Agriculture, Ecosystems and Environment 231 (2016) 68–78

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Rhizobacterial-plant interactions: Strategies ensuring plant growth promotion under drought and salinity stress

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ARTICLE INFO

Article history:
Received 20 March 2016
Received in revised form 6 June 2016
Accepted 19 June 2016
Available online xxx

Keywords:
Drought
Aalinity
IST
Rhizobacteria
Microarray
Signalling

ABSTRACT

Drought and salinity are major environmental stresses resulting in secondary stresses such as osmotic and oxidative stress (common to both stresses) as well as ionic stress (during salinity) causing alterations in physiological, biochemical and molecular processes in plants resulting in substantial loss to crop productivity. The major physiological parameters studied in plants during stressed conditions are malondialdehyde (MDA) content and relative electrical conductivity in leaves, relative water content (RWC), stomatal conductance (gs), Chl content and Chl-fluorescence. Plants inoculated with plant growth promoting rhizobacteria (PGPR) induce morphological and biochemical modifications resulting in enhanced tolerance to abiotic stresses defined as induced systemic tolerance (IST). Molecular approaches such as RNA differential display (RNA-DD), reverse transcriptase PCR (RT-PCR) microarray analysis, real time PCR, differential display PCR (DD-PCR) and illumina sequencing revealed PGPR inoculation caused upregulation of drought stress related genes such as *ERD15* (Early Response to Dehydration 15) and ABA-responsive gene, *RAB18* in *Arabidopsis* genes, *APX1* (ascorbate peroxidise), *SAMS1* (S-adenosyl-methionine synthetase), and *HSP17.8* (heat shock protein) in leaves of wheat, *Cadhn* (dehydrin-like protein), *VA* (Vacuolar ATPase), *sHSP* (Plant small heat shock proteins) and *CaPR-10* (Pathogenesis-related proteins) in pepper, dehydration responsive element binding protein (*DREB2A*), catalase (*CAT1*) and dehydrin (*DHN*) in mung, salt stress responsive genes such as *RAB18* (LEA), *RD29A*, *RD29B* regulons of ABRE (ABA-responsive elements) and DRE (dehydration responsive element) in *Arabidopsis*.

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http://dx.doi.org/10.1016/j.agee.2016.06.031
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1. Introduction

World population is increasing at an alarming rate and sufficient food production is a major challenge for the 21st century. However chemical fertilizers used in intensive agriculture to increase crop productivity creates serious environmental and health hazards. This is even more aggravated by climate change that causes environmental stresses such as drought and salinity which are major deterrents to plant growth responsible for decreased agricultural productivity (Zhang et al., 2010). Water deficit caused by drought lowers soil water potential, causing cell dehydration ultimately inhibiting cell expansion and cell division, thus resulting in osmotic stress (Fig. 1). In addition reactive oxygen species (ROS) produced during drought causes oxidative stress in plants (Vurukonda et al., 2016). Salinity in early phase creates water deficit conditions as higher ionic concentration alters the basic texture of the soil causing decreased soil porosity and subsequently reducing water uptake. Salinity creates osmotic stress thus it can be considered a form of a physiological drought however later higher accumulation of salts in transpiring leaves causes ionic toxicity in plants inducing leaf senescence (Munns and Tester, 2008). Thus cross talks occur between components of drought and salinity stress resulting in secondary stresses such as osmotic and oxidative stress (common to both) as well as ionic stress (during salinity) responsible for plant demise (Gill and Tuteja, 2010). The use of beneficial microbes as an integral component of agricultural practice is technology which should be endorsed to enhance crop productivity in a sustainable and environmentally friendly manner under environmental stress conditions (Gill et al., 2016).

Plant growth promoting rhizobacteria (PGPR) commonly known as rhizobacteria encompasses bacteria inhabiting rhizosphere and facilitating plant growth either through direct mechanisms which include production of phytohormones, enhanced availability of nutrients or by indirect mechanisms that include suppression of pathogens by antibiosis, synthesis of lytic enzymes and induced systemic resistance (ISR) (Glick, 2014). Plant growth promotory activities of rhizobacteria have been reported during drought stress in maize (Vardharajula et al., 2010), cucumber (Wang et al., 2012), mung bean (Sarma and Saikia, 2014) as well during salinity stress in tomato (Mayak et al., 2004), maize (Bano and Fatima, 2009), wheat (Tiwari et al., 2011) and white clover (Han et al., 2014). PGPR induces salt and drought stress tolerance in plants through elicitation of so-called induced systemic tolerance (IST) process (Fig. 2) that involves various physiological and biochemical changes (Yang et al., 2009). It includes modulation of phytohormonal levels (Egamberdieva, 2012; Liu et al., 2013; Glick, 2014; Kang et al., 2014b; Belimov et al., 2015; Cohen et al., 2015) (Fig. 2a), antioxidant defence (Wang et al., 2012; Armada et al., 2014) (Fig. 2b), osmotic adjustment (Sarma and Saikia, 2014) (Fig. 2c), stress responsive genes (Kim et al., 2014) (Fig. 2d), bacterial exopolysaccharides (Vardharajula et al., 2011; Timmusk et al., 2014) (Fig. 2e) and volatile organic compounds (Zhang et al., 2008) (Fig. 2f) that can improve stress tolerance in plants. Kaushal and Wani (2015) has reviewed rhizobacterial-induced drought endurance and resilience (RIDER) mechanisms, however it lacked salinity issues which is a major constraint along with drought characteristic of drylands and recent work. Present review is an attempt to provide an insight on the mechanism exhibited by rhizobacteria that promotes plant growth and

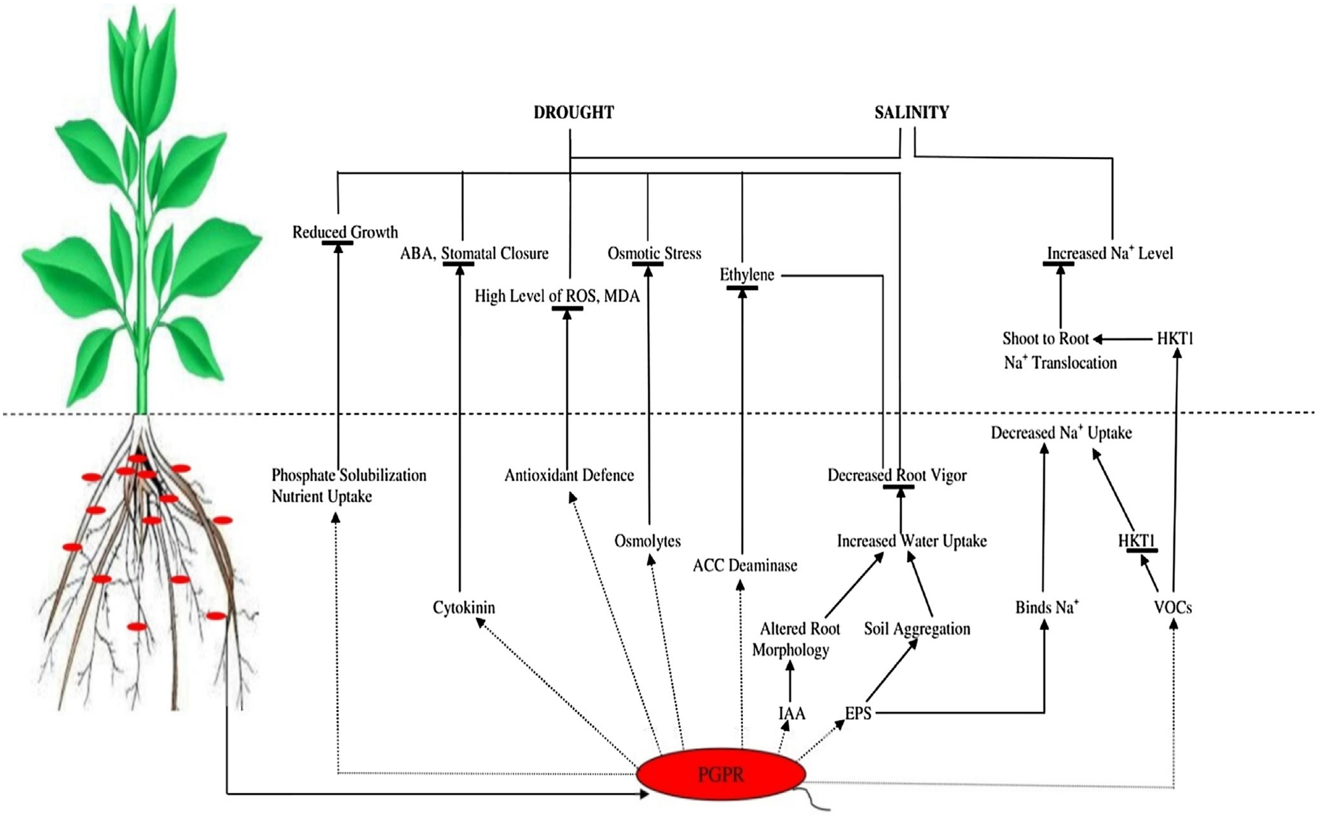

Fig. 1. Plant growth promoting activities exerted by PGPR (rhizobacteria) in relation to the specific mechanisms during drought and salinity stress. Solid arrows indicate drought and salinity stress induced effects on plants; broken arrows indicate rhizobacterial components negating stress effects.
Abbreviations: ABA, abscisic acid; ROS, reactive oxygen species; MDA, malondialdehyde; *HKT1*, high affinity K$^+$ transporter; ACC, 1-aminocyclopropane-1-carboxylate; VOCs, volatile organic compounds; IAA, indole-3-acetic acid; EPS, exopolysaccharides.

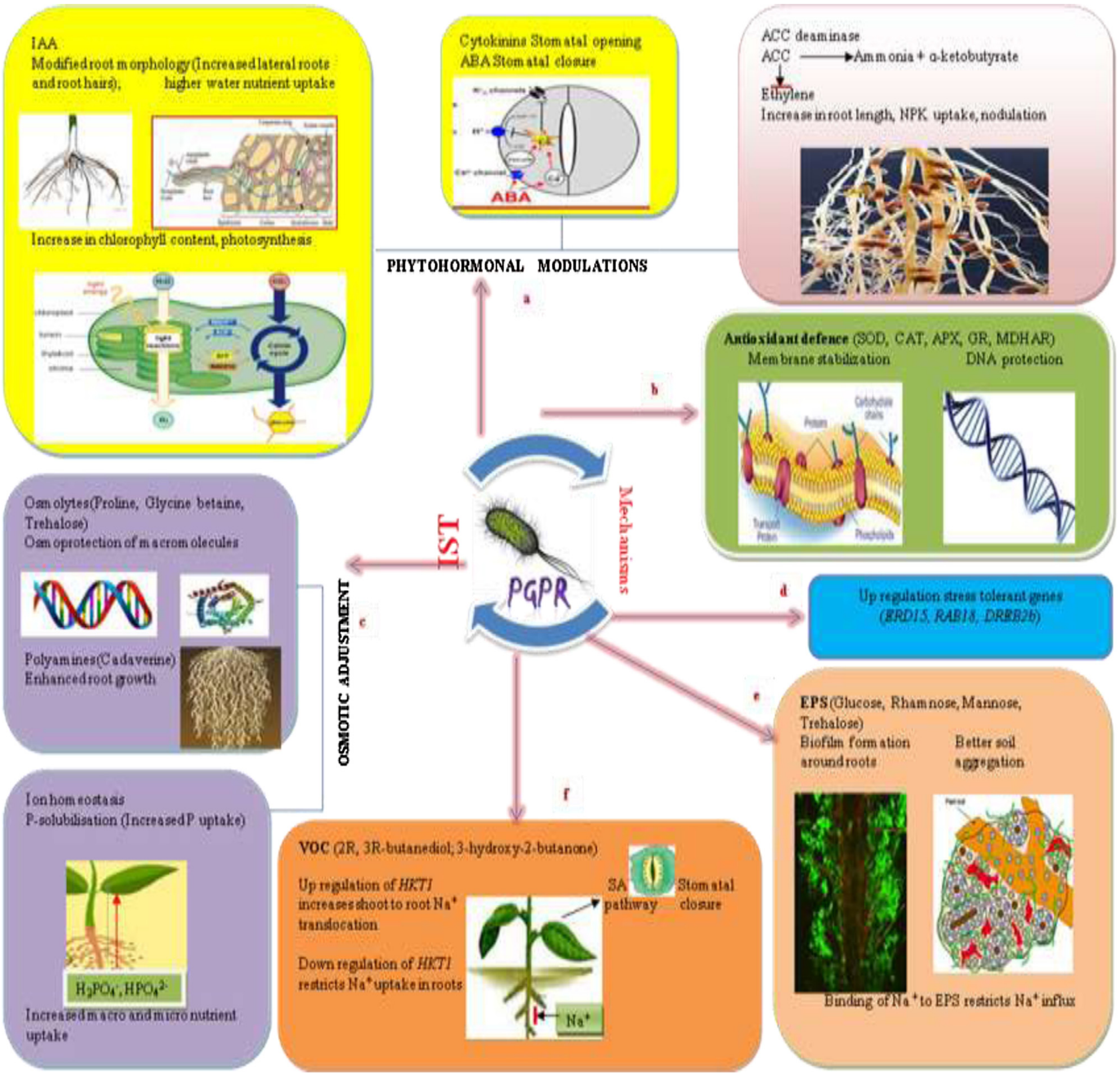

Fig. 2. Induced systemic tolerance (IST) mechanisms exhibited by rhizobacteria (PGPR) enhancing stress tolerance in plants.

productivity through enhanced salt and drought tolerance including updated research done in this context.

2. Demonstrated effects of rhizobacteria on stressed plants

Water deficit caused by both stresses triggers physiological, biochemical and molecular responses in plants to rescue plants from these stresses (Gill and Tuteja, 2010). Exposure of plants to both stresses causes physiological changes such as reduced turgor pressure, leading to closing of stomata and leaf senescence (Alcazar et al., 2011). Leaf senescence alters chlorophyll (Chl) properties and photosynthesis. The Malondialdehyde (MDA) content and relative electrical conductivity in leaves, relative water content (RWC), stomatal conductance (gs), Chl content and Chl-fluorescence are major physiological parameters studied in plants during stress (Murchie and Lawson, 2013). RWC and gs are important physiological parameters frequently employed to measure water status as they correspond to uptake of water by the roots, water lost by transpiration and stomatal closure. Chl content is important physiological trait measured during stress (Ma et al., 2012) as salinity and drought result in Chl peroxidation thus decreasing its content. An elevation of Chl content in plants leads to higher photosynthetic rate and starch production, which supports plant growth under salinity and drought stressed environment. Chl-fluorescence analysis an indicator of plant health is used to estimate PSII activity during stress which varies with plant water status thus is one of widely used parameters for measuring leaf physiological status. Dark adapted measurement of F_v/F_m (ratio of variable to maximal fluorescence) reflects maximum quantum efficiency of PSII photochemistry (Baker, 2008). Decrease in F_v/F_m indicates extent of increased leaf damages. MDA is among cytotoxic aldehydes produced and accumulated as a result of lipid peroxidation responsible for cell membrane damage. Increased MDA level and relative electrical conductivity in leaf are most intensively used as indicators of oxidative stress induced damage at the cellular level (Miao et al., 2010). PGPR strains affects plant physiology by increasing RWC, Chl content, F_v/F_m and reducing leaf MDA content thus enhancing plant growth under stress situations.

Wang et al. (2012) reported that cucumber plants inoculated with a consortium of three PGPR strains called BBS (*Bacillus cereus* AR156, *Bacillus subtilis* SM21 and *Serratia* spp. XY21) reduced both MDA content as well as relative electrical conductivity and increased Chl content (Chl a, b and a + b increased by 25.9%, 31.5%, and 27.4%, respectively) in leaves over control during drought. Similar

Table 1
Rhizobacterial role in alleviation of drought and salinity stress in plants.

Type of stress	Organism	Mechanism	Crop	References
Drought	*Pantoea agglomerans*	Exopolysaccharides (EPS)	Wheat	Amellal et al. (1998)
Drought	*Paenibacillus polymyxa*	Production of drought responsive genes *ERD15*, *RAB18*	*Arabidopsis*	Timmusk and Wagner (1999)
Drought	*Rhizobium* spp.	EPS	Sunflower	Alami et al. (2000)
Drought	*Bacillus*	Cytokinin	Lettuce	Arkhipova et al. (2007)
Drought	*Rhizobium tropici, Paenibacillus polymyxa*	Increased nodulation and nitrogen content	Common bean	Figueiredo et al. (2008)
Drought	*Variovorax paradoxus*	Decreased ethylene due to ACC deaminase (ACCd)	Pea	Belimov et al. (2009)
Drought	*Pseudomonas putida*	Improved soil aggregation due to EPS production	Sunflower	Vardharajula et al. (2009)
Drought	*Bacillus* spp.	Proline, Decreased ascorbate peroxidase (APX), glutathione peroxidase (GPX), catalase (CAT), EPS	Maize	Vardharajula et al. (2011)
Drought	*Bacillus cereus*, *Bacillus subtilis*, *Serratia* spp.	Expression of genes *cAPX*, *rbcL*, *rbcS*, Increased chlorophyll content	Cucumber	Wang et al. (2012)
Drought	*Variovorax paradoxus*	Increased nutrient uptake, Accd decreased root ABA	Pea	Jiang et al. (2012)
Drought	*Bacillus licheniformis*	Expression of genes *Cadhn, VA, sHSP, CaPR-10*, IAA	Pepper	Lim and Kim (2013)
Drought	*Bacillus thuringiensis*	Increased activity of glutathione reductase (GR),CAT, superoxide dismutase (SOD), Alginate, IAA, Reduced emissions of stress volatiles	Wheat	Timmusk et al. (2014)
Drought	*Pseudomonas aeruginosa*	IAA, Up regulation of *DREB2A, CAT1, DHN*, Increased activity of SOD, peroxidase (POX), CAT	Mung bean	Sarma and Saikia (2014)
Drought	*Acinetobacter, Pseudomonas*	IAA, EPS, Siderophore production	Grapevine	Rolli et al. (2014)
Drought	*Pseudomonas* spp.	EPS increased soil aggregation and water uptake	Maize	Naseem and Bano (2014)
Drought	*Burkholderia phytofirmans, Enterobacter* spp.	ACCd activity, Increased chlorophyll content	Maize	Naveed et al. (2014)
Drought	*Bacillus thuringiensis*	Decrease of GR, APX, Increased K$^+$ content, Micronutrient uptake	*Lavandula*	Armada et al. (2014)
Drought	*Bacillus thuringiensis*	Proline, APX activity decreased	*Trifolium repens*	Ortiz et al. (2015)
Drought	*Azospirillum brasilense*	High ABA, Proline	*Arabidopsis thaliana*	Cohen et al. (2015)
Drought, Salinity	*Achromobacter piechaudii*	ACCd	Tomato	Mayak et al. (2004)
Salinity	*Bacillus amylolequifaciens, Bacillus insolitus Microbacterium* spp., *P. syringae*	Restricted Na$^+$ influx due to rhizosheath formation by EPS	Wheat	Ashraf et al. (2004)
Salinity	*Pseudomonas fluorescens*	ACCd	Groundnut	Saravana Kumar and Samiyappan (2007)
Salinity	*Pseudomonas putida*	ACCd	Canola	Cheng et al. 2007
Salinity	*Bacillus subtilis*	VOCs regulates *HKT1* expression	*Arabidopsis thaliana*	Zhang et al. (2008)
Salinity	*Pseudomonas fluorescens, Enterobacter* spp.	ACCd, Increased NPK uptake	Maize	Nadeem et al. (2009)
Salinity	*Pseudomonas syringae, Pseudomonas fluorescens, Rhizobium phaseoli*	ACCd	Moong bean	Ahmad et al. (2011)
Salinity	*Bacillus subtilis, Arthrobacter*	Proline, Decreased CAT	Wheat	Upadhyay et al. (2011a,b)
Salinity	*Pseudomonas pseudoalcaligenes, Bacillus pumilus*	Increased concentration of glycine betaine (compatible solute) Decrease in APX, Increase in nitrate reductase activity	Rice	Jha et al. (2011)
Salinity	*Pseudomonas putida, Enterobacter cloacae, Serratia ficaria, Pseudomonas fluorescens*	Improved nutrition	Wheat	Nadeem et al. (2013)
Salinity	*Azotobacter chroococcum*	Increased chlorophyll, polyphenol, Increased K$^+$/Na$^+$ ratio	Maize	Rojas-Tapias et al. (2012)
Salinity	*Pseudomonas chlororaphis*	IAA	Cucumber, Tomato	Egamberdieva (2012)
Salinity	*Bacillus subtilis*	Chlorophyll content, Improved K$^+$/Na$^+$ ratio	White clover	Han et al. (2014)
Salinity	*Pseudomonas Aeruginosa*	EPS	Sunflower	Tewari and Arora (2014)
Salinity	*Exiguobacterium oxidotolerans*	Phosphate nutrition, Proline, K$^+$ uptake, Increased CAT, APX activity	Mentha	Bharti et al. (2014)
Salinity	*Bacillus* spp.	Increased activity of SOD, CAT, phenols, Increased proline, K$^+$ uptake	Gladiolus	Damodaran et al. (2014)
Salinity	*Pseudomonas* spp.	ACCd, Higher chlorophyll content	Tomato	Ali et al. (2014)
Salinity	*Enterobacter* spp.	IAA, Increased expression of salt stress responsive genes such as *DREB2b*, *RD29A*, *RD29B*, *RAB18* in *Arabidopsis*, Higher APX activities	Tomato, *Arabidopsis*	Kim et al. (2014)
Salinity	*Burkholdera cepacia, Promicromonospora* spp., *Acinetobacter calcoaceticus*	Reduced activities of CAT, POD, polyphenol peroxidase (PPO), Increased gibberellins	Cucumber	Kang et al. (2014a)

observation was reported during saline conditions as *Bacillus subtilis* strain GB03 inoculation increased Chl content and reduced MDA content in leaves of white clover (Han et al., 2014). It implicated ability of PGPR strains to reduce peroxidation of plasmalemma thus imparting protection to leaf cell membrane against damage caused due to drought and saline stress. Seedlings of the *Pinus halepensis* inoculated with *Pseudomonas fluorescens* Aur6 enhanced F_v/F_m and electron transport rate during drought stress (Rincon et al., 2008) *Arabidopsis* inoculation with *A. brasilense* inoculation increased relative leaf water content decreased gs and MDA content in plants subjected to drought (Cohen et al., 2015). Higher values of net photosynthesis (Pn), transpiration (E) and gs were observed in grapevine rootstocks K5BB plantlets inoculated with strains *Pseudomonas* spp., *Delftia* spp. in comparison to uninoculated control plants (Rolli et al., 2014). Naveed et al. (2014) reported that *Burkholderia phytofirmans* inoculation to cultivar Mazurka of maize improved photosynthesis (net-rate of CO_2 assimilation under light saturation) (75%), Chl content (22%) and efficiency of PSII (10%) as compared to control. Decrease in relative membrane permeability (RMP) was also observed in Mazurka (38–43%) and in Kaleo (29–41%), respectively as compared to control under reduced irrigation. *Arabidopsis* inoculation with *A. brasilense* showed elevated proline levels and relative leaf water content alongwith decreased gs and MDA content. As the basic mechanisms behind both stresses are similar they are discussed together under common headings (summarized in Table 1, Figs. 1 and 2).

2.1. Phytohormonal modulations

Production of phytohormones by various PGPR strains can modulate hormonal balance of plant hormones thus enhancing plant growth under stressed conditions. Drought and salinity are considered to be root borne stresses as the corresponding root metabolism during water deficit and ionic stress mainly affects the photosynthesis process. Thus the dynamic modulation of root system architecture (RSA) under stress conditions is a stress defensive mechanism (Postma and Lynch, 2011). The underlying mechanism of PGPR inoculation in facilitating plant growth under stressed conditions includes their capability to cause modifications in RSA which includes increase in number of root tips and root surface area (Vacheron et al., 2013) consequently increasing water and nutrient conductance (Egamberdieva and Kucharova, 2009). Production of indole-3-acetic acid (IAA) in inoculated plants increased shoot and root biomass alongwith increased water uptake thus ensuring plant growth and survival during drought (Marulanda et al., 2009). Increased root growth was observed in inoculated wheat seedlings, tomato and cucumber plants as IAA production by *P. chlororaphis* TSAU13 increased phytohormonal content in plants consequently enhancing water conductance and as compared to the uninoculated plants under saline conditions (Egamberdieva and Kucharova, 2009; Egamberdieva, 2012). Enhanced IAA synthesis due to up regulation of indole-3-pyruvate decarboxylase gene in *Azospirillum* caused morphological changes in the coleoptile xylem architecture (wider xylem vessels) in inoculated wheat seedlings. This lead to enhanced water conductance in coleoptiles that enabled plant to cope with osmotic stress (Pereyra et al., 2012). An increase in lateral root density and length as well as root hair density and length (59% and 200%), respectively was observed in drought-stressed *Bacillus thuringiensis* inoculated wheat plants due to bacterial production of IAA and ACCd (1-aminocyclopropane-1-carboxylate deaminase) (Timmusk et al., 2014). Kechid et al. (2013) highlighted role of *NRT2.5* and *NRT2.6* transporter genes of the *NRT2* family, in plant growth promotion by the PGPR strain STM196, these are involved in regulation of shoot: root biomass allocation and root development through improved plant nitrogen status. It would be interesting to investigate role of these transporter genes affecting IAA distribution in inoculated and noninoculated plants during drought and salinity conditions.

The endogenous gibberellin (GAs) affects process of seed germination, stem elongation, flowering, sex expression and senescence (Daviere and Achard, 2013). Production of GAs by *Azospirillum lipoferum* in inoculated maize plants conferred drought tolerance (Cohen et al., 2009). Elevated endogenous GAs in PGPR (*Burkholdera cepacia* SE4, *Promicromonospora* spp. SE188 and *Acinetobacter calcoaceticus* SE370) treated cucumber plants as compared to control plants augmented plant growth under drought and salinity stress (Kang et al., 2014a). Gibberellins secreting rhizobacterium, *Pseudomonas putida* H-2-3 inoculation to soybean plants alleviated drought and salinity stress (Kang et al., 2014b).

Cytokinins stimulate cell division, cell enlargement, shoot growth and causes stomatal opening. *Bacillus subtilis*, a cytokinin-producing rhizobacteria stimulated shoot biomass and reduced the root to shoot ratio in lettuce plants growing in drying soil (Arkhipova et al., 2007) implicating considerable root-to-shoot cytokinin signalling. Inoculating *Platycladeus orientalis* container seedlings with *Bacillus subtilis* (a cytokinin producing rhizobacteria) alleviated drought stress however the potential damage to *P. orientalis* seedlings of increased cytokinins on stomatal opening was reversed by elevated abscisic acid (ABA) level (Liu et al., 2013).

In response to water deficit stress caused by drought and salinity conditions, endogenous ABA is rapidly produced causing stomatal closure to minimize transpirational loss of water, mediates root branching to enhance water uptake in plants hence inducing leaf growth (Tardieu et al., 2010). Plant hormones jasmonic acid (JA) and salicylic acid (SA) protects the plants from oxidative stress damages (Iqbal and Ashraf, 2010). An elevated ABA content was observed in maize plants inoculated with *Azospirillum lipoferum* (Cohen et al., 2009) and in *Arabidopsis* plants inoculated with *Azospirillum brasilense* which augmented plant growth by modulating root architecture through increased lateral roots, stimulating photosynthetic pigments and retarded water loss by decreasing stomatal conductance during drought stress (Cohen et al., 2015). However a significant increase in leaf area and reduced ABA content was observed in PGPR (*Burkholdera cepacia* SE4, *Promicromonospora* spp. SE188 and *A. calcoaceticus* SE370) treated cucumber plants during salt and drought stress (Kang et al., 2014a). Similarly ABA reduction was observed in *P. putida* H-2-3 inoculated soybean plants over the control thus concluding that less stress was felt by inoculated plants. An increase in JA levels during both stresses was also observed however SA levels increased during drought and decreased during salinity (Kang et al., 2014b). Xiong and Yang (2003) showed activation of ABA induced mitogen activate protein kinases (MAPK) during biotic and abiotic stresses in rice plants but its suppression resulted in reduced tolerance to abiotic stresses thus their role in rhizobacterial IST should be investigated during drought and salinity.

During drought and salinity stress endogenous ethylene production increases which negatively affects root development and ultimately plant growth. Glick, (2014) reported that ACC (ethylene precursor), produced by the plant ACC synthase (ACS) in roots is exuded in the rhizosphere, where it is taken up by PGPR strains possessing enzyme ACC deaminase (ACCd) which hydrolyzes it to ammonia and a-ketobutyrate, subsequently lowering ethylene levels. Drought and salinity stress were alleviated in tomato and pepper plants on inoculation with *Achromobacter piechaudii* ARV8 having ACCd thus reducing ethylene levels and causing significant increases in fresh and dry weights (Mayak et al., 2004). Inoculating pepper plants with *Bacillus licheniformis* K11 promoted growth during drought stress due to decreased ethylene levels by ACCd activity (Lim and Kim 2013). *Pisum* plants inoculated with *Pseudomonas* spp. possessing ACCd activity showed elongated roots thus increasing water uptake during drought (Zahir et al., 2008). Inoculation of pea plants with *Variovorax paradoxus* 5C-2 attenuated increased xylem ACC levels caused due to drying soils thereby reducing shoot ethylene production thus negating drought induced reduction in nodulation and nitrogen seed content (Belimov et al., 2009). There have been numerous reports implicating plant growth-promoting role of ACCd producing rhizobacteria under salinity stress (Siddikee et al., 2010; Ali et al., 2014; Bharti et al., 2014). Nadeem et al. (2009) reported that rhizobacteria capable of producing ACCd improved mineral nutrition in plants which mitigated salt stress. Wang et al. (2005) reported in *Arabidopsis* plants colonization by *Pseudomonas fluorescens* FPT9601-T5 caused up regulation of auxin regulated genes but down regulation of ethylene responsive genes during biotic stress conditions. Root growth in PGPR inoculated plants by IAA through reduced ethylene levels is attributed to correlation between IAA and ethylene precursor ACC (Lugtenberg and Kamilova 2009). *V. paradoxus* 5C-2 (ACCd containing rhizobacteria) inoculation to pea plants decreased root ABA concentrations and accumulation by 40–60% but effect of ACCd on root to shoot ABA signalling needs to be investigated, thus implicating correlation between ACCd and ABA (Jiang et al., 2012).

2.2. Redox homeostasis: antioxidant defence

During normal growth conditions production of reactive oxygen species (ROS) as by-products of cellular metabolism is generally low in various plant organelles. However drought and salinity induces overproduction of ROS, causing altered redox homeostasis of cell. Increased ROS levels results in oxidative stress responsible for cell damages and ultimately cell death. Thus oxidative stress is generation of ROS above threshold levels causing imbalance in cell homeostasis. Elevated ROS level causes disruption of membrane bound proteins, decreased membrane fluidity, inhibition of protein synthesis, DNA damage and loss of enzymatic activities. Under stress conditions lipids are major targets, ROS attacks polyunsaturated fatty acids present in membrane phospholipids and initiates lipid peroxidation. As a result fatty acids are degraded leading to formation of variety of products, aldehydes being one of them (Gill and Tuteja, 2010). Plants are equipped with antioxidant defence system constituting enzymatic and non-enzymatic components to protect themselves against detrimental effects of ROS (Miller et al., 2010). Enzymatic components comprises superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR) and non-enzymatic components includes cysteine, glutathione, tocopherols and ascorbate. Usually higher activities of enzymatic components are correlated to oxidative stress resistance in plants, however at elevated levels detrimental effects of ROS are evident but it has recently become apparent that ROS at low levels acts as signalling molecule thus activating stress-response and defence pathways (Pitzschke et al., 2006). It has been reported that feedback and feedforward interactions occur between ROS and phytohormones for example hydrogen peroxide induces ethylene accumulation, ROS also affects auxin biosynthesis, transport, metabolism and signalling (Tognetti et al., 2012). Therefore, it is important to maintain equilibrium between ROS production and ROS quenching systems to manage oxidative damage and signalling events. There is substantial evidence reported that PGPR inoculated plants can survive under oxidative stress through manipulation of antioxidant enzymes (Han and Lee, 2005; Vardharajula et al., 2010; Wang et al., 2012; Kim et al., 2014). Salinity significantly increased GR and APX activity in lettuce leaves however PGPR inoculated plants displayed decreased activity of these enzymes as compared to control (Han and Lee, 2005). An increased activity of SOD, phenylalanine lyase and CAT was observed in PGPR inoculated gladiolus plants than uninoculated control plants during saline stress (Damodaran et al., 2014). Application of BBS consortium stimulated activity of SOD and *cAPX* transcription levels in cucumber plants that helped plants to combat oxidative stress caused during drought (Wang et al., 2012). CAT, peroxidase (POX) and SOD activity was accelerated in mung bean plants inoculated with *Pseudomonas* strain GGRJ21 under drought stress. It was also observed that CAT activity increased over 15–36 days and then declined however POX and SOD activities increased over 15–43 days (Sarma and Saikia, 2014). Kim et al. (2014) reported that tomato seedlings treated with *Enterobacter* spp. EJ01 showed higher APX activities (3.2 μmol/min/g fresh weight) than uninoculated seedlings (2.6 μmol/min/g fresh weight) under saline stressed conditions. It implied that PGPR inoculated plants can tolerate stress better than uninoculated ones. However decreased levels APX, CAT, glutathione peroxidase (GPX) was observed in maize plants inoculated with *Pseudomonas putida* GAP-P45, thus concluding that rhizobacterial inoculated plants experienced less stress as compared to uninoculated plants (Vardharajula et al., 2010). A similar adaptive drought response in *Bacillus thuringiensis* inoculated *Lavandula* plants was observed which was attributed to decrease of GR and APX activity (Armada et al., 2014). Reduced activities of CAT, POX, polyphenol oxidase and total polyphenol were observed in PGPR inoculated cucumber plants as compared to control which mitigated oxidative stress caused by drought and salinity (Kang et al., 2014a). Thus it can be concluded that PGPR inoculated plants have the ability to abate the oxidative damage but the mechanisms underlying behind variations found in the antioxidant enzymes levels as affected by PGPR in plants imparting stress are not clear yet. Various factors such as host plant, PGPR strain, type and duration of stress might be responsible for such variations in enzymatic levels. Moreover research should be done to examine ROS cross talks with phytohormones during PGPR plant interactions.

2.3. Production of stress-responsive genes

Genes induced in plants during drought and salinity stress forms gene products which are categorized into two major groups as functional proteins and regulatory proteins. The former group act directly in abiotic stress tolerance and includes chaperones, late embryogenesis-abundant proteins (LEA), mRNA-binding proteins, enzymes for osmolyte biosynthesis, water channel proteins and various proteases however latter group proteins are involved in signal transduction or expression of stress-responsive genes includes transcription factors, protein kinases and phosphatases, and calmodulin-binding proteins (Shinozaki and Yamaguchi-Shinozaki, 2007). A hallmark of stressed cells involves synthesis of heat shock proteins (HSPs) or molecular chaperones which act to prevent protein misfolding and aggregation to maintain protein homeostasis, also called proteostasis. These are classified according to their molecular weight as HSP70 (*DnaK*), HSP60 (*GroEL, GroES*), HSP90 and HSP100 (*ClpB,ClpA/C*) and the small HSP (*sHSP*) (Wang et al., 2004). LEA are small molecular weight proteins produced and accumulated during late embryo development and their expression correlates with the acquisition of tolerance against abiotic stresses (Shih et al., 2008).

Inoculation of plants with rhizobacteria causes up regulation of genes involved in stress tolerance. An up regulation of genes involved in stress tolerance, carbon and nitrogen metabolism was observed during macroarray analysis of 7200 expressed sequence tags from nodules of common bean plants inoculated with *Rhizobium etli* overexpressing trehalose-6-phosphate synthase gene (Suarez et al., 2008). Drought responsive genes, *ERD15* (Early

Response to Dehydration 15) and ABA-responsive gene, *RAB18* (LEA) were induced in *Arabidopsis* plants inoculated with *Paenibacillus polymyxa* in response to drought conditions (Timmusk and Wagner, 1999). BBS treatment maintained the transcriptional levels of ribulose-1,5-bisphosphate carboxy/oxygenase (RuBisCO) large and small subunits (*rbcL* and *rbcS)* genes in cucumber leaves thus helping plant to maintain photosynthesis under drought stress (Wang et al., 2012). Lim and Kim, (2013) reported that inoculating pepper plants with *Bacillus licheniformis* K11 induced expression of genes *Cadhn (*dehydrin-like protein)*, VA* (Vacuolar ATPase)*, sHSP* (Plant small heat shock proteins) and *CaPR-10* (Pathogenesis-related proteins) during drought stress. RT-PCR analysis revealed an upregulation of stress related genes *APX1* (ascorbate peroxidise)*, SAMS1* (S – adenosyl – methionine synthetase), and *HSP17.8* (heat shock protein) in leaves of wheat on priming with *Bacillus amyloliquefaciens* 5113 and *Azospirillum brasilense* NO40 thus mitigating drought stress (Kasim et al., 2013). Illumina sequencing (HiSeq 2000system) technique showed activation of ABA-dependent signalling genes in sugar cane cv. SP70-1143 on inoculation with *Gluconacetobacter diazotrophicus* PAL5 which imparted drought tolerance to sugarcane plants (Vargas et al., 2014). An up regulation of three drought stress-responsive genes, i.e., dehydration responsive element binding protein (*DREB2A*), catalase (*CAT1*) and dehydrin (*DHN*) were observed in mung plants inoculated with *Pseudomonas aeruginosa* GGRJ21 as compared to uninoculated plants which alleviated drought stress (Sarma and Saikia, 2014). *Enterobacter* spp. treatment in *Arabidopsis* increased the expression of salt stress responsive genes such as *RAB18* (LEA), *RD29A*, *RD29B* regulons of ABRE (ABA-responsive elements) and DRE (dehydration responsive element) as well as of transcription factor *DREB2b* (dehydration responsive element binding proteins), which modulates transcription of *RD29A*, *RD29B*, however activation of *DREB2b*, showed ABA-independent activation during salt stress (Kim et al., 2014).

2.4. Rhizobacterial exopolysaccharides (EPS) production

Bacterial EPS constituting homo or hetero polysaccharides attached to cell surface as a capsule or slime are responsible for architectural structure of biofilms. Polysaccharide composition varies among different species however common monomers include glucose, galactose and mannose. Neutral sugars (rhamnose and fucose), uronic acids (glucuronic and galacturonic acids), aminosugars (N-acetylamino sugars), organic ester-linked substituents and pyruvate ketals are other constituents of EPS. The acyl group confers EPS an anionic character, thus increasing its lipophilic character ultimately affecting its interactions with other polysaccharides and cations (Davey and O'Toole, 2000). EPS composition and production is influenced by bacterial growth phase, medium composition (carbon/nitrogen ratio) and environmental conditions (De Vuyst and Degeest, 1999). It has been reported that stress conditions triggers formation of guanine cyclises in cells subsequently leading to production of EPS (Borlee et al., 2010). In *A. brasilense* Sp7, *noeJ* and *noeL* genes encoding mannose-6-phosphate isomerise and GDP-mannose 4, 6-dehydratase respectively, are involved in EPS synthesis (Lerner et al., 2009). The enzymes encoded by these genes are involved in synthesis of mannose and fucose, constituents of EPS in *A. brasilense* (Vanbleu et al., 2005). In *P. aeruginosa,* water deficit conditions induces synthesis of *alg* genes in the alginate biosynthesis gene cluster having intricate role in alleviating drought stress (Chang et al., 2007).

EPS production by PGPR strains play significant role in supporting plant growth under water (Bensalim et al., 1998) and saline stress conditions, as it forms hydrophilic biofilms colonizing plant roots imparting protection against desiccation (Rossi et al., 2012). Water retention ability of PGPR strains varies according to polysaccharide constituents of EPS and it may exceed 70 g water per g polysaccharide (Vu et al., 2009). EPS producing bacteria *Azospirillum* enhanced resistance to water stress in plants due to amendments in the soil structure and aggregation properties (Bashan et al., 2004). Sunflower plants inoculated with *Rhizobium* spp. strain YAS34 (EPS-producing rhizobacteria) displayed improved dry biomass, nitrogen nutrition and water uptake of plants which was attributed to increased RAS/RT (root-adhering soil/root tissue) ratio and RAS macroporosity (Alami et al., 2000). Improved soil aggregation in rhizosphere of wheat seedlings was observed due to EPS production by rhizobia thus ameliorating plant growth under stress (Kaci et al., 2005). EPS production by drought tolerant *Pseudomonas* and *Bacillus* spp. increased RAS/RT ratio and macroaggregate stability which enhanced water and nutrient uptake from soil reserve (Vardharajula et al., 2009; Vardharajula et al., 2011). EPS production by PGPR strains during water deficit conditions results in development of extensive root system, increased shoot growth and total dry weight in plants (Ahn et al., 2007; Awad et al., 2012). Thus soil aggregation and water regulation affected in rhizosphere is a function of EPS. Production of exopolymeric substances having EPS by *Pseudomonas* spp. and *Acinetobacter* spp. promoted plant growth during water stress by formation of a hydrophilic biofilm around the roots that acted as an additional sheath to protect the root system from soil hardness (Rolli et al., 2014). EPS can act as emulsifiers imparting protection to biomembranes and in quenching ROS, hence conferring resistance to plant against water stress (Dimitrova et al., 2013). Alginate production induced drought tolerance in wheat plants inoculated by *Bacillus thuringiensis* (Timmusk et al., 2014). Wheat plants inoculated with EPS producing rhizobacteria were able to combat saline stress as rhizosheaths formed around plant roots due to EPS restricted Na^+ influx into the stele (Ashraf et al., 2004). Binding of Na^+ ions to EPS produced by PGPR alleviates salt toxicity as content of Na^+ available for plant uptake is reduced (Upadhyay et al., 2011a,b), thus resulting in improved plant nutrition and growth. EPS production by *P. aeruginosa* PF23 ameliorated salt stress in sunflower plants. Moreover variation in saccharide composition of EPS was observed during low saline levels EPS constituted mainly of glucose and galactose however during salinity EPS constituted glucose, rhamnose, mannose and trehalose protective role of these sugars in stress amelioration has been explained earlier (Tewari and Arora, 2014). There has been considerable research done so far implicating role of elevated levels of EPS produced by PGPR in alleviating stress conditions in plants but more detailed investigations need to be explored regarding variations in EPS composition under different stresses as structure and water retaining capacity of every constituent polysaccharide differs considerably. It has been reported that plant polysaccharides (arabinogalactan, pectin and xylan) act both as an environmental cue and building blocks for matrix synthesis in *Bacillus subtilis*. These polysaccharides induced matrix gene expression and were converted to UDP-galactose, which was utilized as a sugar source for EPS synthesis (Beauregard et al., 2013). Thus it is possible that during drought and salinity plants increase secretion of polysaccharides for EPS production in rhizosphere to protect themselves from stressed conditions.

2.5. Rhizobacterial and plant volatile organic compounds (VOCs)

Rhizobacterial VOCs are lipophilic liquids having high vapour pressures however their production is species-specific, they are involved in communications among organisms, cell to cell signalling and growth-promotion (Kai et al., 2009). Two VOCs, 2R, 3R-butanediol and 3-hydroxy-2-butanone (acetoin) produced by both *Bacillus amyloliquefaciens* IN937a and *Bacillus subtilis* GB03 enhanced growth in *Arabidopsis* plants by modulating expression of genes involved in cell wall structure (Ryu 2004). Zhang et al. (2007) reported that bacterial VOCs produced by *Bacillus subtilis* GB03 caused up regulation of transcripts involved in auxin homeostasis in *Arabidopsis* plants. VOCs also stimulated biosynthesis of choline and glycine betaine thus enhancing plant tolerance to osmotic stress (Zhang et al., 2010). VOCs produced by *Bacillus subtilis* caused tissue-specific gene regulation of high affinity K^+ transporter (*HKT1*) which restricted Na^+ uptake in roots and increased shoot to root translocation, ultimately imparting IST to plants against salinity (Zhang et al., 2008). 2R, 3R-butanediol, a VOC produced by *Pseudomonas chlororaphis* O6 caused stomatal closure in *Arabidopsis* plants thus inducing IST to drought however it involved various phytohormone signalling pathways comprising SA, ethylene and JA (Cho et al., 2008).

In plants VOCs are generally emitted from leaves in low levels but their levels are raised under stress situations (Opris et al., 2013). These act as signals to trigger stress defensive responses but production results in carbon losses which is fixed by photosynthesis (Holopainen, 2004). Timmusk et al. (2014) reported that seven terpenoid and benzenoid compounds (a-pinene, limonene, *para*-cymene, a-phellandrene, camphene, benzaldehyde, b-pinene and geranyl acetone) were emitted from wheat leaves during drought stress. Production of three VOCs (benzaldehyde, b-pinene and geranyl acetone) raised with increasing drought stress however *B. thuringiensis* primed wheat stressed plants displayed decreased emission of these VOCs as compared to nonprimed stressed plants thus resulting in reduced carbon loss and increased growth and productivity.

2.6. Osmotic adjustment

2.6.1. Production of macromolecular osmolytes

Accumulation of compatible solutes to maintain the cell turgidity within boundaries acceptable for normal cellular physiology known as osmotic adjustment is a major physiological mechanism occurring in plants to combat osmotic stress caused by drought and salinity (Gill and Tuteja, 2010). Production of compatible osmolytes by PGPR strains and plants in response to drought and salinity stress, acts in synergism to facilitate plant growth (Paul and Nair, 2008). Substrate availability in rhizosphere and duration of osmotic stress are key factors involved in production of a particular osmolyte in bacteria during stressed conditions. Trehalose synthesis and accumulation occurs in absence of organic osmolytes however glycine betaine and proline are accumulated preferentially by uptake (Burg and Ferraris, 2008). Proline is a major osmolyte produced in plants due to hydrolysis of proteins (Krasensky and Jonak, 2012) to encounter osmotic stress. During salinity and drought conditions proline has multifunctional role such as adjusting cytosolic acidity, reducing lipid peroxidation by scavenging ROS and stabilization of proteins and membranes (Gill and Tuteja, 2010). Plants inoculated with rhizobacteria display enhanced proline levels during drought and salinity (Vardharajula et al., 2011; Bharti et al., 2014; Damodaran et al., 2014; Sarma and Saikia, 2014) but whether it's due to denovo synthesis in plant i.e. due to up regulation of proline biosynthesis pathway (Yoshiba et al., 1997) or is absorbed from rhizosphere has not been clarified. Introduction of *proBA* genes derived from *Bacillus subtilis* into *A. thaliana* under the control of a strong promoter cauliflower mosaic virus 35 S (*CaMV35S*) increased proline production thus conferring osmotolerance to transgenic plants (Chen et al., 2007). Inoculation of tomato plants with *Bacillus polymyxa* showed higher proline secretion which helped plants to cope up with the drought stress (Shintu and Jayaram, 2015).

Accumulation of soluble sugars due to starch hydrolysis was observed in maize seedlings inoculated with PGPR strains to combat negative effect of drought stress (Bano and Fatima, 2009; Vardharajula et al., 2011). Biosynthesis of trehalose imparts osmotolerance to plants inoculated with PGPR as it stabilizes membranes and proteins. Inoculation of plants with PGPR strains which were genetically engineered to overexpress trehalose biosynthetic genes imparted drought tolerance by increasing osmolyte content. Enhanced trehalose synthesis was observed in common bean plants inoculated with *Rhizobium etli* (overexpressing trehalose-6-phosphate synthase) in comparison to plants inoculated with wild type strain (Suarez et al., 2008). Rodriguez-Salazar et al. (2009) reported that inoculating maize plants with *Azospirillum brasilense* overexpressing trehalose biosynthetic genes enhanced accumulation of trehalose thus conferring drought tolerance.

Glycine betaine like quaternary compounds imparts stress tolerance to plants as it is involved in stabilization of proteins, membranes, activity of RuBisCO (Chen and Murata, 2008). *Arabidopsis* plants inoculated with *Bacillus subtilis* GB03 displayed elevated glycine betaine and choline levels however this lacked in *xipotl* mutant of *Arabidopsis* (Zhang et al., 2010). It was reported that higher concentration of glycine betaine conferred salinity tolerance to rice plants inoculated with *Pseudomonas pseudoalcaligenes* (Jha et al., 2011).

Polyamines are low molecular weight compounds having aliphatic nitrogen structure, existing in almost all organisms and are implicated in cell division, root elongation, floral development, fruit ripening, leaf senescence, programmed cell death, DNA synthesis, transcription and translation (Alcazar et al., 2011). Enhanced root growth was observed in *Oryza* seedlings inoculated with *Azospirillum brasilense* Az39 due to cadaverine (polyamine) production by rhizobacteria which promoted plant growth during osmotic stress (Cassan et al., 2009).

2.6.2. Ion homeostasis and increased nutrition

Salinity inhibits plant growth due to increased Na^+ concentration and low K^+/Na^+ ratio in plant. During saline stress plants can protect themselves by restricting Na^+ entry, expelling Na^+ from roots and retrieving Na^+ from xylem stream for recirculation to roots (Chinnusamy et al., 2006). There has been several reports that PGPR inoculation to plants avoided the over accumulation of Na^+ and maintained the ion homeostasis under salinity stress conditions (Mayak et al., 2004; Bharti et al., 2014; Kang et al., 2014b; Tewari and Arora, 2014). VOCs produced from *Bacillus subtilis* decreased transcriptional expression of a high-affinity K^+ transporter (*HKT1*) in roots of *Arabidopsis* but it's up regulation in shoots, thereby decreasing Na^+ uptake by roots and Na^+ expulsion from the shoot (Zhang et al., 2008). Gladiolus plants inoculated with *Bacillus* spp. showed higher uptake of K^+ as compared to Na^+, resulting in lower Na^+/K^+ ratio during saline conditions (Damodaran et al., 2014).

Drought and salinity creates nutritional imbalances due to disturbance in conserved intracellular ionic milieu, thus to increase plant growth through increased nutrition of elements is essential to rescue plant under such conditions. Maize plants inoculated with ACCd producing rhizobacterial strain showed higher N, P and K uptake resulting in increased K^+/Na^+ ratio in plants thus improving growth under saline conditions (Nadeem et al., 2009). Inoculating pea plants with ACCd containing rhizobacterium *V. Paradoxus* 5C-2 enhanced nodulation thus increasing seed nitrogen content grown in drying soil. Ethylene inhibits nodulation thus by attenuating a drought induced elevation in xylem sap ACC content rhizobacteria promoted plant growth during drought (Belimov et al., 2009). Increased content of macronutrients (K^+, Ca^{2+} and Mg^{2+}) as well as micronutrients (Zn^{2+}

Mn^{2+} and Cu^{2+}) was observed in shoots of *Lavandula* plants inoculated with *B. thuringiensis* during drought conditions. Increased K^+ ions decreased stomatal conductance and evapotranspiration thus maintaining turgor pressure during water deficit conditions (Armada et al., 2014).

High salinity restricts uptake of phosphorus (P) in plants thereby inhibiting plant growth. Thus inoculating plants with PGPR strains capable of P solubilisation can enhance crop productivity under such stressed conditions (Prasad et al., 2012). PGPR strains which acts as P solubilizers causes mobilisation of insoluble phosphates thus enhancing P uptake in plants (Prasad et al., 2015). Bharti et al. (2014) reported that increased phosphate nutrition promoted growth and salinity stress tolerance in mentha plants inoculated with *Exiguobacterium oxidotolerans*.

2.7. Conclusions and perspectives

Rhizobacteria can play an important role in conferring resistance to plants against drought and salinity stresses thus ensuring increased crop yield. Although considerable information has been accumulated regarding rhizobacterial inoculated plant responses to drought and salinity stress, one major hindrance is in the understanding of cross talks between rhizobacteria and plants that mediate these responses. Deciphering knowledge generated from rhizobacterial mediated biotic stress tolerance i.e. ISR can help to understand in which direction future research should be focussed to unravel the underlying molecular mechanisms behind IST so as to increase abiotic stress tolerance and hence productivity in agricultural crops.

Conflict of interest

Authors declare no conflict of interest.

Acknowledgement

Financial help provided by ICRISAT is highly acknowledged.

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