004; Coleman-Derr and Tringe, 2014).

Determining the underlying mechanisms of plant adaptations to drought stress is a key step for the development of drought-tolerant varieties and cost efficient management practices. Plant response to drought stress mechanisms involves multiple physiological, molecular and biochemical pathways and quantitative traits that control different metabolic processes, such as water and nutrient relations, carbohydrate metabolism, protein metabolism, hormone metabolism as well as antioxidant defenses (Huang et al., 2014). These adaptations of plants to aid in survival during periods of drought stress have been comprehensively reviewed (e.g. Farooq et al., 2009; Huang et al., 2014) and are not included in this review article.

In this review, we summarize published studies on how beneficial microbes, specifically PGPR, help plants tolerate drought (Table 1). We also present suggestions and recommendations for future research on bacterial-mediated drought tolerance studies in agricultural crop plants.

2. PGPR improve physiological processes associated with drought resistance

2.1. Rooting characteristics for water uptake

Among the many adaptive traits that plants possess to endure drought, root system architecture is one of the most important (Bacon et al., 2002; Yu et al., 2007; Huang et al., 2014). Root system architecture integrates root system topology, spatial distribution of primary and lateral roots, and the number and length of various diameters of roots (de Dorlodot et al., 2007; Vacheron et al., 2013). Roots exhibit morphological plasticity in response to soil physical conditions (Bengough et al., 2006; Forde, 2009; Tuberosa, 2012), a uniqueness that allows plants to adapt better to the chemical and physical properties of the soil, particularly under drought conditions (Bacon et al., 2002; Yu et al., 2007). Specific root traits associated with maintaining plant productivity under drought conditions include increases in numbers of roots with smaller diameters and a deeper root system (Blum, 1988, 2011; Addington et al., 2006; Pemán et al., 2006; Chirino et al., 2008; Comas et al., 2013). A correlation between a deep and prolific root system with drought resistance has been established in several crops including soybeans (Sadok and Sinclair, 2011), chickpea (*Cicer arietinum* L.) (Varshney et al., 2011), maize (Tuberosa et al., 2003, 2007, 2011; Landi et al., 2010; Hund et al., 2011), and wheat (*Triticum aestivum* L.) (Wasson et al., 2012). Similarly, increases in numbers of roots with small diameters enable plants undergoing drought to increase hydraulic conductance by increasing the surface area in contact with soil water as well as increasing the volume of soil that can be explored for water (Comas et al., 2013). From these studies, it can be argued that plants with a more prolific and deeper root system would be able to tolerate drought stress better than plants with fewer roots, as roots are the only organ capable of extracting water from the soil profile (Turner et al., 2001; Kavar et al., 2007; Gowda et al., 2011).

Treatment of plants with PGPR has been reported to promote root growth and to alter the root architecture (Kloepper, 1992; Kloepper et al., 2004; Ngumbi, 2011). It has further been argued that bacterial-induced alterations in root architecture may lead to an increase in total root surface area, and consequently lead to improved water and nutrient uptake, with positive effects on plant growth as a whole (Somers et al., 2004; Timmusk et al., 2014). In a study with maize, Naseem and Bano (2014) applied strain *Alcaligenes faecalis* (AF3) to seeds in growth chamber tests. Three weeks after planting, drought stressed PGPR treated plants showed an increase in root length by 10% compared to drought stressed noninoculated control plants (Table 1). They argued that development of root system as a result of PGPR treatment led to an increase in water uptake which allowed treated plants to tolerate drought stress. Naveed et al. (2014) reported that maize plants inoculated with *Burkholderia phytofirmans* strain PsJN had significantly increased root biomass by 70 and 58% in Mazurka and Kaleo

Table 1
List of studies on applications of rhizobacteria for drought tolerance.

Scientific name	Plant	Identification	Experimental system and soil used	Means of applying drought	Morphological, physiological or molecular plant traits assessed	Synopsis of the aim of study, results and conclusions	References
Arabidopsis thaliana	Arabidopsis	*Paenibacillus polymyxa* B2, B3, and B4	**Experimental system**: - Growth chamber studies **Inoculation design**: - Plants inoculated by soaking their roots overnight in cultures of bacteria in L medium at a concentration of 10^8 cfu/ml.	- Drought applied by opening the lids of culture dishes for 3 days.	- Expression of abiotic stress induced genes including *RAB18*,*LT178*, *ERD15*, and biotic stress related genes including *PR-1*, *HEL*, and *ATVSP*	**Objectives**: - To investigate changes of plant gene expression following inoculation by root-invading PGPR *P. polymyxa*. **Conclusions**: - Inoculation of Arabidopsis plants with PGPR *P. polymyxa* conferred resistance to biotic stress and tolerance to drought stress. Drought tolerance was correlated with increased expression of genes associated with abiotic stress (*ERD15*, *RAB18*).	Timmusk and Wagner (1999)
Arabidopsis thaliana	Arabidopsis	*Phyllobacterium brassicacearum* strain *STM196*	**Experimental system**: - Growth chamber studies **Soil used**: - Mixture (1:1, v/v) loamy soil and organic compost **Inoculation design**: - Inoculation of soil with bacteria at 3×10^7 cfu/g.	- Drought applied by stopping irrigation. Drought started when the first two true-leaves emerged.	- Rosette expansion, leaf production dynamics and phenology, whole-plant leaf morphology, leaf and shoot development, stomata and cell density, and net photosynthetic and transpiration rates - Sucrose and leaf abscisic acid (ABA) contents	**Objectives**: - To investigate the growth and physiological responses of *A. thaliana* inoculated with *P. brassicacearum* under long-term water deficit. **Conclusions**: - PGPR induced a suite of developmental and physiological changes in Arabidopsis plants that contributed to the observed drought tolerance and water-use efficiency. - PGPR also enhanced Arabidopsis plants' performance and tolerance to stress via coordinated changes in transpiration, photosynthesis, and ABA content. These PGPR-induced changes resulted in higher water-use efficiency. - Inoculation with PGPR induced a delay in the transition from vegetative to reproductive phase, and this delay contributed to increased tolerance of Arabidopsis plants to water deficit.	Bresson et al. (2013)
Arabidopsis thaliana	Arabidopsis	*Azospirillum brasilense* Sp 245 strain	**Experimental system**: - Petri dishes and growth chamber studies **Soil used**: - Sterilized soil maintained at field capacity **Inoculation design**: - Bacteria applied to roots of seedlings at the second leaf stage at 10^6 cfu/ml.	- Drought applied when plants were 30 days old. - Drought applied by stopping watering until visible symptoms of temporary wilting were observed (ca. 10 days after water was withheld).	- Plant growth parameters - Abscisic acid - Water loss - Relative water content - Stomatal conductance - Lipid peroxidation - Proline concentration - Survival - Photosynthetic efficiency	**Objectives**: - To investigate the mechanisms involved in PGPR- treated plants under drought conditions. - To examine Arabidopsis development and reproductive successes as affected by PGPR treatment, abscisic acid, and drought. **Conclusions**: - PGPR helped Arabidopsis plants tolerate drought stress through several morphophysiological and biochemical changes including increase in photosynthetic pigments, ABA, proline and lipid peroxidation. - PGPR treated plants had augmented photosynthetic and photoprotective pigments. In addition, the observed PGPR effect may have been the result of better control of stomata closure mediated by ABA together with a more developed root system.	Cohen et al. (2015)

Capsicum annuum	Pepper	*Bacillus licheniformis* strain K11	**Experimental system**: - Growth chamber **Soil used**: - Sterilized soil - 200 g of soil **Inoculation design**: - Bacteria were applied to transplanted seedlings at 7.0×10^8 cfu/ml.	- Progressive drought by withholding water for 15 days. - Drought introduced 5 days after transplanting.	- Stress proteins - Stress-related genes including *Cadhn*, *VA*, *sHSP* and *CaPR-10* were monitored using two dimensional polyacrylamide gel electrophoresis and differential display PCR	**Objectives**: - To study the molecular effects induced during pepper-PGPR interactions under drought stress conditions. **Conclusions**: - PGPR *Bacillus licheniformis* K11 that produce auxin and ACC deaminase can alleviate drought stress in pepper plants via the regulation of stress-proteins and stress-related genes; *Cadhn*, *VA*, *sHSP* and *CaPR-10*.	Lim and Kim (2013)
Cucumis sativa	Cucumber	*Bacillus cereus* strain AR156 *B. subtilis* strain SM21 *Serratia* sp. strain XY21	**Experimental system**: - Greenhouse studies **Soil used**: - Sterilized soil - Plastic pots 355.46 cm^3 **Inoculation design**: - 20 ml of bacterial cell suspension at 5×10^8 cfu/ml was poured on the pots around the roots of seedlings in each pot.	- Drought applied by withholding watering for 13 days. - Drought started 15 days after transplanting cucumber seedlings that were 15 days old.	- Leaf monodehydroascorbate - Proline content - Root vigor - Chlorophyll content - Antioxidant enzymes - Gene expression studies that monitored transcript levels of *rbcS*, *rbcL*, and *cAPX*	**Objectives**: - To examine the effects of a consortium of PGPR on a range of physiological indicators of drought tolerance. **Conclusions**: - PGPR provided tolerance to drought without involving ACC-deaminase. This was achieved via several mechanisms including reductions in leaf monodehydroascorbate content and relative electrical conductivity, reduced expression of drought-triggered genes *cAPX*, *rbcL*, *rbcS* and, and increases in the contents of chlorophylls *a*, *b*, and *a* + *b*. These mechanisms help to protect the leaf cell membrane from damage. - PGPR increased proline which serves as an osmolyte that helps to stabilize the osmotic potential in cucumber plants under drought stress. - Mixtures of PGPR can be used to confer drought tolerance by maintaining root recovery intension and by reducing peroxidation of the plasma lemma, maintaining photosynthesis efficiency, and increasing the activities of the antioxidant enzymes SOD in the leaves.	Wang et al. (2012)
Helianthus annuus	Sunflower	*Achromobacter xylosoxidans* (SF2) *Bacillus pumilis* (SF3 and SF4)	**Experimental system**: - Growth chamber studies **Soil used**: - Sterilized sand soil **Inoculation design**: - Four days after planting, seedlings were singly inoculated with bacteria SF2, SF3, or SF4 (1 ml at 10^8 cfu/ml) or co-inoculated with a combination of SF2/SF3, SF2/SF4, or SF3/SF4 (0.5 ml of each).	- Drought introduced by watering with polyethylene glycol (PEG) 6000 at a concentration sufficient to produce $\Psi a = -2.03$ MPa.	- Relative water content - Plant growth parameters - Phytohormones—Abscicic acid, salicylic acid and jasmonic acid	**Objectives**: - To study effects of bacterial single inoculation and co-inoculation on growth and phytohormone production of sunflower seedlings under water stress. **Conclusions**: - Increased salicylic acid in shoots of PGPR-treated plants suggests that water stress in sunflower activates the isochorismate synthase pathway, and that salicylic acid may also be a phytohormone directly related to drought stress. - Treatment with PGPR improved plant growth parameters and increased relative water content. - Treatment with PGPR helped sunflower seedlings tolerate stress via the regulation of phytohormones. - Different PGPR may impart drought tolerance via different mechanisms.	Castillo et al. (2013)

Table 1 (*Continued*)

Scientific name	Plant	Identification	Experimental system and soil used	Means of applying drought	Morphological, physiological or molecular plant traits assessed	Synopsis of the aim of study, results and conclusions	References
Hyoscyamus niger	*Hyoscyamus niger* (Medicinal plant)	*Pseudomonas putida* strain (PP) *Pseudomonas fluorescens* strain (PF)	**Experimental design**: - Greenhouse studies **Soil used**: - Sterilized soil - 8 kg of soil maintained at 30%, 60% and 90% percent water holding capacity **Inoculation design**: - Applied bacterial solutions to seedlings at 10^9 cfu/ml.	- Progressive drought by withholding water for 60 days. - Drought introduced when plants were 45 days old.	- Plant growth parameters - Chlorophyll pigment - Proline content - Relative water content in leaves - Antioxidant enzymes (superoxidase dismutase (SOD), peroxidase (POX), and catalase (CAT)	**Objectives**: - To investigate the role of plant growth-promoting rhizobacteria on antioxidant enzyme activities and tropane alkaloid production of *Hyoscyamus niger* under water deficit stress. **Conclusions**: - Treatment of *Hyoscyamus* plants with PGPR had positive effects on root and shoots growth, improved leaf relative water content, increased leaf numbers, stimulated the activities of antioxidant enzymes, increased proline accumulation and improved alkaloid content. These changes account for enhanced drought tolerance by PGPR.	Ghorbanpour et al. (2013)
Pisum sativum	Pea	*Pseudomonas* spp.	**Experimental system**: - Semi-field studies using pots **Soil used**: - Sterile sandy clay loam soil **Inoculation design**: - Seed treatment - Concentration was 10^8-10^9 cfu/ml.	- Drought applied by skipping irrigation when plants were at the vegetative growth stage (ca. 3 weeks after germination) or at flowering stage (ca. 7 weeks after germination) or at the pod formation stage (ca. 8 weeks after germination). - Re-watered plants when symptoms of wilting were observed.	- Root architecture traits - Shoot weight - Chlorophyll content	**Objectives**: - To study the effects of bacteria that produce ACC-deaminase on growth, yield and ripening of peas under drought stress conditions applied at different stages. **Conclusions**: - Treatment of plants with ACC-deaminase-producing PGPR helped reduce the effects of drought stress. This may have been due to the suppression of ethylene by ACC-deaminase or by longer roots, which might have helped plants to get water from deep soil. However, this was dependent on the stage upon which drought was applied. - Treatment of plants with PGPR also increased root weight, shoot length, number of pods, and the total grain yield and chlorophyll contents.	Arshad et al. (2008)
Solanum Lycopersicum *Capsicum annuum*	Tomatoes Peppers	*Achromobacter piechaudii* ARV8	**Experimental system**: - Growth chamber studies **Soil used**: - Vermiculite soil - 7 cm diameter pot **Inoculation design**: - Bacteria were applied to 10 day old seedlings.	- Drought applied by withholding watering two weeks after transplanting seeds. - Rewatered plants after 7 or 12 days.	- Plant growth parameters - Levels of ethylene - Relative water content	**Objectives**: - To evaluate bacteria from arid and salty environments for conferring resistance to water stress in tomato and pepper plants. **Conclusions**: - ACC-deaminase- producing PGPR that reduce the production of ethylene may be effective in alleviating water stress and may provide means to facilitate plant growth in arid environments.	Mayak et al. (2004)

Solanum tuberosum	Potato	*Bacillus pumilus* strain DH-11 *Bacillus firmus* strain 40	**Experimental system**: - Greenhouse studies **Soil used**: - Sterilized soils **Inoculation design**: - Bacteria were applied to the roots at 10^8 cfu/g - Reinoculation was done one week later and was applied as a soil drench (10^8 cfu/g substrate).	- Drought applied by watering them with 10% PEG. - Drought started 2 weeks after inoculating plants with PGPR.	- Antioxidant enzymes - Putative changes in the expression of genes encoding the Reactive oxygen species-scavenging enzymes and ethylene biosynthesis	**Objectives**: - To investigate the potential of PGPR to enhance drought tolerance in potato plants. **Conclusions**: - PGPR increased proline content and the level of three antioxidant enzymes: ascorbate peroxidase, superoxide dismutase and catalase. - PGPR induced changes in the expression of reactive oxygen species-scavenging enzymes and enhanced the photosynthetic efficiency of potato plants. - Changes in photosynthetic parameters may be used to investigate changes in photosynthetic machinery of plants under stress conditions.	Gururani et al. (2013)
Sorghum bicolor	Sorghum	*Bacillus* spp strains KB122, KB129, KB133, KB142	**Experimental system**: - Greenhouse studies **Soil used**: - Sterilized field soil - 900 g of soil maintained at 50 and 75% water holding capacity **Inoculation design**: - After seedling emergence, plants were treated with 1 ml of bacterial culture at 10^8 cfu.	- Progressive drought by withholding water for 5 days. - Drought introduced when plants were 27 days old.	- Plant growth parameters - Leaf relative water content - Levels of proline - Sugar content	**Objectives**: - To evaluate drought-tolerant rhizobacteria isolated from semiarid zones in India for their effect on growth promotion and physiological parameters of sorghum seedlings under drought stress. **Conclusions**: - Treatment of plants with PGPR resulted in increased shoot length, root dry biomass, relative water content, sugar, chlorophyll, soil moisture content and proline content thereby improving sorghum seedlings growth and health under stress conditions.	Grover et al. (2014)
Triticum aestivum	Wheat	*Azospirillum lipoferum* AZ1 *A. lipoferum* AZ9 *A. lipoferum* AZ45	**Experimental system**: - Greenhouse studies **Soil used**: - Field soil maintained at 80% water holding capacity **Inoculation design**: - Seedlings were soaked in bacterial solution at 3.2×10^9 cfu/ml for 3 h.	- Drought applied by withholding water for 6 days or 12, 18, and 24 days. - Drought started 50 days after planting. - Had three drought intensities: control, moderate and high drought. - Restored irrigation after drought stress.	- Soil and plant measurements - Leaf water potential - Relative water content - Soil matrix potential - Grain yield and yield component	**Objectives**: - To test if inoculation of wheat plants with the isolated strains of *Azospirillum* sp. can alleviate drought stress. **Conclusions**: - Treatment of plants with PGPR enhanced the tolerance of plants to drought by increasing relative water content and decreasing leaf water potential. Consequently, plant growth and yield was improved under drought. - Different strains of PGPR performed differently under different drought intensities.	Arzanesh et al. (2011)
Triticum aestivum	Wheat	*Bacillus amyloliquefaciens* 5113 *Azospirillum brasilense* N040	**Experimental system**: - Greenhouse studies **Soil used**: - Sterile soils **Inoculation design**: - Primed seeds by soaking them in bacterial strains containing 10^7 bacteria per ml for 2 h.	- Progressive drought by withholding water for 4, 5, or 7 days. - Drought introduced when plants were 12 days old.	- Fresh and dry weights - Antioxidant enzymes - Expression of stress marker genes *APX1*, *SAMS1*, and *HSP17.8*	**Objectives**: - To explore the potential to improve drought tolerance of wheat through priming with PGPR. **Conclusions**: - Beneficial bacteria are a promising approach to reduce drought stress in wheat plants. - Priming resulted in improved growth, which increased survival, fresh and dry weights, and water content under drought. In addition, primed and drought-stressed plants showed lower antioxidant enzymes activity; strongly supporting the ability of bacterial priming to reduce reactive oxygen species levels in drought stressed plants.	Kasim et al. (2013)

Table 1 (*Continued*)

Scientific name	Plant	Identification	Experimental system and soil used	Means of applying drought	Morphological, physiological or molecular plant traits assessed	Synopsis of the aim of study, results and conclusions	References
						- Priming resulted in lower activities of ascorbate peroxidase (APX) and reduced transcript levels of the stress-related genes (ascorbate peroxidase (*APX1*), S-adenosyl-methionine synthetase (*SAMS1*), and the heat shock protein (*HSP17.8*) - Different PGPR may impart drought tolerance via different mechanisms.	
Triticum aestivum	Wheat	*Bacillus. thuringiensis* AZP2 *Paenibacillus polymyxa B*	**Experimental system**: - Greenhouse studies **Soil used**: - Soaked seeds in bacterial solutions containing 10^7 bacteria per ml for 4 h **Inoculation design**: - 450 g of soil maintained at 75% water holding capacity	- Progressive drought by withholding water for 10 days (plants grown in sand soil) or 14 days (plants grown in sand soil mixed with 10% greenhouse soil). - Drought introduced 10 days after seed germination.	- Plant survival - Seedling germination - Antioxidant enzymes - Foliage gas exchange - Volatiles - Ethylene emission rates - Root adhering soil - Water use efficiency-ratio of total plant dry mass to total water use during the experiment	**Objectives**: - To systematically compare bacterial isolates from stressed and mild environments for the capacity to enhance drought stress tolerance in wheat. - To gauge if volatiles can be used to assess differences in plant stress tolerance. **Conclusions**: - Bacteria isolated from harsh environments enhanced drought tolerance in wheat more than those collected from moderate environments. - Bacterial priming improved seedling germination, increased plant dry mass and the number of lateral roots and enhanced production of antioxidant enzymes. - Measurements of plant volatile profiles provide a novel approach to characterize efficiency of different bacterial strains in priming for drought tolerance. Three key volatiles were identified as the most responsive to drought stress: benzaldehyde, beta-pinene and geranyl acetone.	Timmusk et al. (2014)
Vigna radiata	Green gram	*Pseudomonas fluorescens* strain Pf1 *Bacillus subtilis* EPB5, EPB22, *and* EPB 31	**Experimental system**: - Greenhouse Studies **Soil used**: - Sterilized soil **Inoculation design**: - Seeds were soaked in 10 ml of bacterial suspension at 10^8 cfu/ml.	- Progressive drought by withholding water for 6 days. - Drought introduced when plants were 30 days old.	- Plant growth parameters - Stress-related enzymes - Proline content	**Objectives**: - To evaluate promising strains of *P. fluorescens* and *B. subtilis* ability to enhance drought resistance on green gram plants. - To study the differential enzymatic and protein activity during water stress conditions. **Conclusions**: - PGPR improved several plant growth parameters including roots and shoot length, and increased the content of proline and the antioxidant enzymes catalase and peroxidase. Accumulation of proline and other enzymes may have enhanced the ability of green gram plants to tolerate water stress. Therefore, the use of PGPR can mitigate water stress in crop plants and may be an adoptable strategy to manage drought conditions.	Saravanakumar et al. (2011)

Vigna radiata	Mung bean	*Pseudomonas aeruginosa* strain GGRJ21	**Experimental system**: - Greenhouse studies **Soil used**: - Sterilized soils **Inoculation design**: - Seeds were inoculated with 10 ml of bacterial cell suspension containing 0.1% of carboxymethyl cellulose - Seeds were incubated for 3 h.	- Drought applied by withholding watering 10 days after planting.	- Up regulation of drought stress responsive genes: *DREB2A*, *CAT1*, and *DHN* - Levels of antioxidant enzymes - Cell osmolytes	**Objectives**: - To investigate the potential of the mung bean rhizosphere-associated *Pseudomonas aeruginosa* GGRJ21 strain on drought stress alleviation. **Conclusions**: - Strain GGRJ21 improved germination rate and seedling vigor, increased plant growth and development in mung bean plants under water-stressed environments. - Treatment with PGPR increased relative water content, root length, concentrations of antioxidant enzymes and the expression of three drought stress responsive genes: *DREB2A*, *CAT1*, and *DHN* - The alleviation of drought stress is related to increased levels of antioxidants, cell osmolytes, and consistent up-regulation of stress-responsive genes.	Sarma and Saikia (2014)
Zea mays	Maize	*Pseudomonas entomophila* strain BV-P13 *P. stutzeri* strain GRFHAP-P14 *P. putida* strain GAP-P45 *P. syringae* strain GRFHYTP52 *P. monteilli* strain WAPP53	**Experimental system**: - Growth chamber studies **Soil used**: - Sterilized field soil - 2 kg of soil maintained at 75% water holding capacity. **Inoculation design**: - Talc-based formulation with 10^8 cells/g.	- Progressive drought by withholding water for 6 days. - Drought introduced after 21 days of germination.	- Plant growth - Osmoregulation - Antioxidative enzymes - Relative water content - Leaf water retention - Levels of free Proline contents - Total soluble sugars - Total amino acids - Leaf protein analysis - Electrolyte leakage	**Objectives**: - To study the effect of inoculation of five drought-tolerant *Pseudomonas* spp. strains on growth, osmoregulation and antioxidant status of maize seedlings under drought stress. **Conclusions**: - Treatment of maize seedlings with PGPR improved physiological and biochemical parameters including relative water content. Treated plants had increased antioxidant enzymes activity and increased levels of proline, sugars, and free amino acids. Soluble sugars and proline are key osmolytes contributing towards osmotic adjustment. Subsequently, inoculated plants were more tolerant to drought.	Sandhya et al. (2010)
Maize	*Zea mays*	*Azospirillum lipoferum* strain GQ255950	**Experimental system**: - Greenhouse studies **Soil used**: - Sterile soils - 12 kg soil maintained at field capacity **Inoculation design:** - Applied 1 ml of bacterial inoculum.	- Drought started at the vegetative stage by maintaining the soil moisture content at 15 ± 1%.	- Free amino acid levels - Soluble sugars - Proline - Soluble protein - Relative water content - Leaf osmotic potential	**Objectives**: - To investigate the effects of maize inoculation with PGPR on biochemical attributes and growth of maize plants under drought stress. **Conclusions**: - *Azospirillum lipoferum* strain mitigated the deleterious effects of drought on maize through a variety of mechanisms including increase in the relative water content, accumulation of free amino acids and accumulation of important osmolytes like proline.	Bano et al. (2013)
Zea mays	Maize	PGPR isolate 1 K, 9 K and KB	**Experimental system**: - Greenhouse studies **Soil used**: - Sterilized soil **Inoculation design**: -	- Drought introduced after 7 days of germination by withholding watering for 6 days.	- Soil and moisture contents - Plant growth parameters - Relative water content	**Objectives**: - To screen PGPR isolates from semi-arid regions and assess their capacity to alleviate drought stress in maize plants.	Yasmin et al. (2013)

Table 1 (*Continued*)

Scientific name	Plant	Identification	Experimental system and soil used	Means of applying drought	Morphological, physiological or molecular plant traits assessed	Synopsis of the aim of study, results and conclusions	References
			Seeds were inoculated with bacteria at 10^8 cells/g for 2–4 h			**Conclusions**: - Inoculation with PGPR isolates 1 K, 9 K and KB resulted in increases in shoot and root length, leaf area, root and shoot dry mass, and leaf relative water content. These allowed maize plants to grow better under drought conditions. - Isolate 9 K performed better than the other isolates.	
Zea mays	Maize	*Proteus penneri* strain (Pp1) *Pseudomonas aeruginosa* strain (Pa2) *Alcaligenes faecalis* strain (AF3)	**Experimental system**: - Growth chamber studies **Soil used**: - Sterilized soil **Inoculation design**: - Soaked seeds in 48-h-old and 10-d-old bacterial culture solutions for 3–4 h.	- Progressive drought by withholding water for 10 days. - Drought introduced after 1 week of seed germination.	- Relative water content - Proteins and sugars - Proline content - Soil moisture content	**Objectives**: - To characterize the EPS-producing bacteria from arid and semiarid regions of Pakistan and evaluate the drought tolerance potential of these PGPR on maize. **Conclusions**: - Treatment of maize plants with PGPR induced drought tolerance by improving soil moisture content, plant biomass, root and shoot length, relative water content, protein and sugar concentration in leaves, and proline.	Naseem and Bano (2014)
Zea mays	Maize	*Burkholderia phytofirmans* strain PsJN *Enterobacter* sp. strain FD17	**Experimental system**: - Greenhouse studies - Two maize varieties were tested; Mazurka and Kaleo **Soil used**: - Field collected soil - 15 kg of soil **Inoculation design**: - Seeds were incubated in bacterial suspension at 10^8–10^9 cfu/ml for 2 h.	- Progressive drought by stopping irrigation of plants and observing for wilting signs. - Drought introduced when plants were 45 days old.	- Water status - Photosynthetic activity - Relative water content - Membrane permeability - Shoot fresh and dry weight	**Objectives**: - To evaluate the potential of two endophytic bacterial strains for improving physiology and growth of maize under drought stress. **Conclusions**: - Bacterial inoculation improved the physiological traits and growth of both maize cultivars and enhanced their capacity to tolerate drought via several mechanisms including an increase in shoot biomass, root biomass, leaf area, chlorophyll content, photosynthetic rate, relative water content, and photochemical efficiency. - Bacterial strain and plant genotype affect the outcome of bacterial-mediated drought tolerance.	Naveed et al. (2014)
Zea mays	Maize	*Bacillus amyloliquefaciens* strain HYD-B17 *B. licheniformis* strain HYTAPB18 *B. thuringiensis* strain HYDGRFB19 *Paenibacillus favisporus* strain BKB30 *B. subtilis* strain RMPB44	**Experimental system**: - Growth chamber **Soil used**: - Sterilized field soil maintained at 75% water holding capacity **Inoculation design**: - Talc-based formulation of bacteria was applied to seeds at a population of 10^8cells/g.	- Progressive drought by withholding water for 6 days. - Drought introduced when plants were 21 days old.	- Intracellular amino acids - Relative water content of leaves - Leaf water retention - Proline content - Total soluble sugars - Amino acids - Leaf proteins - Plant antioxidative enzymes	**Objectives**: - To study PGPR traits and stress-adaptive mechanisms at the cellular level with drought- tolerant *Bacillus* spp. isolated from arid and semi-arid zones of India. - To select efficient drought-tolerant plant growth-promoting *Bacillus* spp. and analyze their ability to increase maize stress tolerance. **Conclusions**: - Inoculation of maize plants with drought-tolerant *Bacillus* spp improved tolerance of maize plants to tolerate abiotic stress and improved plant development via an increase in plants biomass, relative water content, leaf	Vardharajula et al. (2011)

						water potential, antioxidant enzymes and enhanced production of proline, amino acids and soluble sugars. Inoculation with PGPR also improved protein content in leaves .	
Maize	*Zea mays*	*Burkholderia* sp. strain LD-11	**Experimental system**: - Rainout shelter studies **Soil used**: - 3 kg soil (loamy clay and peat mixture (3:1, v/v) **Inoculation design**: - 10 ml of bacteria at 5×10^7 cfu/g was applied to the surface soil near root-stem transition. - Multiple re-inoculations. - Five watering regimes (80, 60, 45, 35, and 25% of soil water capacity).	- Drought introduced by withholding watering for 10 days when plants reached the 4 leaves stage.	- Plant growth parameters - Leaf water potential and gas exchange measurements - Lipid peroxidation and reactive oxygen species - Antioxidant enzymes - Abscisic acid	**Objectives**: - To understand the physiology and biochemistry of plant growth promotion induced by PGPR under different water deficits. **Conclusions**: - Treatment with PGPR improved tolerance to drought by maize plants via several mechanisms including increasing the concentration of antioxidant enzymes, reducing production of reactive oxygen species, and lowering abscisic acid levels. Consequently, PGPR treated plants had enhanced water- use efficiency. - Treatment with PGPR improved plant growth parameters. This improvement was dependent on the intensity of water deficits and plant genotype. Treated plants had longer and larger root systems which may have contributed to the observed drought tolerance.	Fan et al. (2015)

cultivars, respectively. Likewise, inoculation of plants with *Enterobacter sp.* strain FD resulted in 47 and 40% increase in root mass in Mazurka and Kaleo cultivars respectively compared to control plants under drought stress conditions. They suggested that the observed increase in root biomass led to improved water uptake by plants during drought stress. Similarly, Yasmin et al. (2013) reported that under drought stress, maize plants inoculated with PGPR isolate 9 K enhanced root length by 43.3%. Timmusk et al. (2014) reported that wheat plants treated with *Bacillus thuringiensis* AZP2 had two to three times longer root hairs and longer and denser lateral roots, effects that were more pronounced when plants experienced drought stress. The observed bacterial-mediated alterations in root architecture of wheat plants may have helped the plants to tolerate drought stress (Timmusk et al., 2014) (Table 1).

PGPR may help plants tolerate drought stress via the enhancement and alteration of root parameters. More studies are needed to investigate the correlation between bacterial-mediated improved root architecture and drought tolerance. Moreover, functional structural modelling studies of root systems in interaction with their soil environment could be very pertinent (Doussan et al., 2006; Dunbabin et al., 2013). Furthermore, more studies will be needed to identify the ideal root traits that help plants the most under drought stress. Identified specific traits could be incorporated in breeding programs that aim to breed plants with root traits to enhance productivity under drought stress.

2.2. Shoot growth characteristics

One of the key responses to drought stress is the inhibition of shoot growth, which benefits plants by limiting the leaf area available for evaporative loss of limited water reserves (Sinclair and Muchow, 2001; Wang and Yamauchi, 2006; Neumann, 2008; Skirycz and Inzé, 2010). In addition, inhibiting shoot growth allows plants to divert essential solutes from growth requirements to stress-related house-keeping functions, such as osmotic adjustment. Therefore, inhibition of shoot growth is considered an adaptive response that helps plants to tolerate drought stress (Neumann, 1995, 2008; Aachard et al., 2006).

However, drought tolerance mechanisms that increase plant survival by inhibiting shoot growth will likely decrease plant size and hence limit yield potential (Sinclair and Muchow, 2001; Neumann, 2008; Claeys and Inzé, 2013). Hence, inhibition of shoot growth could be a counter-productive response in the case of crop plants exposed to moderate drought stress. In such cases, plant survival might not be threatened, but drought stress-induced reductions in shoot growth would still limit yield potential. Therefore, development of crop varieties with an ability to maintain near-normal shoot growth rates during moderate drought stress might be advantageous for crop production (Neumann, 2008).

Treatment of plants with PGPR typically increases shoot growth. Consequently, under drought stress, plants inoculated with effective PGPR strains could maintain near-normal shoot growth rates, resulting in increased crop productivity. For example, Vardharajula et al. (2011) showed that inoculation of corn plants with plant growth-promoting *Bacillus* spp. improved shoot growth. In this study, under drought stress conditions, all the plants inoculated with the tested *Bacillus* spp. showed significantly greater shoot length and dry biomass compared to non-inoculated plants. Similarly, Timmusk et al. (2014) showed that under drought stress, wheat plants treated with PGPR had 78% higher biomass than non-treated plants, confirming the potential of PGPR to enhance plant performance under drought stress. Similarly, Lim and Kim (2013) showed that pepper plants treated with *Bacillus licheniformis* K11 and exposed to drought stress had 50% higher biomass than non-treated plants. The plant shoot length was also increased. Increases in shoot and plant growth under drought stress as a result of PGPR treatment have also been reported in other crops including sorghum (*Sorghum bicolor* L.) (Grover et al., 2014), sunflower (*Helianthus annuus* L.) (Castillo et al., 2013), wheat (Arzanesh et al., 2011; Kasim et al., 2013), green gram (*Vigna radiata* L.) (Saravanakumar et al., 2011) mung bean (*Vigna radiata* L.) (Sarma and Saikia, 2014) and maize (Sandhya et al., 2010; Naseem and Bano, 2014; Naveed et al., 2014) (Table 1).

Taken together, the above studies clearly show that treatment of plants with selected strains of PGPR leads to increase in shoot growth and improvements in plant growth which help plants tolerate drought stress. Consequently, improved shoot growth, and plant growth may translate to increased yield and increased plant productivity.

2.3. Relative water content

Relative water content (RWC) in plant leaves is considered one of the best criteria for measuring plant water status because it is involved in the metabolic activity in tissues. A decline in RWC reflects a loss of turgor that results in limited cell expansion and, consequentially, reduced growth in plants (Ashraf, 2010; Lu et al., 2010; Castillo et al., 2013). It has been observed that species that are better adapted to dry environments have high RWC (Jarvis and Jarvis, 1963). Therefore, an increase in RWC should be considered an important drought tolerance enhancement strategy. RWC could be used as a parameter in screening PGPR for drought stress-alleviating potential. Indeed, many studies investigating the ability of PGPR to help plants tolerate drought stress have measured RWC in treated and non-treated plants under drought stress. Several studies have shown that under drought stress, PGPR-treated plants maintained relatively higher RWC compared to non-treated plants, leading to the conclusion that PGPR strains that improve survival of plants under drought stress generally increase RWC in the plants. For example, Grover et al. (2014) reported that sorghum plants treated with PGPR, *Bacillus* spp strain KB 129 under drought stress showed 24% increase in RWC over plants that were not treated with PGPR. Similar results have been demonstrated in maize (Sandhya et al., 2010; Vardharajula et al., 2011; Bano et al., 2013; Naveed et al., 2014; Naseem and Bano, 2014) (Table 1). Studies reported above have indicated that higher RWC may help plants counteract the oxidative and osmotic stresses caused by drought stress, potentially contributing to greater productivity under stress.

While studies have reported a correlation between increased RWC with PGPR treatment, the mechanisms behind these phenomena are yet to be uncovered. Casanovas et al. (2002) suggested that the high RWC in maize treated with *Azospirillum brasilense* BR11005spp. was a result of bacterial absicisic acid (ABA) that induced stomatal closure and mitigated drought stress. Dodd et al. (2010) proposed that the increase in RWC may have been a result of alterations of the sensitivity of physiological processes such as stomatal closure. Such contrasting views emphasize the need to understand mechanisms behind observed bacterial-mediated drought tolerance via increased RWC. It is yet to be established whether the observed increase in RWC remains constant as drought stress increases.

2.4. Osmotic adjustment for drought tolerance

Osmotic adjustment is one of the key adaptations at the cellular level that helps plants tolerate drought-induced damage (Blum, 2005; Farooq et al., 2009). It protects enzymes, proteins, cellular organelles and membranes against oxidative damage (Hoekstra and Buitink, 2001; Farooq et al., 2009; Huang et al., 2014). Osmotic adjustment is the active accumulation of organic and inorganic solutes, also referred to as compatible solutes (Kiani et al., 2007), in response to drought stress (Nilsen and Orcutt, 1996). These solutes maintain cellular turgor and help plants lower water potential without decreasing actual water content (Serraj and Sinclair, 2002). They include ammonium compounds such as glycine betaine, sugars (e.g. sucrose), poly-ols (e.g. mannitol), organic acids (e.g. malate), inorganic ions (e.g. calcium), and non-protein amino acids (e.g. proline). Drought stress is often accompanied by an increase in compatible solutes, specifically proline (Farooq et al., 2008).

Proline is one of the most important osmolytes that accumulate in plants experiencing drought stress (Yoshiba et al., 1997; Verbruggen and Hermans, 2008; Farooq et al., 2009; Huang et al., 2014). Apart from acting as an osmolyte for osmotic adjustment, proline contributes to stabilizing sub-cellular structures (e.g. proteins and membranes), scavenging free radicals and buffering cellular redox potential (Ashraf and Foolad, 2007; Hayat et al., 2012). In many plants, an increase in proline levels under drought stress has been correlated with drought tolerance (Sankar et al., 2007). For example, proline content increased under drought stress in pea (*Pisum sativum* L.) (Alexieva et al., 2001), chickpea (*Cicer arietinum* L.) (Mafakheri et al., 2010), rice (*Oryza sativa* L.) (Lum et al., 2014), and soybean (Silvente et al., 2012). These studies indicate that plants with increased levels of proline would be better able to tolerate drought stress.

Treatment of plants with PGPR has been shown to lead to an increase in proline levels. This has been demonstrated in maize (Sandhya et al., 2010; Vardharajula et al., 2011; Naseem and Bano, 2014), sorghum (Grover et al., 2014), potato plants (Gururani et al., 2013), mung bean (Sarma and Saikia, 2014), and Arabidopsis (*Arabidopsis thaliana* L.) (Cohen et al., 2015) (Table 1). For example, Wang et al. (2012) reported that treatment of cucumber (*Cucumis sativa* L.) plants with a mixture of three PGPR strains (*Bacillus cereus* AR156, *Bacillus subtilis* SM21, and *Serratia* sp. XY21) increased leaf proline contents 3–4 fold relative to untreated controls. They suggested that the observed increase in leaf proline contributed to the observed drought tolerance by protecting the cucumber plants from over-dehydration. Treatment with PGPR has also been shown to increase concentrations of free amino acids and soluble sugars in maize (Sandhya et al., 2010; Vardharajula et al., 2011; Bano et al., 2013) (Table 1). Consequently, plants with increased levels of free amino acids and soluble sugars are suggested to tolerate drought stress.

2.5. Antioxidant metabolism

One of the inevitable consequences of drought stress is enhanced production of a variety of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), superoxide radical (O_2^-), and the hydroxyl radical ($HO^\bullet$) (Helena and Carvalho, 2008). These ROS slow down normal plant metabolism through oxidative damage to lipids, proteins and other macromolecules and may ultimately cause cell death (Mittler, 2002; Farooq et al., 2009; Hasanuzzaman et al., 2014).

To avoid the deleterious effects of ROS, plants have enzymatic and non-enzymatic oxidants also known as scavenging enzymes that act in an efficient and cooperative manner (Helena and Carvalho, 2008; Simova-Stoilova et al., 2008). These enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), glutathione reductase (GR), and ascorbate peroxidase (APX). ROS and the scavenging enzymes have been extensively reviewed (Helena and Carvalho, 2008; Farooq et al., 2009; Gill and Tuteja, 2010; Hasanuzzaman et al., 2014). Measuring activities of specific antioxidant enzymes is one of the approaches used to assess involvement of the scavenging system during drought stress. Several studies have detected a direct correlation between the level of induction of the antioxidant system and the degree of drought tolerance (Contour-Ansel et al., 2006; Guo et al., 2006). Drought-tolerant plants, therefore, develop effective ROS scavenging systems (Apel and Hirt, 2004; Huang et al., 2014).

Experiments investigating bacterial-mediated tolerance have measured activities of antioxidant enzymes as a way to assess the involvement of the scavenging system during drought stress. Specifically, these studies have investigated if treatment of plants with PGPR led to increases in the levels of antioxidant enzymes. Elevated accumulation of antioxidant enzymes, such as CAT, POX, and POX, serves to minimize oxidative injury and contributes to the drought tolerance. Treatment of potato plants with two PGPR strains, *Bacillus pumilus* str. DH-11 and *Bacillus firmus* str. 40, induced an increase in the levels of ROS-scavenging enzymes including ascorbate peroxidase and catalase. Gururani et al. (2013) reported a significant increase in several scavenging enzymes including APX, SOD, and CAT. The specific activity of CAT, for example, was up to 1.8 times higher under drought stress in PGPR-treated plants compared with that in non-treated plants. The elevation in ROS-scavenging enzymes was suggested as the main reason for the observed tolerance to drought stress in PGPR-treated potato plants. Saravanakumar et al. (2011) reported an increase in the activity of CAT in green gram plants treated with *Pseudomonas fluorescens* Pf1 and *Bacillus subtilis* EPB. This increase was correlated with the observed drought tolerance. An association of CAT production and drought tolerance has also been observed in cucumber plants (Wang et al., 2012), maize (Sandhya et al., 2010; Sarma and Saikia, 2014; Vardharajula et al., 2011), and wheat (Kasim et al., 2013) (Table 1).

Results generated from the above studies clearly point out an important role of ROS-scavenging enzymes in PGPR-mediated drought tolerance. Treatment of plants with selected PGPR induces the over-production of these ROS-scavenging enzymes, which in turn reduce levels of over-produced ROS, thereby conferring drought tolerance. However, there are several key questions to be answered that include determining the following: (1) whether the observed increases are dependent on the physiological status of the plant or the PGPR strain used; (2) if certain strains induce the production of certain ROS-scavenging enzymes; (3) whether there is a correlation between increases in ROS-scavenging enzymes with increasing drought duration; (4) if ROS-scavenging enzymes vary depending on the type of crop investigated; (5) if there are other ROS-scavenging enzymes not traditionally considered that may be induced solely by PGPR; and (6) how the observed results of PGPR treatment translate to the overall improved fitness of the plant.

2.6. Plant growth substances

Plant growth and development including shoot growth (see Section 2.2) is under the control of plant growth regulators (substances applied externally) and several phytohormones, including auxins, gibberellins (GAs), cytokinins (CKs), ethylene (ET), and abscisic acid (ABA) (Farooq et al., 2009). GAs and CKs promote plant growth while ethylene and abscisic acid inhibit growth (Taiz and Zeiger, 2010). Drought stress leads to an increase in the concentrations of substances that inhibit growth, thereby allowing the plants to regulate their water budget (Farooq et al., 2009). PGPR treatment promotes plant growth in the presence of drought stress by manipulating and modifying the phytohormone content (Dodd et al., 2010; Bresson et al., 2014). Such modifications include decreasing ET production (Glick et al., 1998; Belimov et al., 2009) and changing the balance of CKs and ABA (Figueiredo et al., 2008; Cohen et al., 2009) or IAA signaling (Contesto et al., 2010). These modifications have all been associated with drought stress tolerance when PGPR are applied and may contribute to the observed bacterial-mediated drought tolerance.

2.6.1. Auxin

Auxin, also referred to as indole-3-acetic acid (IAA), is an important regulator of plant growth and development, which influences a large number of diverse cellular functions including differentiation of vascular tissues, initiation of lateral and adventitious roots, stimulation of cell division, elongation of stems and roots, and orientation of root and shoot growth in response to light and gravity (Glick, 1995). Treatment of clover (*Trifolium repens* L.) plants with PGPR (*P. putida* and *B. megaterium*) increased shoot and root biomass and water content under drought stress, and these increases were correlated with increased IAA production also elicited by the applied PGPR (Marulanda et al., 2009). Treatment of Arabidopsis plants with PGPR *Phyllobacterium brassicacearum* strain STM196 resulted in increased lateral root length and modifications of the root architecture that led to the observed drought tolerance (Bresson et al., 2014). These increases in root length and modifications of the root architecture were correlated with increased IAA concentrations in rhizobacteria-treated plants (Contesto et al., 2010). These results suggest that bacterial-mediated drought tolerance may be partly mediated by IAA.

2.6.2. Ethylene and ACC deaminase

Ethylene (ET) is synthesized at higher rates as a result of several stress signals, including mechanical wounding, chemicals and metals, flooding, extreme temperatures, pathogen infection and drought (Johnson and Ecker, 1998). 1-Aminocyclopropane-1-carboxylate (ACC) is the immediate precursor of ET in higher plants. Its regulation has been suggested as the principal mechanism by which bacteria exert beneficial effects on plants under abiotic stress, including drought stress (Saleem et al., 2007). Some PGPR contain the enzyme ACC deaminase that hydrolyzes ACC into ammonia and alpha-ketobutyrate (Glick et al., 1998; Shaharoona et al., 2006) instead of converting it to ET. This cleavage reduces ACC and ethylene levels in the rhizoplane, thus providing a sink for ACC. Reduced ACC levels lead to a reduction in the levels of endogenous ET, thus eliminating the inhibitory effect of higher ET concentrations (Glick et al., 1998). Consequently, plants are able to maintain normal growth (Siddikee et al., 2011). Several other studies have documented the positive effect ET has on plants experiencing drought stress. For example, treatment of pea plants with *Pseudomonas* spp. containing ACC deaminase partially eliminated the effects of drought stress (Arshad et al., 2008). Similarly, treatment of tomato (*Solanum lycopersicum* L.) and pepper (*Capsicum annuum* L.) seedlings with *Achromobacter piechaudii* ARV8 reduced the production of ET, which may have contributed to the observed drought tolerance (Mayak et al., 2004). Lim and Kim (2013) showed that pepper plants treated with PGPR *Bacillus licheniformis* K11 tolerated drought stress and had better survival compared to non-treated plants. The authors argued that part of the observed drought tolerance may have been due to the fact that the PGPR applied produced ACC deaminase that reduced ET concentrations by cleaving ACC. It is important to point out that other studies have not found a correlation between ACC deaminase-producing bacteria and drought tolerance. For example, Wang et al. (2012) showed that the observed bacterial-mediated tolerance in cucumber plants did not involve the action of ACC deaminase. In addition, production of ACC deaminase is assayed *in vitro*, under culture conditions different from those found in soil. Hence, production *in vitro* does not assure production on roots growing under field conditions.

2.6.3. Abscisic acid

Abscisic acid (ABA) plays important roles in many physiological processes in plants and is crucial for the response to environmental stresses such as drought (Porcel et al., 2014; Cohen et al., 2015). Elevated ABA contents in plant organs under drought stress result in physiological changes that modulate plant growth (Farooq et al., 2009). PGPR that elevate the concentrations of ABA can enhance plants' ability to tolerate drought stress. Arkhipova et al. (2007) showed that *Bacillus* sp.-treated lettuce (*Lactuca sativa* L.) plants had increased amounts of ABA when compared to non-treated plants. They related the observed drought tolerance to increased ABA levels. Similarly, Cohen et al. (2008) reported that Arabidopsis plants that were treated with PGPR *Azospirillum brasilense* Sp245 had higher ABA content than non-treated plants, and they correlated the observed drought tolerance to the elevated ABA content. There are other explanations that have been advanced to explain the mechanisms by which ABA is able to enhance drought tolerance. One of the explanations is that ABA enhances drought tolerance via regulation of leaf transpiration and root hydraulic conductivity (Aroca et al., 2006). Another explanation is that ABA enhances drought tolerance via the up regulation of aquaporins (Zhou et al., 2012). From these explanations, it is clear that more research is required to understand exactly how bacterial-mediated modifications of ABA contents lead to the observed enhancement of drought tolerance in plants. Apart from ABA, cytokinins have also been reported to have a positive effect on plant growth under drought stress conditions (Timmusk and Wagner, 1999; Arkhipova et al., 2007; Liu et al., 2013).

3. Conclusion

This review of the literature indicates that certain strains of PGPR can help plants tolerate drought stress. Some of the physiological mechanisms that have been proposed include alterations in root architecture which results in improved water and nutrient uptake, with positive effects on the overall plant growth, increase in relative water content, increase in several organic and inorganic solutes as well as an increase in the synthesis of osmolytes including proline, increase in antioxidant enzymes that scavenge for reactive oxygen species, and manipulation of phytohormones including IAA, ABA, and CK. The research that has been published so far offers a glimpse into the intricate, complex and intriguing mechanisms underlying bacterial-mediated drought tolerance. New studies on these mechanisms will help improve strategies for the use of PGPR in mediating drought tolerance.

Although it is clear that various PGPR strains help plants mitigate drought stress, the mechanisms involved remain largely speculative. Understanding the mechanisms behind the observed PGPR-observed-drought tolerance mechanisms is important and will contribute to our ability to improve strategies for the use of these beneficial bacteria in mediating drought tolerance. Some of the fundamental questions that remain unanswered are: Is the observed bacterial-mediated drought tolerance due to IAA or there are other mechanisms that are yet to be discovered? Does the observed bacterial-mediated drought tolerance change with plants physiological status?

To understand fully the mechanisms behind the observed bacterial-mediated drought tolerance, there is a need for more systematic studies and screening protocols that would allow scientists to obtain accurate data that can be replicated with greater precision. Currently, it is difficult to compare the responses of plants submitted to a progressive drought stress, imposed by withdrawing water for several days, to the responses of PGPR-treated plants submitted to a more immediate drought stress, imposed by watering with an osmotically active agent such as PEG for several hours. Similarly, it is difficult to compare results generated from using sterilized soils to results obtained from agriculturally relevant soils. Moreover, there is the need to take into consideration the diversity of physical-chemical characteristics of soils which may be impacted by drought stress and the PGPR, and which may also further impact beneficial microbes including PGPR (Bérard et al., 2015). Further, results generated from using plants that have been subjected to different screening protocols cannot be easily compared.

Among the many adaptive traits that plants possess to endure drought, root system architecture is one of the most important. Plant growth-promoting rhizobacteria and microbial inoculants are specifically known for their excellent ability to promote root growth and significantly improve root architecture; changes that increase the volume of soil explored and consequently the uptake of water and nutrients. These alterations in root architecture are important traits for drought tolerance. However, there are fewer studies that have looked into understanding if the ability of PGPR to improve root growth and parameters, hence, enhanced drought tolerance can be harnessed in breeding programs.

Under natural environments, drought hardly ever occurs in the absence of other stress factors. Most important are biotic stressors such as plant diseases, pathogens and insects. Bacterial inoculants are widely known for their ability to induce systemic resistance to biotic stresses including plant diseases and insects. Therefore, identification of bacterial strains with potential to confer tolerance to biotic and abiotic stress would be valuable. Similarly, understanding how the mechanisms behind ISR and those behind observed bacterial-mediated drought tolerance overlap would be valuable.

The review of literature also suggests that bacterial collections from drought-prone areas performed better in increasing plants' tolerance to drought stress than those that were isolated from areas that do not experience drought. However, this relation, drawn from a few studies, needs to be validated in more cases. While there have been suggestions for this, it is not clear if higher percentages of PGPR isolated from dry environments will confer drought tolerance compared to collections of PGPR from “normal” agricultural fields. Overall, there is a continuing need to screen collections of PGPR for drought tolerance from diverse environments.

When designing methods to screen PGPR for drought tolerance, researchers face two complementary requirements. The first is to simplify the system in order to facilitate elucidation of the most important drought-adaptive features that may be expressed in plants that are treated with beneficial microbes. The second is to evaluate the broader value of these PGPR-related, drought-adaptive features in a breeding and agronomically sound context. Therefore, it is important to develop screening protocols that can be used by many scientists to evaluate PGPR-related, drought-adaptive features. This will help scientists create accurate data that can be replicated with greater precision. Although there are many studies reporting the capacity of PGPR to improve plants' tolerance of drought stress, the methods employed in the studies have been quite diverse. Additionally, most of the studies used sterile soils, and hence the relevance of the reported results to “real” field conditions is unclear. Moreover, soil sterilization may induce changes in soil physical-chemical characteristics. Such changes in the soil may affect plants response to drought stress (Bérard et al., 2015).

The outcome of PGPR-mediated drought tolerance may depend on the interaction between the strain of PGPR used and soil type (Cairns et al., 2009, 2011) as well as the plants ability to benefit from PGPR populations occurring naturally in the soils (Den Herder et al., 2010). Coarse sandy or gravelly soils have been reported to allow for thinner roots to develop, which lead to improved soil penetration, and may ultimately translate to drought tolerance (Cairns et al., 2009). In addition, the outcome of PGPR-mediated drought tolerance may be influenced by the duration and severity of the stress and the age and stage of the plant's development at the point of drought exposure. Moreover, the performance of effective PGPR strains must be evaluated under field conditions where plants are more likely to experience cyclic drought rather than continuous drought. In these evaluations the effect of PGPR on overall crop yield should be documented. Ultimately, integrating testing of PGPR strains into plant breeding strategies for drought tolerance may help agriculture adapt to continued climate change.

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