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REVIEW ARTICLE

Plant-growth-promoting rhizobacteria: drought stress alleviators to ameliorate crop production in drylands

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Abstract Drylands are known for being a drought stressed environment, which is an alarming constraint to crop productivity. To rescue plant growth in such stressful conditions, plant-growth-promoting rhizobacteria (PGPR) are a bulwark against drought stress and imperilled sustainability of agriculture in drylands. PGPR mitigates the impact of drought stress on plants through a process called rhizobacterial-induced drought endurance and resilience (RIDER), which includes physiological and biochemical changes. Various RIDER mechanisms include modification in phytohormonal levels, antioxidant defense, bacterial exopolysaccharides (EPS), and those associated with metabolic adjustments encompass accumulation of several compatible organic solutes like sugars, amino acids and polyamines. Production of heat-shock proteins (HSPs), dehydrins and volatile organic compounds (VOCs) also plays significant role in the acquisition of drought tolerance. Selection, screening and application of drought-stress-tolerant PGPRs to crops can help to overcome productivity limits in drylands.

Keywords Drought stress · PGPR · LapA · EPS · VOCs · RIDER

Introduction

Drylands (arid, semi-arid and dry sub-humid ecosystems) occupy approximately 40 % of the terrestrial surface and are so

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characterized due to low inputs of mean annual precipitation relative to mean annual potential evapotranspirational losses (Millennium Ecosystem Assessment 2005). Drought stress conditions prevailing in drylands impede crop production (Debaeke and Abdellah 2004), as restricted water availability changes physiological and biochemical processes that affect growth and yield. Drought stress engenders cellular dehydration, which evokes osmotic stress, thus hampering cell expansion (Bartels and Sunkar 2005). A water deficit causes diminished water potential and turgor loss, stomatal closure, and disruption of membrane integrity along with protein denaturation. Stomatal closure in response to water deficit causes a decline in the rate of photosynthesis. (Hoekstra et al. 2001; Chen and Murata 2008; Yang et al. 2010; Alcazar et al. 2011). A decrement in above-ground vegetative biomass accumulation due to water deficit subsequently trammels plant yield (Vile et al. 2012). Inoculation of plants with PGPR can amplify productivity of crops under a drought stress environment (Chanway and Holl 1994). Plant-growth-promoting rhizobacteria (PGPR) possess tremendous potential for modulating the physiological response to water deprivation, thus ensuring plant survival under such stressful conditions (Marasco et al. 2012). It has also been reported (Marulanda et al. 2007) that PGPR inoculated plants display increases in growth and yield to remarkable levels, as well as drought tolerance in arid and semiarid areas. Inoculation of *Arabidopsis thaliana* with *Phyllobacterium brassicacearum* strain STM196 enhanced resistance to moderate water deficit through a reproductive delay and changes in transpiration rate (Bresson et al. 2013). Inoculating cucumber plants with BBS (*Bacillus cereus* AR156, *Bacillus subtilis* SM21 and *Serratia* sp. XY21), a consortium of three plant-growth-promoting rhizobacterium strains decreased leaf monodehydroascorbate (MDA) content, and enhanced superoxide dismutase (SOD) activity, leaf proline content and photosynthetic activity in

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leaves over control under drought stress (Wang et al. 2012). It has also been reported that *Pinus halepensis* inoculated with *Pseudomonas fluorescens* (Rincon et al. 2008) and *Azospirillum*-inoculated rice (Ruiz-Sanchez et al. 2011) displayed increased photosynthetic capacity. Studies show that *Phyllobacterium brassicacearum* strain STM196 increased the length of lateral root (Kechid et al. 2013) as well as density and length of root hairs, which led to a greater exchange surface area with soil, and thus a higher water flux through the whole root system up to the leaves of the plant. The present review elucidates the role of PGPR to mitigate drought stress prevailing in drylands, and provides a new avenue of investigation to improve drought tolerance in agricultural crops.

Mechanism of action of PGPR to alleviate drought stress

Several mechanisms of drought resistance in plants have been proposed to be induced by PGPR, through elicitation of the so-called rhizobacterial-induced drought endurance and resilience (RIDER) process that involves various physiological and biochemical changes. It includes modifications in phytohormonal content (Khalid et al. 2006) and antioxidant defense. PGPR also produce osmolytes and bacterial exopolysaccharides (EPS) to ensure survival of plants under drought stressed conditions (Vanderlinde et al. 2010). Production ofheat-shock proteins (HSPs), (Berjak 2006), dehydrins (Timmusk and Wagner 1999) and volatile organic compounds (VOCs) (Ryu 2004) have been reported to impart drought tolerance to plants.

Phytohormonal modifications

One of the mechanisms employed by PGPR strains ensuring plant survival under drought stress is modification in content of bacterial phytohormones, such as auxins, gibberellins, cytokinins, ethylene and abscisic acid (ABA). Indole-3-acetic acid (IAA) has been reported to be effective in imparting osmotic stress tolerance to bacteria (Boiero et al. 2006). IAA production by PGPR causes modifications in root system architecture by increasing the number of root tips and the root surface area, thus increasing water and nutrient acquisition (Mantelin and Touraine 2004), which helps plants to cope water deficit (Egamberdieva and Kucharova 2009). Plants inoculated with *Pseudomonas putida* were able to survive drought stress due to the production of IAA (Marulanda et al. 2009). It has also been reported that bacterial VOCs from *Bacillus subtilis* strain GB03 cause growth promotion in *Arabidopsis* by upregulating transcripts involved in auxin homeostasis (Zhang et al. 2007). Pereyra et al. (2012) reported

that wheat seedlings inoculated with *Azospirillum* were able to cope with osmotic stress due to morphological modifications in coleoptile xylem architecture. This was attributed to upregulation of the indole-3-pyruvate decarboxylase gene and enhanced IAA synthesis in *Azospirillum*. Physiological modifications in soybean plants inoculated by the gibberellins secreting rhizobacterium *P. putida* H-2–3 improved plant growth under drought conditions (Sang-Mo et al. 2014). Production of ABA and gibberellins by *Azospirillum lipoferum* alleviated drought stress in maize plants (Cohen et al. 2009). Cellular dehydration induces biosynthesis of ABA, which is commonly known as a stress hormone because of its prodigious accumulation during water deficit. ABA is involved in water loss regulation by control of stomatal closure and stress signal transduction pathways (Yamaguchi et al. 1994). *Arabidopsis* plants inoculated with *Azospirillum brasilense* Sp245 had elevated levels of ABA compared to non-inoculated ones (Cohen et al. 2008). PGPR *Phyllobacterium brassicacearum* strain STM196, isolated from the rhizosphere of *Brassica napus*, improved osmotic stress tolerance in inoculated *Arabidopsis* plants by elevating ABA content, leading to decreased leaf transpiration (Bresson et al. 2013). Inoculation of *Platycladus orientalis* container seedlings with cytokinin-producing PGPR (*Bacillus subtilis*) has been reported to interfere with suppression of shoot growth, thus conferring drought stress resistance (Liu et al. 2013). Ethylene biosynthesis is increased during drought stress that results in reduced root and shoot growth. Investigations have indicated that certain PGPR strains possess enzyme ACC deaminase (Glick 2007), which can cleave the plant ethylene precursor ACC to ammonia and a-ketobutyrate, thereby lowering the ethylene level (Shaharoona et al. 2006). The deleterious effect of ethylene is abated by the removal of ACC, thus ameliorating plant stress and promoting plant growth (Glick 2007). Bacterial ACC deaminase (produced by PGPR strain *Achromobacter piechaudii* ARV8) confers tolerance against water deficit in tomato and pepper, resulting in significant increases in fresh and dry weights (Mayak et al. 2004). Inoculating pepper with *Bacillus licheniformis* K11 increased ACC deaminase production, thus imparting tolerance to cope with drought stress (Hui and Kim 2013). A co-relationship between IAA and the ethylene precursor ACC demonstrates the positive effects of IAA on root growth through the reduction of ethylene levels (Lugtenberg and Kamilova 2009). Inoculation of *Pisum* with *Pseudomonas* spp. (ACC deaminase containing bacteria) induced longer roots, which led to an increased uptake of water from soil under drought stress conditions (Zahir et al. 2008). Hontzeas et al. (2004) reported an increase in transcripts of genes related to cell division and proliferation and a downregulation of genes related to stress in canola plants colonized by the ACC-deaminase-producing strain *Enterobacter cloacae* UW4. Furthermore, it was also observed that auxin responsive genes were upregulated and those involved in ethylene

responses were downregulated in *Arabidopsis* plants colonized by *P. fluorescens* FPT9601-T5 (Wang et al. 2005).

Antioxidant defense

Generation of reactive oxygen species (ROS) such as super oxide radicals, hydrogen peroxide and hydroxyl radicals is generally at low levels in various plant organelles during ideal growth conditions (Apel and Hirt 2004). Water deficit conditions disrupt photosynthetic machinery and increase photorespiration, thus altering the normal homeostasis of cells, subsequently resulting in amassed production of ROS. Plants are armed with antioxidant defense systems constituting both enzymatic and non-enzymatic components that work in concert to alleviate the oxidative damage occurring during drought by the scavenging of ROS (Miller et al. 2010). Enzymatic components include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR). Non-enzymatic components contain cysteine, glutathione and ascorbic acid. Excess ROS results in enhanced lipid peroxidation and subsequent damage to proteins, DNA and lipids (Pompelli et al. 2010), but ROS also act as a signal for the activation of stress-response and defense pathways (Pitzschke et al. 2006). Therefore, it is imperative to regulate ROS levels through the coordination of ROS production and ROS scavenging systems to manage oxidative damage and simultaneously modulate signalling events. High activities of antioxidant enzymes are linked with oxidative stress tolerance in plants (Stajner et al. 1997). A significant relation exits between drought stress and antioxidant enzyme activity, but inoculation with PGPR mitigates the adverse effect of drought stress on antioxidant enzyme activity (Han and Lee 2005). Maize plants inoculated with *Bacillus* species developed protection against drought stress by reducing activity of the antioxidant enzymes APX and GPX (Vardharajula et al. 2011). Decreased activity of APX, CAT and GPX enzymes has also been reported in maize plants inoculated with EPS-producing bacteria, subsequently conferring stress tolerance to plants (Naseem and Bano 2014).

Accumulation of osmolytes

Plants under water deficit conditions have a greater requisite to adjust osmotically, in order to alleviate cell turgidity losses. The accumulation of osmolytes, such as proline, glycine betaine and trehalose, is the most frequent acclimatization response observed in plants and bacteria under water deficit conditions (Sakamoto and Murata 2002; Chen et al. 2007; Gruszka et al. 2007; Rodriguez et al. 2009). Protecting membrane integrity to prevent protein denaturation is essential

under drought stress (Hoekstra et al. 2001; Farooq et al. 2009). Elevated levels of amino acids, which are considered to be an indication of drought tolerance (Zhu 2002), have been reported in sorghum, pepper and wheat (Yadav et al. 2005). Accumulation of amino acids is due to hydrolysis of proteins, which occurs in response to changes contributing to osmotic adjustments (Iqbal et al. 2011; Krasensky and Jonak 2012). Proline synthesis results in osmotic adjustment, free radical scavenging and stabilization of subcellular structures in plant cells to overcome the detrimental effects of drought (Hare et al. 1998). Elevated proline levels have been reported to confer drought in plants (Valentovic et al. 2006; Chen et al. 2007). The repressed catabolic pathway leads to a colossal increase in proline content, which helps plants to amputate oxidative damage (Nayer and Reza 2008). PGPR exudate osmolytes in response to drought stress, which act synergistically with plant-produced osmolytes and stimulate plant growth (Paul and Nair 2008). Proline synthesis has been observed to be increased in osmotically stressed plants in the presence of *Burkholderia* (Barka et al. 2006). Inoculation with *Bacillus* strains significantly increased proline content in plants under drought stress; this is attributed to the upregulation of genes for P5CS, which acts during the biosynthesis of proline, as well as inhibiting expression of the gene for ProDH, which acts during metabolism of proline (Yoshiba et al. 1997). Introduction of proBA genes derived from *Bacillus subtilis* into *A. thaliana* lead to enhanced proline production, which is correlated to acquisition of osmotic tolerance in transgenic plants (Chen et al. 2007). Maize plants inoculated with *Bacillus* spp. displayed higher levels of proline, sugars and free amino acids, thus increasing plant biomass, relative water content, leaf water potential and root adhering soil/root tissue ratio (Vardharajula et al. 2011). Elevation of leaf proline levels in maize plants was triggered during drought stress, which was further enhanced on inoculation with *P. fluorescens* (Ansary et al. 2012). *Azospirillum lipoferum* has been reported to increase maize growth, while accumulating free amino acids and soluble sugars during drought stress (Qudsaia et al. 2013).

Accumulation of soluble sugars as osmolytes is another adaptive mechanism contributing towards osmotic adjustment under drought stress. It was reported that starch hydrolysis leads to higher sugar levels (Enebak et al. 1997). An increase in soluble sugar content in drought-stressed plants was observed (Dekankova et al. 2004). Starch depletion and higher sugar content were simultaneously observed in grapevine leaves (Patakas and Noitsakis 2001) during drought stress. Maize seedlings inoculated with *Bacillus* strains displayed higher sugar content due to starch degradation, thus imparting resistance to plants during drought stress (Nayer and Reza 2008). Sandhya et al. (2010) demonstrated that adverse effects of drought stress on plant growth under

uninoculated condition may be attributed to declining sugar levels. Maize seedlings inoculated with *Pseudomonas* spp. once increased soluble sugar content compared to uninoculated, thus indicating that inoculation leads to hydrolysis of starch, subsequently providing sugar for osmotic adjustment to negate the effect of drought stress (Bano and Fatima 2009). It is also well documented that enhanced biosynthesis of glycine betaine, like quaternary compounds, increases plants adaptability to various types of abiotic stresses (Sakamoto and Murata 2002; Chen and Murata 2008). While glycine betaine does not scavenge ROS directly, its synthesis produces H_2O_2 that activates ROS-scavenging enzymes and thus mitigates oxidative stress. Rapid accumulation of glycine betaine in *Oryza* inoculated with *Pseudomonas pseudoalcaligenes* has been reported to confer stress tolerance (Jha et al. 2011). *Arabidopsis* inoculation with the VOC-emitting strain *Bacillus subtilis* GB03 induced elevated glycine betaine content and its precursor choline levels in plants, imparting them with drought tolerance. However, GB03-induced drought tolerance was lost in the *xipotl* mutant of *Arabidopsis* with reduced choline production (Zhang et al. 2010). Trehalose, a non-reducing disaccharide, acts as osmoprotectant by stabilizing dehydrated enzymes and membranes; thus, its biosynthesis imparts osmoprotection in bacteria (Yang et al. 2010). Biosynthesis of trehalose in *A. brasilense* increased drought tolerance and biomass production in maize plants (Rodriguez et al. 2009). Enhanced trehalose accumulation was noticed in *Phaseolus vulgaris* plants inoculated with *Rhizobium etli*, which bestows drought stress tolerance to plants. A microarray analysis of 7200 expressed sequence tags from nodules of plants inoculated with PGPR overexpressing trehalose-6-phosphate synthase gene displayed upregulation of genes involved in stress tolerance, elucidating a plant signalling mechanism responding to bacterial trehalose (Suarez et al. 2008). Co-inoculation of *Rhizobium tropici* and *Paenibacillus polymyxa* (overexpressing a trehalose-6-phosphate synthase gene) increased plant growth and nodulation of *Phaseolus vulgaris* L. submitted to 3 weeks of drought stress, compared with plants inoculated with *Rhizobium* alone (Figueiredo et al. 2008). Mannitol, N-acetyl glutaminyl glutamine amide (NAGGN) and betaine are other compatible osmolytes that have been reported in *P. putida* (Kets et al. 1996). Polyamines are aliphatic nitrogen compounds ubiquitous in bacteria, plants and animals, and are involved in various metabolic and hormonal pathways that regulate plant growth and development as well as plant responses under drought stress (Alcazar et al. 2010). Enhanced root growth caused by cadaverine (polyamine) production helped *Oryza*

seedlings to mitigate osmotic stress when inoculated with *A. brasilense* Az39 (Cassan et al. 2009).

Production of EPS

EPS, components of bacterial biofilms, are hydrated compounds with 97 % water in a polymer matrix that imparts protection against desiccation (Bhaskar and Bhosle 2005). Increased EPS production by *Bacillus amyloliquefaciens* was observed during water stressed conditions as compared to non-stressed conditions. EPS increases microaggregates that improve plant growth under drought stress by increasing aggregate stability and RAS/RT (root-adhering soil/root tissue) ratio. Better aggregation of RAS leads to increased uptake of water and nutrients from rhizosphere soil, thus ensuring plant growth and survival under drought stress (Vardharajula et al. 2011). Colonization of wheat plants with *Pantoea agglomerans* (EPS-producing rhizobacteria) increased RAS dry mass to root tissue (RT) dry mass (RAS/RT) and enhanced water stability of adhering soil aggregates (Amellal et al. 1998). Inoculating sunflower plants with bacterial strain YAS34 (EPS-producing) also increased the RAS/RT ratio as well as RAS macroporosity, which helps to relieve the effect of water stress on sunflower growth, where crops are often subjected to long dry periods (Alami et al. 2000). EPS cause stabilization of soil aggregates and water regulation through plant roots, as they possess unique water-retaining properties (Roberson and Firestone 1992). Bensalim et al. (1998) reported that plants inoculated with EPS-producing bacteria display increased resistance to water stress. Cells under stress trigger production of guanine cyclases, subsequently leading to production of cyclic-di-GMP, protein adhesins and EPS involved in biofilm development (Borlee et al. 2010). EPS production by *Pseudomonas* spp. increased shoot and root length, and total dry weight in plants (Ahn et al. 2007). Inoculation with EPS-producing bacteria results in the development of an extensive root system which further increases shoot growth during water deficit (Awad et al. 2012). EPS-producing bacteria resulted in increased drought tolerance in maize (Naseem and Bano 2014). Almost all *Pseudomonas* species possess the capability to produce alginate, a major EPS (Halverson 2009) that maintains hydration of biofilms and attenuates oxidative stress. Drought tolerance enhancement of alginate might be due to its hygroscopic properties, but can also results from its role in biofilm architecture, which contributes to reduced evaporation loss. Dehydration conditions are known to induce ALG genes in the alginate biosynthesis gene cluster in *Pseudomonas aeruginosa*, which in addition also contains Psl, a mannose 13 galactose-rich EPS polymer, and Pel, a glucose-rich EPS which highlights significant roles of EPS under drought stress conditions (Chang et al. 2007). Recent research studies done on diverse bacterial

species have revealed an inventory of molecular determinants that participate during the process of bacterial colonization of surfaces and biofilm development. LapA and LapF are large extracellular proteins that play a pivotal role in the formation of biofilms by *P. putida*. LapA is first required for initial adhesion of individual bacteria to a surface, while LapF is involved in the development of mature biofilms (Martinez et al. 2014). Expression from the *lapA* promoter increases with high levels of c-di-GMP, while the opposite is true for *lapF*. The transcriptional regulator FleQ is required for modulation of *lapA* expression by c-di-GMP, but has a minor influence on *lapF*. It has also been reported that Fis (a small DNA binding and bending homo dimeric protein) binds to lapF promoter in vitro and represses the expression of LapF in *P. putida* (Lahesaare et al. 2014).

Production of other responses

Cell membrane proteins are at elevated risk of denaturation due to their direct contact with the environment. Desiccation due to water deficit causes protein aggregation, exposure of hydrophobic regions, subsequent inactivation of enzymes and changes in tertiary structure that prohibit their use as structural proteins (Allison et al. 1999). HSPs are upregulated upon exposure to drought stress. HSPs,which are also called chaperones, such as GroEL, DnaK, DnaJ, GroES, ClpB, ClpA, ClpX, sHSPs and proteases are involved in various stress responses (Munchbach et al. 1999). The primary function of these proteins is to govern the folding and refolding mechanism of stress natured proteins. Clp family proteases are implicated in the participation of multiple stress responses, suggesting they are key to bacterial fitness (Ekaza et al. 2001). Plant small heat shock proteins (sHSPs) function as molecular chaperones that facilitate native folding of proteins and play an important role during stress by preventing irreversible aggregation of denatured proteins (Sarkar et al. 2009). *P. aeruginosa* strain AMK-P6 isolated from a semi-arid location displayed induction of HSPs when exposed to high temperature (Ali et al. 2009). Pepper plants inoculated with *Bacillus licheniformis* K11 showed increased expression of genes *Cadhn*, *VA*, *sHSP* and *CaPR-10* under drought stress (Hui and Kim 2013). Timmusk and Wagner (1999) reported that induction of the drought responsive gene ERD15 (Early Response to Dehydration 15) and of an ABA-responsive gene, RAB18, confers drought tolerance in *A. thaliana* inoculated with *Paenibacillus polymyxa*. These genes, known as dehydrins (Group II late embryogenesis abundant proteins), are related to drought and cold stresses, whose expression is commonly upregulated by cellular water deficits. Many dehydrins are believed to function via stabilization of large-scale hydrophobic interactions such as membrane structures or hydrophobic patches of proteins (Borovskii et al. 2002).

Rocha et al. (2007) reported differential expression of 93 genes in sugarcane, including drought-responsive genes such as *MRB* and *WRKY* transcription factors under drought conditions; however, cotreatment of the same plant with *Herbaspirillum* spp. and *Gluconacetobacter diazotrophicus* resulted in the induction of stress resistance and salicylic acid biosynthesis genes. VOCs are commonly emitted from plants leaves, and these emissions are known to increase substantially under stress situations. VOCs released by *Bacillus* play a role in stress tolerance response (Ryu 2004). VOCs released by *Bacillus subtilis* strain GB03 stimulated *Arabidopsis* biosynthesis of choline (precursor of glycine betaine), a compatible solute involved in maintaining cell turgor under dehydrating conditions (Zhang et al. 2007). Another VOC, 2R, 3R-butanediol, has been reported to induce stomata closure in plants colonized by *Pseudomonas chlororaphis* O6, subsequently imparting stress resistance by interferring with various hormone signalling pathways comprising salicylic acid, ethylene, ABA and jasmonic acid (Cho et al. 2008).

Future prospects

The future trend needs to be in developing genetically modified PGPR over transgenic plants for boosting plant performance under drought stress, as it is simpler to modify a bacterium than complex higher organisms. Moreover, instead of engineering individual crops, a single, engineered inoculant can be employed for several crops, especially when using a non-specific genus like *Azospirillum*. PGPR strains development is hampered mainly by the fact that these organisms are sometimes unable to survive harsh environmental conditions, including high concentrations of environmental contaminants, salts, extremities of pH and temperature. Genetic engineering can be used to develop PGPR strains that are effective at low inoculum doses and under a variety of environmental conditions. It is urgent to develop more effective PGPR strains with longer shelf-lives to achieve sustainable crop production in drylands. Recent advances in the fields of microbiology, biotechnology, molecular biology and bioinformatics have opened up the way to identify novel genes involved in drought tolerance. Concepts of microbiotechnology application in agriculture should be employed to isolate indigenous PGPR from the stress-affected soils, and screening on the basis of their stress may be useful in rapid selection of efficient strains that could be used as bioinoculants for crops grown in drylands. Applications of bionanotechnology could also provide new avenues for the development of carrier-based microbial inocula. Use of nanoformulations may enhance the stability of PGPR with respect to dessication, heat and UV inactivation.

Conclusions

Drought stress hampers plant growth and development due to impaired biochemical and physiological mechanisms. It is perceived that RIDER mechanisms elicited by PGPR play a vital role in ensuring plant survival under drought stress in drylands, as they help plants to counteract osmotic and oxidative damages. Stress-tolerant abilities of PGPR strains can be harnessed for the betterment of dryland agriculture; identification, cloning and functional characterization of genes in such bacteria that confer resistance towards drought stress are needed.

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