CrossMark

Mechanisms of plant response to salt and drought stress and their alteration by rhizobacteria

Cinzia Forni · Daiana Duca · Bernard R. Glick

Abstract

Background Soil salinity and drought are an enormous worldwide problem for agriculture, horticulture and silviculture. The initial responses of plants to drought and salinity are similar; both are attributed to water deficit which inhibits plant growth and development.

Scope In this review, an overview of the major physiological and biochemical changes that occur in plants as a consequence of salt and drought stress is presented. In addition, the role of beneficial plant growth-promoting bacteria in ameliorating many of the deleterious consequences of salt and drought stress is discussed. Mechanisms used by plant growth-promoting bacteria to ameliorate the effects of these stresses include the production of cytokinin, indoleacetic acid, ACC deaminase, abscisic acid, trehalose, volatile organic compounds, and exopolysaccharides.

Conclusion Given the fundamental understanding of many of the mechanisms operating in plant-bacterial interactions, it is expected that the practical use of beneficial bacteria in agriculture, horticulture and silviculture will grow dramatically in the coming years.

C. Forni (✉)
Dipartimento di Biologia, Università degli Studi di Roma "Tor Vergata", Via della Ricerca Scientifica, 00133 Rome, Italy
e-mail: forni@uniroma2.it

D. Duca · B. R. Glick
Department of Biology, University of Waterloo, Waterloo, ON N2L 3G1, Canada

Introduction

During their lifetime, plants may face a wide range of environmental stress conditions, including temperature extremes, drought, salinity, flooding, pollutant toxicity and various oxidative stresses, all of which may negatively affect growth and limit plants from reaching their full growth potential. Worldwide, these abiotic stresses affect both natural settings and yields of many major crops (Mahajan and Tuteja 2005). More recently, climate change has shown a trend that leads to differences in rainfall patterns, temperature extremes, and soil composition changes, including salinization (Verslues et al. 2006). Given the many environmental challenges facing the agriculture industry, significant genetic improvement of crops (Araus et al. 2008) or the use of plant growth-promoting bacteria that interact with those crops (Glick 2012) are needed to maintain or increase crop yields, in the presence of suboptimal conditions including drought and high salinity

A. The problem of salt and drought stress

Drought and soil salinity threaten the sustainability of agriculture by negatively impacting plant growth and crop production (Bray et al. 2000). Therefore, a better understanding of the physiological variations in plants caused by stress is required to facilitate the identification of effective tolerance mechanisms.

In arid and semi-arid areas, even though irrigation helps to increase productivity, the over-exploitation of irrigation schemes, land clearing and some ill-conceived agricultural practices often leads to soil salinization. At the present time, nearly 20 % of all cultivated and irrigated lands (equivalent to 62 million ha) are negatively salt affected with some estimates being as high as 50 % (Khan et al. 2015). Soils are classified as saline when the electrical conductivity of a saturated paste soil extract (ECe) is 4 dS/m or more. This is equivalent to approximately 40 mM NaCl and generates an osmotic pressure of approximately 0.2 MPa (Munns and Tester 2008). Such an ECe significantly reduces the yield of most crops. In saline soils, NaCl is the most prevalent soluble salt, but a range of other dissolved salts, such as Na_2SO_4, $MgSO_4$, $CaSO_4$, $MgCl_2$, KCl, and Na_2CO_3, can also contribute to salinity stress (Munns and Tester 2008).

Besides salinity, frequent occurrences of drought and abnormal weather events have lately been observed all over the world (McNutt 2014). Almost every year, some region of the earth is hit by drought, damaging crops and disrupting agricultural production.

B. Differences and similarities between drought and salt stress

In principle, plants can be divided into those sensitive and those tolerant towards abiotic stresses (Dolferus 2014). Unfortunately, the difference between sensitivity and tolerance of a species to these stresses is often difficult to define, however, for crop plants it is usually related to yield.

Water deficit induces different responses in plants depending on three distinct stage of soil dehydration as reported by Serraj and Sinclair (2002). Most of the research on stress tolerance has been performed in laboratory experiments applying severe stress conditions, while the effect of milder stress has been less comprehensively studied. In field conditions, plants may be exposed to a wide natural variation in stresses that need to be considered to optimize crop performance (Collins et al. 2008). The more severe conditions that have been studied in some lab experiments have pointed the way towards successful (although still somewhat limited) field experiments (for example Saravanakumar and Samiyappan 2007).

The plant phenological stage, the severity and the length of exposure to the stress play an important role in the growth arrest or in determining the damage caused by stress. Osmotic stress can be a consequence of either salt or drought. Leaf growth is generally more sensitive to osmotic stress than root growth, e.g. mild osmotic stress can inhibits the growth of stems and leaves (Nonami and Boyer 1990; Bartels and Sunkar 2005). Reduced leaf size is generally considered to be beneficial to plants under water deficit conditions because of a concomitant reduced rate of transpiration, even though it may impact on the photosynthetic rate. In moderately dry climates such a strategy is not always as successful as expected, due to the direct evaporation from the soil when it remains partially wet (Tardieu 2005). Many mature plants subjected to drought respond by accelerating senescence and abscission of the older leaves (Gepstein and Glick 2013). This process is also known as leaf area adjustment, while the roots continue to elongate (Sharp et al. 1988). During drought stress, continued root elongation can be explained by the plant's need to reach groundwater (Brunner et al. 2015). In salt stress, heavier roots can accumulate higher amounts of chloride. Moya et al. (1999) determined the rate of chloride uptake by detecting this ion depletion in the media and reported that in *Citrus* species under saline conditions the root chloride uptake is a passive process. According to the authors the shoot to root ratio has a role in modulating chloride uptake in sensitive or tolerant species. The authors found differences in the amount of chloride uptake based on the growth of shoot/root ratio that tended to increase (in sensitive species) or decrease (in tolerant species) chloride uptake. Root pruning and defoliation showed a dependence of the uptake on root system size. Leaf biomass was responsible of leaf chloride accumulation.

At a cellular level the osmotic stress, caused by salt and drought, leads to different degrees of effects depending on the severity of the stress applied. Under severe stress, cell dehydration is a consequence of water removal from the cytoplasm into the extracellular space, thereby decreasing cytosolic and vacuolar volumes (Bartels and Sunkar 2005). These osmotic stresses limit plant growth due to photosynthetic decline and result in the production of reactive oxygen species (ROS) that may damage cell components as described below. Another consequence of osmotic stress involves autophagy, an intracellular degradation process that delivers cytoplasmic constituents to the vacuole (Han et al. 2011); this is considered to be a central component in the integrated stress response (Kroemer et al. 2010). Under osmotic stress, cytosolic and organelle proteins may have reduced activity or even undergo complete denaturation. The ability of autophagy to scavenge

oxidized proteins and to regulate ROS levels suggests its probable role in salt and drought stress. Some of the ATG genes (termed AuTophaGy-related genes), involved in the autophagocytosis, such as *AtATG8* in *Arabidopsis* have been reported to function in response to salt stress (Slavikova et al. 2008). Under normal growth conditions AtATG8 encoded proteins are assembled within autophagosome-resembling structure in the vacuoles, they modulate the effect of cytokinin on root architecture. Under salt stress the expression of recombinant protein AtAtg8 prevents the inhibition of primary root growth, the mechanism behind this effect is still unknown (Slavikova et al. 2008).

The major factor affecting plant water relations is the large difference in the concentration of water vapor between the plant's substomatal pore and the atmosphere, i.e. the driving force for the movement of water through the soil–plant–atmosphere continuum. The flux of water through the plant carries essential nutrients to the shoots, but in a saline environment, within the transpiration stream, any dissolved solutes can also be carried from the soil to the leaves, where they must be either re-circulated or excreted in order to prevent the toxicity of some ions. All plants have the ability to acquire ions that are then compartmentalized in the vacuoles. Under high salinity, excessive accumulation of Na^+ and Cl^- ions occurs and is detrimental to biochemical processes (Munns and Tester 2008) and interferes with nutrient availability as the soil dries. Na^+ uptake, transport and compartmentation are crucial for plant survival in environments with a high NaCl content, and salt tolerance is also based on appropriate osmotic adjustment that maintains cellular homeostasis.

Two important strategies have been adopted by plants exposed to the cytotoxicity of Na^+, e.g. improving ion compartmentation via use of a tonoplast Na^+/H^+ antiporter and/or increasing active Na^+ extrusion through Na^+/H^+ antiporters located in the plasma membrane, and vacuolar ion sequestration (Sun et al. 2009). The efficiency of these mechanisms confers different degrees of salt tolerance in various plant species, from glycophytes (salt sensitive plants) like rice (*Oryza sativa*), maize (*Zea mays*), soybean (*Glycine max*) and beans (*Phaseolus vulgaris*) to halophytes which can tolerate high salt concentrations (Mahajan and Tuteja 2005). Plant salt tolerance can also be achieved by specific regulation of gene expression involving both universal and unique changes to the transcriptome as indicated below.

According to Tavakkoli et al. (2010), plants grown in the presence of high NaCl concentrations accumulate both Na^+ and Cl^- simultaneously, although the effects of the two ions may differ. High Cl^- concentrations reduce the photosynthetic capacity and quantum yield due to chlorophyll degradation and impaired photosystem II efficiency. High Na^+ interferes with K^+ and Ca^{2+} nutrition, affecting stomatal regulation and decreasing photosynthesis and growth. Significantly, the other major detrimental impacts of drought and salinity on the cellular energy supply and redox homeostasis are balanced by global re-programming of plant primary metabolism and altered cellular architecture. Therefore, the physiological responses of plants to salinity are often similar to other environmental stresses, such as drought (Munns and Tester 2008) and may share common stress-tolerance pathways.

Severe drought stress removes water from cellular membranes, disrupting their normal bilayer structure. A further contribution to the loss of membrane integrity is due to the displacement of membrane proteins causing changes in selectivity, disruption of cellular compartmentalization and a loss of activity of membrane proteins (Mahajan and Tuteja 2005). Regulation of water movement across cellular membranes is controlled by a family of water channel proteins called aquaporins, a highly conserved protein family called major intrinsic protein (MIP) with several homologues in different plants. These proteins facilitate the efficient transport of water molecules, as well as small solutes across the plasma membrane and tonoplast (Chrispeels and Maurel 1994; Khan et al. 2015).

How do salt and drought stress affect the physiology of plants

Perception of stress, signaling and defense response

To cope with salt and drought stress, as well as other stresses, and to guarantee success in the adaptation to and survival of limiting growth conditions, plants have developed diverse stress-responsive signaling pathways and sophisticated defense mechanisms (Huang et al. 2012). Plants have multiple stress perception and signal transduction pathways, which may interact with one another at various steps in the pathways. Plants are also able to display strategic defense responses when two stressors occur at the same time, and this response can

be, in some cases, distinctive from the response to either individual stress (Koussevitzky et al. 2008).

To economize their molecular resources plants share stress protective responses, that require tight coordination of multiple signals.

The master regulators of transcription involved in the stress response and their key roles in plant adaptation during adverse environmental conditions have been described and reviewed (Balderas-Hernández et al. 2013). A small note of caution is relevant here: most of the studies on stress perception and response have been conducted using *Arabidopsis thaliana* and these results are not always applicable to other plant species, since the responses also depend on the genotype and developmental stage of the plant (for example Moya et al. 1999; Pandolfi et al. 2010).

The stress response depends on both genotypes and developmental stages and may exert positive and negative effects over plants status and growth. The response mechanisms confer different degrees of stress tolerance, which are largely determined by genetic plasticity in tolerant species. A gradual adaptation is required by non-tolerant species for expression of genes responsible for the acquisition of some degree of tolerance (Zhu 2001; Bartels and Sunkar 2005), demonstrating to some extent the presence of a genetic program for tolerance in non-tolerant plants. Hundreds of genes have been associated with the abiotic stress response. The latter involves the activation of mechanisms that prepare the plant for adaptation via transcriptional modulation that is crucial for the plant's genetic and biochemical networks. It is a multilevel reorganization that often involves massive changes depending on the severity and duration of one or more stresses (Atkinson and Urwin 2012). Usually the manipulation of such complex mechanisms are performed mainly considering the agronomic point of view and trying to avoid other strategies that might imply a toll in the production.

The proper regulation of stress-responsive genes is important for both recognition and response to stress conditions. The gene network involved in the signaling, responses and governing of diverse physiological functions, include various transcription factors (TFs) (Fig. 1). Recent advances in systems biology have facilitated the identification of a number of TFs that participate in regulating defense and modulate adaptive responses (Balderas-Hernández et al. 2013; Deinlein et al. 2014; Elfving et al. 2011; Golldack et al. 2011; Li et al. 2015; Nakashima et al. 2009; Nuruzzaman et al.

2013; Sakuraba et al. 2015). TFs and *cis*-elements function in the promoter regions of different stress-related genes, and the over-expression or suppression of these genes may improve a plant's tolerance to both biotic and abiotic stress. Therefore, TFs and *cis*-elements are considered important targets for the improvement of stress tolerance in crop species through genetic engineering. During plant development and stress responses another significant role is played by the DEAD-box RNA helicases that in plants are differentially regulated during development and in response to environmental stresses (Tuteja et al. 2014a, b).

A class of small non-coding micro RNAs (miRNAs) regulates gene expression at the post-transcriptional level; they play important roles in plant growth and development as well as abiotic stress responses in diverse species (Jeong and Green 2013; Ferdous et al. 2015). During abiotic stress, miRNAs may modulate the expression of genes involved in the stress response, as demonstrated by the phenotypic analysis of transgenic plants or mutants, in which the expression of either stress-responsive miRNAs or their target genes was modified (Jeong and Green 2013).

In plants, osmotic stress-responsive (OR) genes are normally silent and are activated under stress conditions. Microarray experiments helped to identify several OR genes (Kreps et al. 2002; Seki et al. 2002), including TFs and regulatory sequences in stress-inducible promoters. The role of OR genes involves the protection of cells from stress by the production of important metabolic proteins and the regulation of the downstream genes for signal transduction.

The majority of salt- and drought-induced genes appear to function in damage limitation or repair, e.g. late embryogenesis abundant (LEA) protein, osmotin, antifreeze proteins, chaperones and ubiquitination-related enzymes. *LEA/dehydrin*-type genes help in protecting the partner protein from degradation by proteinases that function to remove denatured and damaged proteins. Protein kinases (such as mitogen activated protein kinase, MAPK; calcium dependent protein kinase, CDPK; and receptor protein kinase), protein phosphatases (phosphoesterases and phospholipase C) and proteinases are also involved in the response (Fig. 1) (Yamaguchi-Shinozaki and Shinozaki 2006).

Downstream transduction of the stress signal, detected by plasma membrane receptors, generates different second messengers including inositol phosphates and oxidative bursts due to over-production of ROS and

Fig. 1 Overview of salt- and drought-stress responses in plants. Salt and drought affect cell physiology and metabolism and as consequence reduce plant growth. Stress signaling is perceived by the cell and elicits stress-signaling pathways that involve transcriptional remodeling, metabolic changes and altered hormonal activity. Bacterial activity may affect the latter. A positive stress response leads to plant tolerance of the stress while a negative response leads to growth inhibition
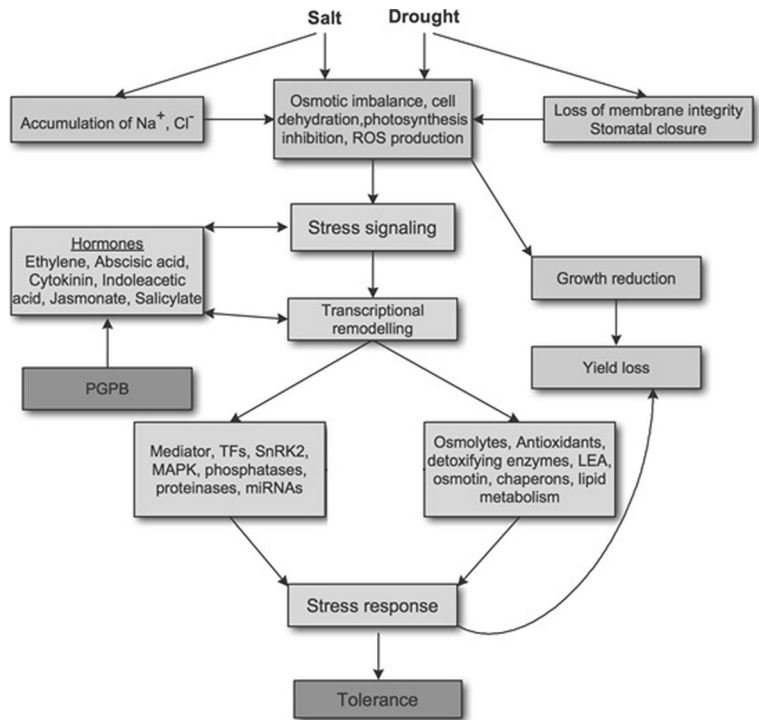
calcium (Mahajan and Tuteja 2005). For example, the presence of NaCl induces a rapid and transient increase of cytosolic calcium, which triggers signal transduction pathways that result in diverse cellular responses (Bartels and Sunkar 2005). Calcium is an important signaling molecule acting as a second messenger, whose intracellular concentration is sensed by calcium binding proteins (Tuteja and Mahajan 2007). These proteins are calmodulin, CDPKs (calcium-dependent protein kinase) and CBLs (calcineurin B-like proteins). These proteins, by interacting with their partners, start a phosphorylation cascade.

The discovery of *SOS* (Salt Overly Sensitive) genes paved the way for elucidation of a pathway linking Ca^{2+} signaling in response to salt stress (Zhu et al. 1998; Zhu 2002), clearly indicating the fundamental role played by this ion in plant abiotic stress response. The SOS pathway results in the exclusion of excess Na^+ ions out of the cell via the plasma membrane Na^+/H^+ antiporter and helps in reinstating cellular ion homeostasis. This pathway has three key components: SOS3, acting as a Ca^{2+} sensor; SOS2, a serine/threonine protein kinase and SOS1, a plasma membrane Na^+/H^+ antiporter (Türkan and Demiral 2009). The stress responsive genes represent the major target of this reaction. The products of

these genes contribute to plant adaptation and survival (Mahajan and Tuteja 2005).

The oxidative bursts, caused by over-production of ROS, depend on the imbalance between ROS production and ROS scavenging that occurs during stress (Miller et al. 2010). Powerful oxidants can react with most cellular components, producing severe damage to proteins, lipids and nucleic acids (oxidative stress situations) (Del Rio 2015). Plant cells try to overcome the detrimental effects of increased ROS concentrations either by eliciting the production of antioxidant compounds or by enhancing the activity of enzymes involved in ROS scavenging or both. Secondary metabolites, like phenolics, may play a protective role as antioxidant molecules in salt and drought stress. Thus, increasing phenolic concentrations has been reported in white clover and an interspecific hybrid of *Trifolium* exposed to drought (Ballizany et al. 2012; Nichols et al. 2015), and wild genotypes of barley exposed to either salt or drought or both stresses (Ahmed et al. 2015). Anthocyanins are also reported to increase in response to salt stress (Parida and Das 2005), while their concentration decreases in salt sensitive species (Daneshmand et al. 2010). Moreover, plant tissues containing anthocyanins are more resistant to drought (Chalker-Scott 1999).

The enhancement of the activity of enzymes involved in ROS-scavenging, such as guaiacol peroxidase (G-POD), superoxide dismutase (SOD), catalase (CAT), as well as enzymes of the ascorbate-glutathione cycle, such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) has also been reported (Noctor and Foyer 1998). Under stressful conditions, the enhanced activities of these enzymes appear to function as important components of the antioxidative defense system (Di Cori et al. 2013; Sharma and Dubey 2005). The coordinated activity of the multiple forms of these enzymes in different cell compartments allows a balance between the rate of formation and removal of ROS, and maintains hydrogen peroxide (H_2O_2) at levels required for cell signaling (Munns and Tester 2008). In fact, the role of ROS as important signal transduction molecules of the plant response to abiotic stresses has been acknowledged and widely accepted (Miller et al. 2010; Del Rio 2015). The key role of ROS as signal transduction molecules involves mediating responses to stresses, programmed cell death and different developmental stimuli (Miller et al. 2010). During ABA-mediated stress responses, ROS act to sustain plant survival under stress conditions.

Since both salt and drought ultimately result in dehydration and osmotic imbalance of the cell, the components of both stresses interact (cross talk) with each other, and the pathways act cooperatively to alleviate stress. Plant cells need to repair the stress damage through detoxification signals, and to then re-establish the homeostasis. The production of osmolytes mediates the osmotic adjustment by overcoming osmotic stress and re-establishing cellular homeostasis (Shinozaki and Yamaguchi-Shinozaki 1997; Zhu 2002). They also help the cells to maintain their hydrated state providing resistance against drought and cellular dehydration. These molecules are proline, glutamate, glycine-betaine, carnitine, mannitol, sorbitol, fructans, polyols, trehalose (Petrusa and Winicov 1997; Nawaz and Ashraf 2010; Redillas et al. 2012), sucrose, oligosaccharides and inorganic ions like K^+ (Mahajan and Tuteja 2005). The maintenance of hydrophilic interactions with membrane lipids and proteins, e.g. the preservation of membrane structural integrity, is based on the hydroxyl group of sugar alcohols that can substitute for the OH group of water. However, the tolerance towards stress is not always related to the presence of osmolytes. In some cases it has been reported that they play a vital role (Aziz

et al. 1998; Nawaz and Ashraf 2010), in other cases no significant changes in osmolyte concentration was detected (Di Cori et al. 2013). Therefore, the protective role of osmolytes seems to be species specific and depends on a number of factors, such as growth conditions and the plant developmental stage. Controversy exists about the role of osmolyte accumulation as a selection criterion in crop breeding programs to improve yield in dry environments; according to Serraj and Sinclair (2002) little evidence for a strong benefit of such accumulation on crop yield has been provided. These authors reported that in the literature a positive correlation between osmotic adjustment and yield is significant under severe drought stress, when the yields are very low.

Roles of hormones in plant stress response

Plant hormones play important roles in regulating the responses to a wide variety of internal and external stimuli. They can have direct and/or indirect effects on multiple plant functions. Hormones also play substantial roles in the response of plants to abiotic stress, in particular, abscisic acid (ABA), salicylic acid (SA), ethylene, jasmonates (JAs), and cytokinins (Fig. 1).

Two signal transduction pathways are triggered by salt and drought stresses based on their dependence on ABA (Takahashi et al. 2004; Golldack et al. 2014; Fujita et al. 2005; Yoshida et al. 2014). ABA, the most studied plant stress-signaling hormone, is the endogenous signal molecule enabling plants to survive severe adverse environmental conditions, such as salt and drought stress. In fact, the synthesis and accumulation of ABA, provides a fast response to abiotic stress, in particular water stress (Nakashima et al. 2009; Peleg and Blumwald 2011). In Arabidopsis thaliana, a large number of genes are associated with ABA de novo biosynthesis and the genes encoding ABA receptors and downstream signaling relays have been characterized (Cutler et al. 2010). However, the stress response may also involve ABA-independent signaling response pathways (Yamaguchi-Shinozaki and Shinozaki 2006). For example, osmotic stress-responsive gene expression is regulated by both ABA-dependent and -independent pathways (Yoshida et al. 2014).

ABA-responsive TFs (AREB/ABF) have a pivotal role in ABA-dependent gene activation, e.g. increased AREB1/ABF2, AREB2/ABF4 and ABF3 expression is induced by drought, high salinity and ABA in

vegetative tissues (Fujita et al. 2005), and based on overexpression data, these three AREB/ABFs are positive regulators of ABA signaling under drought stress conditions (Fujita et al. 2005; Yoshida et al. 2010, 2014). In *Arabidopsis* many drought-regulated genes are ABA-responsive genes; while, about a third of identified drought-regulated genes are not significantly regulated by ABA or ABA analogues, thus belonging to ABA-independent pathway (Huang et al. 2008). It is noteworthy to mention that promoter motif analyses of the latter genes revealed a significant over-representation of ABA-responsive promoter motifs (e.g. ABRE-like, ACGTABREMOTIFA2OSEM, and GADOWNAT) in the promoters of these genes. Therefore the expression of many of these genes could be at least partially linked to the ABA-dependent stress signal pathway (Huang et al. 2008).

The crucial role of DREBs (dehydration-responsive element binding) also referred to as CBF (C-repeat binding factor) proteins in drought, high salinity and heat stress have been pointed out in *Arabidopsis* (Sakuma et al. 2006a, b; Kim et al. 2012). *DREB2A* and *DREB2B* have been reported to function mainly in ABA-independent manner under osmotic, drought,high salinity and heat stress (Yoshida et al. 2014). *DREB2A* seems to function mainly in ABA-independent water stress–inducible gene expression, since its expression is strongly induced by drought and high-salinity stresses but not by ABA treatment (Liu et al. 1998). A better elucidation of the role of DREB2A under water stress has been made by Sakuma et al. (2006b), who reported that DREB2A regulates the drought-stress responsive genes expression, thus enhancing the stress tolerance.

Cytokinins are produced in the root tips and then translocated to the shoot through xylem. The effects of the cytokinins on stress tolerance are rather complex. Several studies have provided strong evidence of the existence of crosstalk among cytokinin, ABA, and stress signaling pathways (Tran et al. 2010; Nishiyama et al. 2011; Nishiyama et al. 2012). According to some authors, cytokinin and ABA may exert antagonistic activities during a number of growth and physiological processes, including stomatal opening, cotyledon expansion and seed germination (Javid et al. 2011).

The exposure of plants to water limiting conditions decreases cytokinin levels while excessive overproduction of cytokinins above a certain threshold causes abnormal organ and tissue development, but not drought tolerance (Gepstein and Glick 2013). In *Arabidospis,*

microarray expression analyses have determined that numerous genes encoding proteins with cytokinin signaling pathways are affected differently by various abiotic stresses. Javid et al. (2011) reported that the exogenous application of a synthetic cytokinin, kinetin, is capable of breaking stress-induced seed dormancy in crop plants such as tomato, barley and cotton. This positive effect of kinetin treatment may be due to the cytokinin activity as a direct free radical scavenger or it may be involved in antioxidant activity related to the protection of purine breakdown (Javid et al. 2011). Moreover, by enhancing root cytokinin synthesis it is possible to modify both shoot hormonal and ion status, thus ameliorating the salinity induced decreases in growth and yield (Ghanem et al. 2011). However, the positive role played by this hormone in ameliorating stress is still controversial based on the analyses of genes involved in stress response and regulated by cytokinin. Improved salt and drought stress tolerance in cytokinin deficient mutants has been reported by Nishiyama and coworkers (Nishiyama et al. 2011; Nishiyama et al. 2012). Tran et al. (2010) reported that the three cytokinin receptors AHK2, AHK3 and AHK4 act as negative regulators in both ABA-dependent and ABA-independent pathways.

JAs are involved in drought tolerance and in the response to salt stress, acting as positive regulators of salt tolerance (Dong et al. 2013; Qiu et al. 2014; Zhao et al. 2014). There is growing evidence that jasmonic acid and biologically active derivatives alleviate salt stress in plants. After methyl jasmonate application, enhanced amount of different antioxidants have been reported (Ahmad et al. 2016). However, it seems that the response to the jasmonate application is depending on the concentration and is species specific (Ahmad et al. 2016). The defensive effects of treatment with jasmonates have been mainly ascribed to the induction of antioxidant activity (Dar et al. 2015). Jasmonic acid enhances the activities of the enzyme cationic peroxidase, pathogenesis related proteins, like PR-1 and PR-10, and salt stress responsive proteins in roots of rice plants (Moons et al. 1997) and antioxidant enzymes in wheat (Qiu et al. 2014).

Much progress has been made to elucidate the role of jasmonates in signaling, cross-talking, jasmonate receptors etc., but not all the mechanisms behind the stress response have been clarified (Ahmad et al. 2016).

Salicylic acid (SA) and ethylene may be generated during stress responses (Mahajan and Tuteja 2005).

These molecules may amplify the initial signal, generating a second round of signaling that may follow either the same pathway or use other components of the signaling pathway. It is well known that SA plays an important role in plant responses to pathogens, but it is also involved in the regulation of plant growth, development, ripening, flowering, and responses to abiotic stresses (Miura and Tada 2014). The involvement of SA in the regulation of drought responses is based on the results obtained in different species (Munne-Bosch and Penuelas 2003; Bandurska and Stroìnski 2005). SA-inducible genes *PR1* and *PR2* are induced by drought stress (Miura and Tada 2014). Controversy still exists about the effect of SA on drought tolerance because some investigators have reported enhancement of drought tolerance by SA application, while others have reported a reduction (Miura and Tada 2014; Kang et al. 2012). An increase in endogenous hormone levels promotes stomatal closure; probably caused by the generation of ROS induced by SA (Melotto et al. 2006). Stomatal closure may also be caused by the exogenous application of SA leading to ROS, H_2O_2, and Ca^{2+} accumulation (Dong et al. 2001; Liu et al. 2003).

Low levels of ethylene have been reported to be involved in the defense against abiotic stress (Forni et al. 2012; Kazan 2015). However, when ethylene is produced above a threshold level, it is considered to be "stress ethylene" which is unfavorable in terms of root/shoot proliferation and other growth parameters and, thus hinders plant growth and development. The synthesis of stress ethylene occurs in two peaks of ethylene that are observed after stress exposure to plants. The first small peak of ethylene is believed to be responsible for transcription of genes that encode plant defensive/protective proteins. The second much larger ethylene peak, termed as "stress ethylene", is detrimental to plant growth and initiates processes like senescence, chlorosis and leaf abscission (Glick et al. 2007). Increased foliar ethylene evolution as a consequence of salinization has been detected as reviewed by Dodd and Pérez-Alfocea (2012). Ethylene production as a consequence of drought depends on the plant species. Thus, rapid drought stress elicits production of this hormone in wheat (Narayana et al. 1991), but not in common bean, cotton, or miniature rose (Morgan et al. 1990). Plant growth inhibition caused by stress ethylene may be reduced by PGPB that possess the enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACCD), as described below.

In contrast to JAs, which promotes stomatal closure, ethylene has been implicated in stomatal movement (Daszkowska-Golec and Szarejko 2013), either by inhibiting ABA-induced stomatal closure, or promoting stomatal closure by promoting NADPH oxidase-mediated ROS production in guard cells (Kazan 2015). Overall, these results are contradictory and the possible effects of ethylene-mediated stomatal movement on drought avoidance require further investigation.

Jung and Park (2011) reported that in transgenic plants the overexpression of the gene *YUCCA3* (*YUC3*), which encodes an auxin biosynthetic enzyme, caused sensitivity to salt in germinating seeds of *Arabidopsis*. High salt stress greatly remodels root architecture by altering auxin accumulation and redistribution. This means that the redistribution of auxin maxima formation in plant tissues is correlated with reduced growth, and therefore the reduction observed under stress conditions could also be the outcome of such altered auxin accumulation and redistribution (Ryu and Cho 2015; Dodd and Pérez-Alfocea 2012). Decreases in root branching in *Arabidopsis* are associated with changes in indole-3-acetic acid (IAA) response following the addition of 150 mM salt (Ulmasov et al. 1997; Dubrovsky et al. 2008; Contreras-Cornejo et al. 2014). Results showed that salinity inhibits auxin-inducible gene expression in primary root tips (Contreras-Cornejo et al. 2014). In another study, the accumulation of IAA in grey poplar trees exposed to 150 mM NaCl was compared to the non-treated controls. The concentration of IAA in poplar trees exposed to salt was decreased by 65–85 % (Luo et al. 2009; Dodd and Pérez-Alfocea 2012). Moreover, *Arabidopsis* mutants with defects in auxin transport were more sensitive to salt stress, suggesting that the transport of IAA between plant cells affects plant response to saline conditions (Wang et al. 2009; Contreras-Cornejo et al. 2014). Plant mutants with defects in transcription factors/receptors involved in the auxin response were dramatically affected by salt, showing up to 50 % inhibition in shoot fresh weight. Based on observations that high salt levels decreased the level of IAA in various plant tissues, researchers have shown that the addition of exogenous IAA could alleviate some of the adverse effects of salt stress (Afzal et al. 2005; Abd El-Samad 2013; Liu et al. 2015).

Polyamines are a group of ubiquitous aliphatic amine compounds, involved in plant development and physiology as well as in modulating the defense response to stress, such as salt and drought (Gill and Tuteja 2010).

The most common polyamines i.e., putrescine, spermidine and spermine, can be found in free, soluble conjugated and insoluble bound forms. A connection among polyamine metabolism, abiotic stress and ABA has been postulated (Jiménez-Bremont et al. 2007; Alcázar et al. 2010).

Under salt stress conditions, enhanced polyamine titre has been correlated with improved salinity tolerance (Zapata et al. 2004; Alcázar et al. 2010). Several authors suggested a possible beneficial activity of exogenous application of polyamines for the improvement of plant tolerance to abiotic stress (Gill and Tuteja 2010), but this is still an unresolved issue. For example, the response may depend on the organ developmental stage, since Pandolfi et al. (2010) reported that in the mature root zone of maize and *Arabidopsis* pre-treatment with 1 mM spermine, spermidine or putrescine prevented salt-induced K+ leak, while in the distal elongation zone opposite effect was observed. The authors suggested the existence of complex mechanism that involves polyamine transport, cyplasmic accumulation, metabolization and functional expression.

Plant growth-promoting bacteria

In healthy soils there are typically around 10^8 to 10^9 bacteria per gram of soil, with this number dropping down to as low as 10^4 in environmentally stressed soils (Schoenborn et al. 2004). Moreover, bacteria are not evenly distributed in soils, with the concentration of bacteria around the roots of plants, i.e., in the rhizosphere, generally being much higher than in the rest of the soil. This is a direct consequence of the many small molecules including sugars, amino acids and organic acids that are exuded from the roots of most plants and serve as a food source for many soil bacteria (Badri and Vivanco 2009). Soil bacteria may affect plants in their vicinity in several different ways. The interaction between soil bacteria and plants may be beneficial, harmful or neutral for the plant. Here, the focus is on beneficial soil bacteria, i.e. plant growth-promoting bacteria (PGPB). These bacteria employ a wide range of mechanisms to facilitate plant growth (Glick 2012). For example, they may promote plant growth directly, generally by either facilitating resource acquisition (e.g. Fe, P and N) or by modulating plant hormone levels. On the other hand, they may promote plant growth indirectly by

decreasing the inhibitory effects of various pathogenic agents on plant growth.

Plant growth is readily facilitated when plants are provided with optimal levels of various plant hormones including cytokinins, gibberellins, indoleacetic acid (IAA) and ethylene. However, a detailed understanding of the role of bacterially produced phytohormones is complicated by the fact that plants simultaneously produce precisely the same molecules. Some PGPB can synthesize either cytokinins or gibberellins or both (Salamone et al. 2001; Joo et al. 2005). Notwithstanding the demonstration that cytokinin producing bacteria may enhance plant growth in drying soil (Arkhipova et al. 2007), scientists have not yet elaborated a detailed understanding of the functioning of bacterial cytokinins or gibberellins in plant growth and development. In this case, the putative roles played by these two phytohormones is largely based on studies where purified hormones have been added to individual plants. While the scientific literature contains descriptions of a number of different naturally occurring auxins, by far the most common and the most studied auxin is IAA. This hormone affects plant cell division, extension and differentiation; stimulates seed and tuber germination; increases xylem and root development; initiates lateral and adventitious root formation; mediates responses to light, gravity and fluorescence; affects pigment formation; and can help to mediate resistance to various stresses (Spaepen and Vanderleyden 2011). Plant roots and shoots are both affected by IAA although at very different concentrations, with the optimal IAA level for roots being approximately five orders of magnitude lower than for shoots. The plant hormone ethylene is also active in modulating plant growth and development in a very wide range of concentrations, i.e. from about 0.05 μL/L to around 200 μL/L (Abeles et al. 1992). Ethylene in plants can promote root initiation, inhibit root elongation, promote fruit ripening and flower wilting, stimulate seed germination, promote leaf abscission, inhibit *Rhizobia* spp. and mycorrhizae plant interaction, and be produced as a response to various environmental stresses (Abeles et al. 1992). The enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase can cleave plant-derived ACC (the immediate biosynthetic precursor of ethylene) and thereby lower ethylene levels in plants (Glick et al. 1998). In practice, this means that PGPB that express ACC deaminase can modulate all of the above mentioned effects of ethylene on plants (Glick et al. 2007). Finally, it is necessary to

keep in mind that the functioning in plants of bacterial phytohormones is complicated by the interaction between these exogenous hormones and the endogenous plant mechanisms that regulate plant hormone homeostasis.

How do PGPB protect plants against stress

Using PGPB to protect plants from salt and drought stress

Many of the mechanisms that PGPB utilize to protect plants from salt and drought stress are interconnected and affect one another. Moreover, a detailed description of the nature of these interconnections remains, for the most part, to be elaborated. In addition, while PGPB can provide some protection against the inhibitory effects of salt or drought stress (e.g. by promoting plant growth), they may also alter plant gene expression so that the plant is less likely to succumb to these stresses. For example, various PGPB have been shown to increase plant production of the metabolites betaine, proline and trehalose as well as the synthesis of enzymes such as SOD and CAT that can detoxify reactive oxygen species (for example, Nautiyal et al. 2013).

Occasionally, conferring salt or drought tolerance upon plants can be unequivocally attributed to one or another specific PGPB mechanism. However, generally speaking, to prove that a particular bacterial mechanism is operative it is necessary to either inactivate a key gene, so that less (or none) of the gene product is made, or to overproduce the product of a key gene so that more of the gene product is made.

The involvement in plant biochemistry/physiology of a PGPB that either overproduces or underproduces a key metabolite or enzyme can then be demonstrated directly by comparing the behavior of the mutant to the wild-type strain. While this may seem obvious, it is nevertheless only very rarely done. Thus, many labs purport to understand the mechanisms that are operative in a specific plant-microbe interaction based solely on the presence of a certain biological activity within the PGPB that they have utilized. In fact, all that these workers have done is to show that there is a correlation between a certain trait and a specific behavior. This approach does not prove the involvement of the trait in question with the observed behavior. In addition, the literature contains a number of reports where the

mechanism(s) employed by a PGPB strain in conferring salt or drought tolerance to a plant is completely unknown (see Table 1). While these bacterial strains may be useful to the lab that reported the work, they do not provide other researchers with any clear mechanistic guidelines for selecting additional PGPB that are able to confer salt or drought tolerance to treated plants. Another problem with some of the literature reports on the use of PGPB to ameliorate the effects of drought or salt stress is that sometimes the work reported in these manuscripts does not include the characterization of the PGPB strain(s) to the genus and species level. Again, this makes it almost impossible for others to reproduce and build upon this published work.

Numerous bacterial traits have been suggested to be involved in conferring salt or drought tolerance to treated plants. These include the production of cytokinin, indoleacetic acid, ACC deaminase, abscisic acid, trehalose, volatile organic compounds, and exopolysaccharides. Some scientists have also reported that beneficial PGPB may synthesize siderophores and have the ability to solubilize phosphate, traits that are unlikely to contribute directly to conferring salt or drought tolerance to treated plants but nevertheless can contribute to a plant's overall health.

Cytokinin

Arkhipova et al. (2007) tested the hypothesis that the lowered levels of cytokinin in drought stressed plants help the plant to adapt to the decreased amount of water by (i) favoring carbon allocation to root growth and (ii) promoting stomatal closure. These workers added a cytokinin-producing *Bacillus* sp. strain to the soil where lettuce seedlings were grown. Inoculation of plants with this bacterium significantly increased both shoot/leaf cytokinin content and biomass (measured 20 days after seedling inoculation) of 12-day-old seedlings that were subjected to various levels of drought. In addition the bacterial treatment resulted in no or only a small increase in root biomass while the root length was decreased. From the results of this study, it was concluded that (i) the added bacterial strain elevated plant cytokinin levels slightly increasing root biomass and increased root sink strength thereby compensating for decreased root length and (ii) the increase in plant cytokinin did not result in the protective closure of stomata. This latter effect is attributed to the rise in plant ABA levels that accompanied the rise in cytokinin levels. The

Table 1 Amelioration of salt and/or drought stress in various plants by PGPB. The entries in this table are grouped according to the mechanisms used by the PGPB with the oldest paper listed first within each mechanism category

Plant	Microorganism	Conditions	Suggested mechanism(s)	Conditions	Reference
Lettuce	Bacillus sp.	Growth chamber	Cytokinin	Drought, 20 days of 30 % of soil water capacity	Arkhipova et al. 2007
Alfalfa	Sinorhizobium meliloti	Greenhouse	Cytokinin	Drought; 3–4 days of no water	Xu et al. 2012
Wheat	Pseudomonas aureantiaca, P. extremorientalis	Growth chamber	IAA	Salt, 100 mM NaCl	Egamberdieva 2009
Medicago truncatula	Sinorhizobium meliloti	Greenhouse, hydroponics	IAA	Salt, 150–300 mM NaCl	Bianco and Defez 2009
Silybum marianum	P. extremorientalis	Growth chamber	IAA	Salt, 25–100 mM NaCl	Egamberdieva et al. 2013
Cotton	P. putida, P. chlororaphis	Growth chamber	IAA	Salt, 100 mM NaCl and 100 mM Mg₂SO₄	Egamberdieva et al. 2015
Wheat	Halobacillus sp., Bacillus halodenitrificans	Laboratory	IAA, P solubilization, siderophores	Salt, 80–320 mM NaCl	Ramadoss et al. 2013
Rice	Serratia sp., P. sp.	Greenhouse	IAA, N-fixation, P solubilization	Salt, Electrical conductivity =0–16 dS/m	Nakbanpote et al. 2014
Sunflower	P. aeruginosa	Growth chamber	IAA, siderophores, exopolysaccharides	Salt, 125 mM NaCl	Tewari and Arora 2014
Arabidopsis thaliana	Micrococcus yunnanensis, Paenibacillus barengoltzii	Growth chamber	IAA, P solubilization, siderophores	Salt, 200 mM NaCl; drought, 5 days of no water	Sukweenadhi et al. 2015
Groundnut	P. aeruginosa	Greenhouse	IAA, P solubilization	Salt, Electrical conductivity =0–6 dS/m	Ghorai et al. 2015
Beans	Rhizobium etli	Greenhouse	Trehalose	Drought, 3 weeks of no water	Suarez et al. 2008
Maize	Azospirillum brasilense	Greenhouse	Trehalose	Drought, 10 days with no water	Rodriguez-Salazar et al. 2009
Beans	Rhizobium etli	Growth chamber	Trehalose	Drought, 5 or 10 days with no water	Reina-Bueno et al. 2012
Wheat	Bacillus thuringiensis	Growth chamber	Volatile organic compounds	Drought, 10 or 14 days with no water	Timmusk et al. 2014
Tomato, pepper	Achromobacter piechaudii	Growth chamber	ACC deaminase	Drought, 7 or 12 days with no water	Mayak et al. 2004a, 2004b
Tomato	Achromobacter piechaudii	Growth chamber	ACC deaminase	Salt, 0–172 mM NaCl	Mayak et al. 2004a
Groundnut	P. fluorescens	Laboratory, field	ACC deaminase	Salt, 120 mM NaCl	Saravanakumar and Samiyappan 2007
Canola	P. putida	Growth chamber	ACC deaminase	Salt, 1 M NaCl at 10 °C and 1 mM NaCl at 20 °C	Cheng et al. 2007
Cucumber	P. putida	Growth chamber	ACC deaminase	Salt, 0–200 mM NaCl	Gamalero et al. 2010
Cucumber	P. fluorescens	Greenhouse	ACC deaminase, siderophore	Salt, 659 mS m⁻¹	Egamberdieva et al. 2011; Cho et al. 2015
Red pepper	Brevibacterium iodinum, Bacillus licheniformis, Zhihengliuela alba	Greenhouse	ACC deaminase	Salt, 100–200 mM NaCl	Siddikee et al. 2011
Barley	Paenibacillus polymyxa, Bacillus megaterium, Bacillus cereus, bacillus pumilus	Field	ACC deaminase	Drought, naturally occurring	Timmusk et al. 2011
Tomato	P. mendocina	Growth chamber, greenhouse	ACC deaminase	Salt, 172–207 mM NaCl	Sadmia et al. 2011
Soybean	P. sp.	Growth chamber	ACC deaminase, IAA	Salt, 200 mM NaCl	Kasotia et al. 2012
Chickpea	Mesorhizobium ciceri	Growth chamber	ACC deaminase	Salt, 0.15 % NaCl	Brigido et al. 2013
Spring wheat	Variovorax paradoxus	Greenhouse	ACC deaminase	Drought. No water until soil matric potential was −30 kPa	Chen et al. 2013
Mung bean, bean, peanut	Bradyrhizobium sp., Enterobacter sp., Chryseobacterium sp.	Growth chamber	ACC deaminase, IAA	Salt, 50 mM NaCl; drought, no water until plants showed visible signs of stress	Tittabutr et al. 2013

Table 1 (continued)

Plant	Microorganism	Suggested mechanism(s)	Conditions	Conditions	Reference
Mung bean	P. syringae, P. fluorescens	ACC deaminase, IAA	Growth chamber	Salt, Electrical conductivity =4–12 dS/m	Ahmad et al. 2013
Cotton	Klebsiella oxytoca	ACC deaminase, IAA	Greenhouse	Salt, 1.3–3.5 g NaCl kg^{-1} soil	Yue et al. 2007; Liu et al. 2013
Pepper	Bacillus licheniformis	ACC deaminase, IAA	Growth chamber	Drought, 10–15 days of no water	Lim and Kim 2013
Wheat	Serratia spp., Aerococcus spp.	ACC deaminase	Jars with soil	Drought, 15–60 % of water holding capacity	Bangash et al. 2013
Mung bean	Rhizobium sp., PGPB	ACC deaminase	Field	Salt, Electrical conductivity =5.6 dS/m	Aamir et al. 2013
Maize	P. syringae, P. fluorescens	ACC deaminase	Field	Drought, water to 50 % of field capacity	Zafar-ul-Hye et al. 2014
Barley, oats	P. putida, P. sp., P. corrugata	ACC deaminase	Greenhouse, field	Salt, Electrical conductivity =9.4 dS/m	Chang et al. 2014
Limonium sinense (Girard) Kuntze	Bacillus, Arthrobacter, Streptomyces, Isoptericola	ACC deaminase	Greenhouse	Salt, 0–250 mMNaCl	Qin et al. 2014
Tomato, Arabidopsis	Enterobacter sp.	ACC deaminase, IAA	Growth chamber	Salt, 200 mM NaCl	Kim et al. 2014
Tomato	P. putida	ACC deaminase	Greenhouse	Salt, 0–190 mM NaCl	Yan et al. 2014
Tomato	P. fluorescens, P. migulae	ACC deaminase	Greenhouse	Salt, 0–185 mM NaCl	Ali et al. 2014
Rice	P. stutzeri	ACC deaminase	Growth chamber	Salt, 120 and 2000 mM NaCl	Han et al. 2015
Potato	Achromobacter xylosoxidans, Pseudomonas oxyzihabitans, Variovorax paradoxus	ACC deaminase	Greenhouse	Drought, 40 % of soil water holding capacity	Belimov et al. 2015
Velvet bean	Rhizobacteria	ACC deaminase	Growth chamber	Drought, 45 % of water holding capacity	Saleem et al. 2015
Barley	Hartmannibacter diazotrophicus	ACC deaminase	Greenhouse	Salt, 200 and 400 mM NaCl	Suarez et al. 2015
Sunflower	PGPB	ACC deaminase	Greenhouse	Salt, Electrical conductivity =8–12 dS/m	Kiani et al. 2015
Canola	Brevibacterium epidermidis, Bacillus aryabhattai	ACC deaminase	Laboratory	Salt, 120 mM	Siddikee et al. 2015
Chinese cabbage	Herbaspirillum sp.	ACC deaminase, IAA, siderophores	Growth chamber	Salt, 0 and 150 mM NaCl	Lee et al. 2015
Chickpea	Bacillus amyloliquefaciens, P. putida	ACC deaminase, IAA, P solubilization	Greenhouse	Drought, 14 days of no water	Kumar et al. 2015
Pea	Variovorax paradoxus	ACC deaminase	Greenhouse	Salt, 70 and 130 mM NaCl	Wang et al. 2016
Maize	Azospirillum spp.	Unknown	Greenhouse	Salt, 0 to −1.6 MPa osmotic potential	Abd El-Samad Hamdia et al. 2004
Rice	Bacillus Pumitus, P. pseudoalcaligenes	Unknown	Greenhouse	Salt, 0.5–2.5 g NaCl/ kg of soil	Jha and Subramanian 2013
Wheat	Azosprillium lipoferum, P. fluorescens	Unknown	Greenhouse	Salt, Electrical conductivity =14 dS/m	Saghafi et al. 2013
Rice	Bacillus amyloliquefaciens	Unknown	Greenhouse	Salt,	Nautiyal et al. 2013

conclusion from these experiments is that in the field, the decreased cytokinin levels that are induced by moderate drought contribute to drought tolerance; however, inoculation with a cytokinin-synthesizing bacterium may also have a beneficial effect. Some of the apparently paradoxical effects of changes in plant cytokinin levels as compared to the effect of adding a cytokinin producing bacterium may relate to the fact that many PGPB affect plants in a variety of different ways and it is often difficult to ascribe every change to a particular bacterial mechanism.

Recently, a strain of *Sinorhizobium meliloti* was engineered to overproduce cytokinin and then tested for the ability to protect alfalfa plants against the senescence that results from drought stress (Xu et al. 2012). The *S. meliloti* transformant expressed an *Agrobacterium ipt* gene under the control of the *trp* promoter and produced ~5 times the level of cytokinin synthesized by the non-transformed strain. After a period of severe drought stress, alfalfa plants inoculated with the engineered strain were significantly larger than plants inoculated with the non-transformed strain. When the plants subjected to drought were rewatered, plants inoculated with the transformed strain grew to a level similar to plants that had not been drought stressed at all. This experiment clearly demonstrates the ability of rhizobial strains synthesizing higher than normal levels of cytokinin to improve the tolerance of alfalfa (and possibly other crops) to severe drought stress.

IAA

To create a PGPB strain to better protect plants against inhibition by high salt, a strain of *Sinorhizobium meliloti* was engineered with an additional pathway for IAA biosynthesis (Bianco and Defez 2009). When the transformed *S. meliloti* strain was used to nodulate *Medicago truncatula* plants, the plants became more resistant to the effects of high salt (0.3 M) and to several other stresses. The bacterially treated plants had a higher proline content and an increase of activity of several antioxidant enzymes including superoxide dismutase, peroxidase, glutathione reductase and ascorbate peroxidase.

When the medicinal plant *Silybum marianum* (milk thistle), inoculated with *Pseudomonas extremorientalis*, was grown in the presence of high salt concentrations, the plant's root and shoot lengths and fresh weight were increased in the presence of the bacterium (Egamberdieva et al. 2013). Since this bacterium doesn't produce ACC deaminase (see below), it was assumed that the tolerance to salt stress was a consequence of bacterially synthesized IAA. These workers did not detail the nature of the changes within the plant other than size and biomass.

Microbial IAA not only serves to mediate the plant-microbe relationship but may also be a mechanism for the bacteria to protect themselves from environmental stress. For example, after osmotic stress about 50 % of untreated bacterial cells died as opposed to only 30 % of IAA-treated cells (Bianco et al. 2006).

ACC deaminase

As mentioned above, abiotic stress such as high salt or drought induces the synthesis of stress ethylene in plants and this ethylene generally inhibits plant growth (Abeles et al. 1992). Thus, it was predicted that a PGPB that possessed the enzyme ACC deaminase would lower the level of stress ethylene, thereby allowing greater plant growth under various abiotic stresses. To test this hypothesis, Mayak et al. (2004a and b) isolated and characterized an ACC deaminase-containing PGPB from a hot, dry and salty environment and tested its ability to promote the growth of tomato plants at high levels of salt or following a period of drought. As predicted, the bacterium significantly increased the biomass of treated plants both in the presence of high salt or following drought conditions. In addition, the bacterium dramatically lowered the amount of ethylene produced by salt treated plants. Subsequent experiments showed that only wild-type PGPB (ACC deaminase-containing), and not mutant PGPB (that lacked ACC deaminase) protected plants from ethylene-mediated growth inhibition, regardless of whether the bacteria were rhizospheric or endophytic in nature (Cheng et al. 2007; Ali et al. 2014; Han et al. 2015). Subsequent to the pioneering experiments of Mayak et al. (2004a), many additional laboratories have successfully utilized ACC deaminase-containing PGPB to ameliorate salt stress with a wide variety of different plants, both in the laboratory and in the field (Table 1).

Based on some of the above-mentioned experiments, many researchers tacitly assume that for PGPB that synthesize IAA and/or produce the enzyme ACC deaminase, the mechanism of drought or salt protection has already been established so that it is not necessary to

generate IAA or ACC deaminase minus mutants to prove the involvement of these mechanisms.

Some workers have studied the effects of ethylene on drought tolerance in considerable detail. For example, Belimov et al. (2009) reported that the ACC deaminase-containing PGPB *Variovorax paradoxus* 5C-2 but not an ACC deaminase minus mutant of this bacterium, improved the growth, yield, and water use efficiency of pea plants subjected to drought. *V. paradoxus* 5C-2 treatment also increased the xylem concentration of ABA as well as the ability of *Rhizobium leguminosarum* bv. *viciae* to nodulate pea plants in the presence of drought stress. In addition, Chen et al. (2013) observed that older more fully expanded wheat leaves partially lost their ability to close their stomata in response to both externally-applied ABA or soil drying (which stimulates ABA production). On the other hand, the ability to close stomata was partially restored when plants were pre-treated with either the ethylene receptor inhibitor 1-methylcyclopropene or the ACC deaminase-containing PGPB *V. paradoxus* 5C-2. These workers have suggested that the insensitivity of older leaves to ABA most likely reflects a decreased sensitivity to ethylene. In another study, comparing well-watered and water-limited potato plants treated with different PGPB, Belimov et al. (2015) suggest that in addition to lowering ethylene levels by ACC deaminase and promoting growth with bacterial auxin, bacteria with these activities may promote growth by modulating plant phytohormone balance. Moreover, treating salinized pea plants with the ACC deaminase-containing PGPB *V. paradoxus* 5C-2 increased K uptake and root to shoot K flow, but decreased Na flow (Wang et al. 2016). This observation is similar to the observation of Mayak et al. (2004a) who reported an increase in K uptake in tomato plants treated with a different ACC deaminase-containing PGPB strain. Thus, both of these reports are consistent with the notion that PGPB that contain both ACC deaminase and auxin ameliorate salt stress in part by improving plant ion homeostasis and water relations.

ABA

It is well known that plant ABA levels increase in response to water deficit and that ABA plays a key role in stomatal closure and the induction of several water-deficit-induced genes (Dodd et al. 2010; Vacheron et al. 2013). ABA is also produced by several PGPB so, for example, when the PGPB *Azospirillum brasilense* Sp245 was grown in the presence of 100 mM NaCl, the level of ABA that it produced increased significantly (Cohen et al. 2008). Some PGPB strains have also been observed to increase levels of plant secreted ABA following the imposition of water stress (by the addition of polyethylene glycol), however it is difficult to ascertain whether the ABA in this case was produced by the bacterium or by the plant (Cohen et al. 2008). In addition, it was reported that the wheat aquaporin gene (encoding water transport) TaAQP7 was upregulated after drought stress (PEG treatment) and was blocked by inhibiting ABA biosynthesis (Zhou et al. 2012), consistent with the involvement of ABA in the upregulating TaAQP7 as a means of enhancing drought tolerance in plants. In other experiments, treating maize plants with fluridone (an inhibitor of ABA synthesis) inhibited plant growth in a manner analogous to drought stress (Cohen et al. 2009). Inoculation of these plants with a PGPB strain of *Azospirillum* completely reversed this effect. Moreover, measurement of the relative water contents of fluridone-treated or drought stressed plants was decreased compared to well-watered plants in both cases, an effect that was reversed by treatment with the bacterial strain.

Trehalose

PGPB can also protect plants from drought and salt stress by synthesizing osmoprotectants such as proline and/or trehalose (Suarez et al. 2008; Rodriguez-Salazar et al. 2009). Trehalose is a highly stable glucoside consisting of two molecules of α-glucose that forms a gel phase (replacing water) as cells dehydrate, thereby decreasing the damage to cells from drought and salt. When mutants of a strain of *Rhizobium etli* that both overproduce and underproduce trehalose were constructed, the trehalose-overproducing strain increased the number of nitrogen fixing nodules per plant while the trehalose-underproducing strain decreased nodule number (Suarez et al. 2008). Higher levels of trehalose had a positive effect on both the survival and yield of bean plants nodulated by these rhizobial strains, especially following periods of drought. In addition, when maize plants were inoculated with a strain of *Azospirillum brasilense* that was transformed with a plasmid carrying a trehalose biosynthesis gene-fusion gene (i.e. *otsA* and *otsB*), 85 % of them survived drought stress compared to 55 % of plants that survived when

they were inoculated with the wild-type strain (Rodriguez-Salazar et al. 2009). Moreover, a 73 % increase was observed in the biomass of maize plants inoculated with transformed *A. brasilense* compared with the wild-type strain. These results clearly demonstrate that PGPB that increase the level of trehalose inside plants can protect those plants against drought or salt stress.

Volatile organic compounds

In the soil, many bacteria and plants communicate with one another by synthesizing a number of different volatile organic compounds. Some of these compounds have the ability to turn on the synthesis of plant genes encoding reactive oxygen species scavenging enzymes such as glutathione reductase, monodehydroascorbate reductase, superoxide dismutase and catalase that can, in turn, protect plants against drought or salt stress (Timmusk et al. 2014). Notwithstanding the simplicity and attractiveness of this mechanism, at the present time, this approach has not been extensively studied.

Exopolysaccharides

Exopolysaccharides (EPS), high-molecular weight carbohydrate compounds attached to the outer surface of bacteria, are responsible for the ability of the bacteria to form biofilms and for the attachment of bacterial cells to surfaces including plant roots and soil particles. In a recent study, scientists isolated and characterized a number of PGPB (all pseudomonads) from the rhizosphere of salt contaminated soils, based on the ability of these bacteria to produce high levels of EPS and to be salt tolerant (Tewari and Arora 2014). One particular strain of *Pseudomonas aeruginosa* was able to grow in up to 12 % salt, produce IAA and siderophores, and facilitate plant growth in the presence of high levels of salt. Following chemical mutagenesis of the bacterium, researchers selected a mutant that produced a significantly decreased level of EPS, while the amount of IAA and siderophores was unchanged. With the decrease in EPS, the mutant lost its ability to grow and promote plant growth in the presence of high levels of salt suggesting that with the loss of the EPS barrier, salt readily entered the bacterium thereby inhibiting its functioning. Furthermore, these researchers believe that, notwithstanding the important role played by EPS, the observed stimulation of plant growth came from IAA synthesis. Since this study did not report the numbers of PGPB, either wild-type or mutant, bound to plant roots, it is not possible to know for certain whether the inability of the mutant to promote plant growth was a consequence of decreased bacterial numbers on the root.

Some notes of caution

As a consequence of a limited number of definitive experiments (some of which are discussed above), many scientists have been encouraged to isolate and characterize new bacterial strains that are able to help plants to overcome the potentially debilitating effects of salt and drought stress. These bacteria have been tested in the lab, under greenhouse conditions and also in the field and have been found to be quite effective. Many of these studies are summarized in Table 1. While most of the experiments referred to in Table 1 were done either in a greenhouse or growth chamber, importantly, a few field experiments with similar results have been reported.

Although it is not always explicitly stated or even tested for by many researchers, most of the PGPB that have been studied to date are thought to be rhizospheric while only a few are likely endophytic. However, more recently, many researchers have specifically focused their efforts on the roles played by endophytic bacteria in promoting plant growth. This is because while both rhizospheric and endophytic bacteria utilize the same mechanisms to promote plant growth, only endophytes are protected from both biotic and abiotic environmental challenge.

Notwithstanding the fact that a particular PGPB strain may perform well in growth chamber or greenhouse studies, this strain may not be suitable for use in the field. Thus, for example, many strains of *P. aeruginosa* (see Table 1) have been associated with human infections so that there is a real question as to whether these strains will be acceptable to regulatory authorities for deliberate release into the environment. In addition, it was previously observed (Glick et al., unpublished experiments) that upon characterizing a PGPB strain with a very high level of ACC deaminase activity, the strain turned out to be the human pathogen *Bacillus anthracis*, an organism that is clearly unsuitable for use in the field as a PGPB.

Many of the PGPB that modulate plant cytokinin, IAA, ethylene or ABA levels may also effect the levels of other plant hormones so that, given the possibility of cross-talk between these hormones, it is not a simple

matter to assign clear and unequivocal roles to each of these hormones in assessing the mechanism(s) that the bacterium uses to help the plant to overcome drought or salt stress. This notwithstanding, some researchers have endeavored to sort out the effects of changes in specific hormone levels by generating plant mutants with altered levels of sensitivity to certain phytohormones. For example, Chen et al. (2013) examined the effects of an ACC deaminase-producing PGPB on the growth and development of wild-type and several ethylene-related mutants of *A. thaliana*. They observed that growth promotion was not observed when ethylene-insensitive mutants were tested, arguing that a completely functional ethylene signal transduction pathway is required for plant growth stimulation (Chen et al. 2013).

Future prospects

In the past 10–20 years plant researchers have developed a sophisticated understanding of how plants, responding to salt and drought stress, alter their gene expression. However, plants by themselves are not always capable of effectively responding to salt and drought stress, and often depend on beneficial soil bacteria to augment their survival strategies. While our current understanding of the mechanisms that PGPB use to facilitate plant growth following salt or drought stress is incomplete, it is nevertheless sufficient so that these organisms may be used in a meaningful way to help plants to grow and thrive following salt and drought stress.

To facilitate the more widespread and efficacious use of PGPB, scientists need to make the leap from greenhouse and growth chamber experiments to field studies, farmers and consumers must be educated about role that PGPB play in plant growth and soil health, greater emphasis needs to be put on the use of endophytic rather than rhizospheric PGPB, and additional research needs to be done on the relationship between PGPB and mycorrhizae. There is no doubt that quite a lot of work remains to be done before PGPB become a mainstay of agricultural, horticultural and silvicultural practice. However, there is every reason to expect this to come to fruition with the next 10–15 years so that we no longer need to depend on chemicals and other traditional approaches.

References

Aamir M, Aslam A, Khan MY, Jamshaid MU, Ahmad M, Asghar HN, Zahir ZA (2013) Co-inoculation with *Rhizobium* and plant growth promoting rhizobacteria (PGPR) for inducing salinity tolerance in mung bean under field condition of semi-arid climate. Asian J Agri. Biol 1:17–22

Abd El-Samad HM (2013) The physiological response of wheat plants to exogenous application of gibberellic acid (GA3) or indole-3-acetic acid (IAA) with endogenous ethylene under salt stress conditions. Int J Plant Physiol Biochem 5:58–64

Abd El-Samad Hamdia M, Shaddad MAK, Doaa MM (2004) Mechanisms of salt tolerance and interactive effects of inoculation on maize cultivars under salt stress conditions. Plant Growth Regulat 44:165–174

Abeles FB, Morgan PW, Saltveit ME Jr (1992) Ethylene in plant biology. Academic Press, New York

Afzal I, Basra S, Iqbal A (2005) The effect of seed soaking with plant growth regulators on seedling vigor of wheat under salinity stress. J Stress Physiol Biochem 1:6–14

Ahmad M, Zahir ZA, Nazli F, Akram F, Arshad M, Khalid M (2013) Effectiveness of halo-tolerant, auxin producing *Pseudomonas* and *Rhizobium* strains to improve osmotic stress tolerance in mung bean (*Vigna radiata* L. Braz J Microbiol 44:1341–1348

Ahmad P, Rasool S, Gul A, Sheikh SA, Akram NA, Ashraf M, Kazi AM, Gucel S (2016) Jasmonates: multifunctional roles in stress tolerance. Front. Plant Sci. 7:813. doi:10.3389/fpls.2016.00813

Ahmed IM, Nadira UA, Bibi N, Cao F, He X, Zhang G, Wu F (2015) Secondary metabolism and antioxidants are involved in the tolerance to drought and salinity, separately and combined, in Tibetan wild barley. Environ Exper. Botany 111:1–12

Alcázar R, Altabella T, Marco F, Bortolotti C, Reymond M, Koncz C, Carrasco P, Tiburcio AF (2010) Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. Planta 231:1237–1249

Ali S, Charles TC, Glick BR (2014) Amelioration of damages caused by high salinity stress by plant growth-promoting bacterial endophytes. Plant Physiol Biochem 80:160–167

Araus JL, Slafer GA, Royo C, Serret MD (2008) Breeding for yield potential and stress adaptation in cereals. Cr rev. Plant Sci 27:6

Arkhipova TN, Prinsen E, Veselov SU, Martinenko EV, Melentiev AI, Kudoyarova GR (2007) Cytokinin producing bacteria enhance plant growth in drying soil. Plant Soil 292:305–315

Atkinson NJ, Urwin PE (2012) The interaction of plant biotic and abiotic stresses: from genes to the field. J Exper. Botany 63:3523–3543

Aziz A, Martin-Tanguy J, Larher F (1998) Stress-induced changes in polyamine and tyramine levels can regulate proline accumulation in tomato leaf discs treated with sodium chloride. Physiol Plant 104:195–202

Badri DV, Vivanco JM (2009) Regulation and function of root exudates. Plant Cell Environ 32:666–681

Balderas-Hernández VE, Alvarado-Rodríguez M, Fraire-Velázquez S (2013) Conserved versatile master regulators in signaling pathways in response to stress in plants. AoB PLANTS 5:plt033. doi:10.1093/aobpla/plt033

Ballizany WL, Hofmann RW, Jahufer MZZ, Barrett BA (2012) Genotype x environment analysis of flavonoid accumulation and morphology in white clover under contrasting field conditions. Field Crops Res 128:156–166

Bandurska H, Stroìnski A (2005) The effect of salicylic acid on barley response to water deficit. Acta Physiol Plant 27:379–386

Bangash N, Khalid A, Mahmood T, Siddique MT (2013) Screening rhizobacteria containing ACC-deaminase for growth promotion of wheat under water stress. Pak J Bot 45(SI):91–96

Bartels D, Sunkar R (2005) Drought and salt tolerance in plants. Crit Rev Plant Sci 24:23–28

Belimov AA, Dodd IC, Hontzeas N, Theobald JC, Safranova VI, Davies WJ (2009) Rhizosphere bacteria containing 1-aminocyclopropane-1-carboxylate deaminase increase yield of plants grown in drying soil via both local and systemic hormone signaling. New Phytol 181:413–423

Belimov AA, Dodd IC, Safronova VI, Shaposhnikov AI, Azarova TS, Makarova NM, Davies WJ, Tikhonovich IA (2015) Rhizobacteria that produce auxins and contain1-amino-cyclopropane-1-carboxylic acid deaminase decrease amino acid concentrations in the rhizosphere and improve growth and yield of well-watered and water-limited potato (*Solanum tuberosum*. Ann Appl Biol 167:11–25

Bianco C, Defez R (2009) *Medicago truncatula* improves salt tolerance when nodulated by an indole-3-acetic acid-overproducing *Sinorhizobium meliloti* strain. J Exp Bot 60: 3097–3107

Bianco C, Imperlini E, Calogero R, Senatore B, Amoresano A, CarpentieriA PP, Defez R (2006) Indole-3-acetic acid improves *Escherichia coli*'s defences to stress. Arch Microbiol 185:373–382

Bray EA, Bailey-Serres J, Weretilnyk E (2000) Responses to abiotic stresses," in biochemistry and molecular biology of plants, eds. B. B. Buchanan, W. Gruissem, and R. L. Jones (Rockville. Am Soc Plant Physiol:1158–1203

Brígido C, Nascimento F, Duan J, Glick BR, Oliveira S (2013) Expression of an exogenous 1-aminocyclopropane-1-carboxylate deaminase gene in *Mesorhizobium* spp. reduces the negative effects of salt stress in chickpea. FEMS Microbiol Lett 349:46–53

Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C (2015) How tree roots respond to drought. Front Plant Sci 6:547. doi:10.3389/fpls.2015.00547

Chalker-Scott L (1999) Environmental significance of anthocyanins in plant stress responses. Photochem Photobiol 70:1–9

Chang P, Gerhardt KE, Huang X-D, Yu X-M, Glick BR, Gerwing PD, Greenberg BM (2014) Plant growth-promoting bacteria that contain ACC deaminase facilitate the growth of barley and oats in salt-impacted soil: potential for phytoremediation of saline soils. Internat J Phytoremed 16:1133–1147

Chen L, Dodd IC, Davies WJ, Wilkinson S (2013) Ethylene limits abscisic acid- or drying-induced stomatal closure in aged wheat leaves. Plant Cell Environ 38:1850–1856

Cheng Z, Park E, Glick BR (2007) 1-aminocyclopropane-1-carboxylate (ACC) deaminase from *Pseudomonas putida* UW4 facilitates the growth of canola in the presence of salt. Can J Microbiol 53:912–918

Cho S-T, Chang H-H, Egamberdieva D, Kamilova F, Lugtenberg B, Kuo C-H (2015) Genome analysis of *Pseudomonas fluorescens* PCL1751: a rhizobacterium that controls root diseases and alleviates salt stress for its plant host. PLoS ONE. doi:10.1371/journal.pone.0140231

Chrispeels MJ, Maurel C (1994) Aquaporins: the molecular basis of facilitated water movement through living plant cells. Plant Physiol 105:9–15

Cohen AC, Bottini R, Piccoli PN (2008) *Azospirillum brasilense* Sp245 produces ABA in chemically-defined culture medium and increases ABA content in *Arabidopsis* plants. Plant Growth Regul 54:97–103

Cohen AC, Travaglia CN, Bottini R, Piccoli PN (2009) Participation of abscisic acid and gibberellins produced by endophytic Azospirillum in the alleviation of drought effects in maize. Botany 87:455–462

Collins NC, Tardieu F, Tuberosa R (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand? Plant Physiol 147:469–486

Contreras-Cornejo HA, Macías-Rodríguez L, Alfaro-Cuevas R, López-Bucio J (2014) *Trichoderma* spp. improve growth of *Arabidopsis* seedlings under salt stress through enhanced root development, osmolite production, and Na$^+$ elimination through root exudates. Molec Plant-Microbe Interact 27: 503–514

Cutler SR, Rodriguez PL, Finkelstein RR, Abrams SR (2010) Abscisic acid: emergence of a core signaling network. Ann rev. Plant Biol 61:651–679

Daneshmand F, Arvin MJ, Kalantari KM (2010) Physiological responses to NaCl stress in three wild species of potato in vitro. Acta Physiol Plant 32:91–101

Dar TA, Uddin M, Khan MMA, Hakeem KR, Jaleel H (2015) Jasmonates counter plant stress: a review. Environ Exp Bot 115:49–57

Daszkowska-Golec A, Szarejko I (2013) Open or close the gate – stomata action under the control of phytohormones in drought stress conditions. Front Plant Sci 4:138

Deinlein U, Stephan AB, Horie T, Luo W, Xu G, Schroeder JI (2014) Plant salt-tolerance mechanisms. Trends Plant Sci 19(6):371–379

Del Rio L (2015) ROS and RNS in plant physiology: an overview. J Exp Bot 66:2827–2837

Di Cori P, Lucioli S, Frattarelli A, Nota P, Tel-Or E, Benyamini E, Gottlieb H, Caboni E, Forni C (2013) Characterization of the response of in vitro cultured *Myrtus communis* L. plants to high concentrations of NaCl. Plant Physiol Biochem 73:420–426

Dodd IC, Pérez-Alfocea F (2012) Microbial amelioration of crop salinity stress. J Exp Bot 63:3415–3428

Dodd IC, Zinovkina NY, Safronova VI, Belimov AA (2010) Rhizobacterial mediation of plant hormone status. Ann Appl Biol 157:361–379

Dolferus R (2014) To grow or not to grow: a stressful decision for plants. Plant Sci 229:247–261

Dong FC, Wang PT, Song CP (2001) The role of hydrogen peroxide in salicylic acid-induced stomatal closure in *Vicia faba* guard cells. Acta Phytophysiol Sin 27:296–302

Dong W, Wang M, Xu F, Quan T, Peng K, Xiao L, Xia G (2013) Wheat oxophytodienoate reductase gene TaOPR1 confers salinity tolerance via enhancement of abscisic acid signaling and reactive oxygen species scavenging. Plant Physiol 161: 1217–1228

Dubrovsky JG, Sauer M, Napsucialy-Mendivil S, Ivanchenko MG, Friml J, Shishkova S, Celenza J, Benková E (2008) Auxin acts as a local morphogenetic trigger to specify lateral root founder cells. Proc Natl Acad Sci U S A 105:8790–8794

Egamberdieva D (2009) Alleviation of salt stress by plant growth regulators and IAA producing bacteria in wheat. Acta Physiol Plant 31:861–864

Egamberdieva D, Kucharova Z, Davranov K, Berg G, Makarova N, Azarova T, Chebotar V, Tikhonovich I, Kamilova F, Validov SZ, Lugtenberg B (2011) Bacteria able to control foot and root rot and to promote growth of cucumber in salinated soils. Biol Fertil Soils 47:197–205

Egamberdieva D, Jabborova D, Mamadalieva N (2013) Salt-tolerant *Pseudomonas extremorintalis* able to stimulate growth of *Silybum marianum* under salt stress. Med Arom Plant Sci Biotechnol 7:7–10

Egamberdieva D, Jabborova D, Hashem A (2015) Pseudomonas induces salinity tolerance in cotton (Gossypium hirsutum) and resistance to Fusarium root rot through the modulation of indole-3-acetic acid. Saudi J Biol Sci: in press

Elfving N, Davoine C, Benlloch R, Blomberg J, Brännstrm K, Müller D, Nilsson A, Ulfstedt M, Ronne H, Wingsle G, Nilsson O, Bjrklund S (2011) The *Arabidopsis thaliana* Med25 mediator subunit integrates environmental cues to control plant development. Proc Nat Acad Sci USA 108: 8245–8250

Ferdous J, Hussain SS, Shi B-J (2015) Role of microRNAs in plant drought tolerance. Plant Biotechnol J 13:293–305

Forni C, Braglia R, Harren FJM, Cristescu SM (2012) Stress responses of duckweed (*Lemna minor* L.) and water velvet (*Azolla filiculoides* lam.) to anionic surfactant sodium-dodecyl-sulphate (SDS). Aquat Toxicol 110–111: 107–113

Fujita Y, Fujita M, Satoh R, Maruyama K, Parvez MM, Seki M, Hiratsu K, Ohme-Takagi M, Shinozaki K, Yamaguchi-Shinozaki K (2005) AREB1 is a transcription activator of novel ABRE-dependent ABA signaling that enhances drought stress tolerance in Arabidopsis. Plant Cell 17:3470–3488

Gamalero E, Berta G, Massa N, Glick BR, Lingua G (2010) Interactions between *Pseudomonas putida* UW4 and *Gigaspora rosea* BEG9 and their consequences on the growth of cucumber under salt stress conditions. J Appl Microbiol 108:236–245

Gepstein S, Glick BR (2013) Strategies to ameliorate abiotic stress-induced plant senescence. Plant Molec. Biol 82:623–633

Ghanem ME, Albacete A, Smigocki AC, Frébort I, Pospisilova H, Martinez-Andùjar C, Acosta M, Sánchez-Bravo J, Dodd IC, Pérez-Alfocea F (2011) Root-synthesized cytokinins improve shoot growth and fruit yield in salinized tomato (*Solanum lycopersicum* L.) plants. J Exp Bot 62:125–140

Ghorai S, Pal KK, Dey R (2015) Alleviation of salinity stress in groundnut by application of PGPR. Int res. J Eng Technol 2: 742–750

Gill SS, Tuteja N (2010) Polyamines and abiotic stress tolerance in plants. Plant Signal Behav 5(1):26–33

Glick BR (2012) Plant growth-promoting bacteria: mechanisms and applications. Scientifica 2012(Article ID 963401):15. doi:10.6064/2012/963401

Glick BR, Penrose DM, Li J (1998) A model for the lowering of plant ethylene concentrations by plant growth promoting bacteria. J Theor Biol 190:63–68

Glick BR, Cheng Z, Czarny J, Duan J (2007) Promotion of plant growth by ACC deaminase-containing soil bacteria. Eur J Plant Pathol 119:329–339

Golldack D, Lüking I, Yang O (2011) Plant tolerance to drought and salinity: stress regulating transcription factors and their functional significance in the cellular transcriptional network. Plant Cell Rep 30:1383–1391

Golldack D, Li C, Mohan H, Probst N (2014) Tolerance to drought and salt stress in plants: unraveling the signaling networks. Front Plant Sci 5, art 151: 1–10. doi:10.3389/fpls.2014.00151

Han S, Yu B, Wang Y, Liu Y (2011) Role of plant autophagy in stress response. Protein Cell 2:784–791

Han Y, Wang R, Yang Z, Zhan Y, Ma Y, Ping S, Zhang L, Lin M, Yan Y (2015) 1-aminocyclopropane-1-carboxylate deaminase from *Pseudomonas stutzeri* A1501 facilitates the growth of rice in the presence of salt or heavy metals. J Microbiol Biotechnol 25:1119–1128

Huang D, Wu W, Abrams SR, Cutler AJ (2008) The relationship of drought-related gene expression in *Arabidopsis thaliana* to hormonal and environmental factors. J Exp Bot 59:2991–3007

Huang G-T, Ma S-L, Bai L-P, Zhang L, Ma H, Jia P, Liu J, Zhong M, Guo Z-F (2012) Signal transduction during cold, salt, and drought stresses in plants. Molec Biol Rep 39:969–987

Javid MG, Sorooshzadeh A, Moradi F, Modarres Sanavy SAM, Allahdadi I (2011) The role of phytohormones in alleviating salt stress in crop plants. Austral. J Crop Sci 5:726–734

Jeong D-H, Green PJ (2013) The role of rice microRNAs in abiotic stress responses. Plant Biol 56:187–197

Jha Y, Subramanian RB (2013) Paddy plants inoculated with PGPR show better growth physiology and nutrient content under saline conditions. Chil J Agri Res 73:213–219

Jiménez-Bremont JF, Ruiz OA, Rodriguez-Kessler M (2007) Modulation of spermidine and spermine levels in maize seedlings subjected to long-term salt stress. Plant Physiol Biochem 45:812–821

Joo GJ, Kim YM, Kim JT, Rhee IK, Kim JH, Lee IJ (2005) Gibberellins-producing rhizobacteria increase endogenous gibberellins content and promote growth of red peppers. J Microbiol 43:510–515

Jung JH, Park CM (2011) Auxin modulation of salt stress signaling in *Arabidopsis* seed germination. Plant Signal Behav 6: 1198–1200

Kang G, Li G, Zheng B, Han Q, Wang C, Zhu Y, Guo T (2012) Proteomic analysis on salicylic acid-induced salt tolerance in common wheat seedlings (*Triticum aestivum* L.). Biochim Biophys Acta 1824:1324–1333

Kasotia A, Jain S, Vaishnav A, Kumari S (2012) Soybean growth-promotion by *Pseudomonas* sp. strain VS1 under salt stress. Pak J Biol Sci 15:698–701

Kazan K (2015) Diverse roles of jasmonates and ethylene in abiotic stress tolerance. Trends Plant Sci 10:219–229

Khan K, Agarwal P, Shanware A, Sane VA (2015) Heterologous expression of two *Jatropha* aquaporins imparts drought and salt tolerance and improves seed viability in transgenic *Arabidopsis thaliana*. PLoS One 10(6):e0128866. doi:10.1371/journal.pone.0128866

Kiani MZ, Ali A, Sultan T, Ahmad R, Hydar SI (2015) Plant growth promoting rhizobacteria having 1-aminocyclopropane-1-carboxylic acid deaminase to induce

salt tolerance in sunflower (*Helianthus annus* L.). Nat Resour 6:391–397

Kim JS, Mizoi J, Kidokoro S, Maruyama K, Nakajima J, Nakashima K, Mitsuda N, Takiguchi Y, Ohme-Takagi M, Kondou Y, Yoshizumi T, Matsui M, Shinozaki K, Yamaguchi-Shinozaki K (2012) *Arabidopsis* growth-regulating factor7 functions as a transcriptional repressor of abscisic acid- and osmotic stress-responsive genes, including DREB2A. Plant Cell 24:3393–3405

Kim K, Jang Y-J, Lee S-M, B-T O, Chae J-C, Lee K-J (2014) Alleviation of salt stress by *Enterobacter* sp. EJ01 in tomato and *Arabidopsis* is accompanied by up-regulation of conserved salinity responsive factors in plants. Mol Cells 37: 109–117

Koussevitzky S, Suzuki N, Huntington S, Armijo L, Sha W, Cortes D, Shulaev V, Mittler R (2008) Ascorbate peroxidase 1 plays a key role in the response of *Arabidopsis thaliana* to stress combination. J Biol Chem 283:34197–34203

Kreps JA, Wu Y, Chang H-S, Zhu T, Wang X, Harper JFH (2002) Transcriptome changes for *Arabidopsis* in response to salt, osmotic, and cold stress. Plant Physiol 130:2129–2141

Kroemer G, Mariño G, Levine B (2010) Autophagy and the integrated stress response. Mol Cell 40:280–293

Kumar M, Mishra S, Dixit V, Kumar M, Agarwal L, Singh P, Chauhan PS, Nautiyal CS (2015) Synergistic effect of *Pseudomonas putida* and *Bacillus amyloliquefaciens* ameliorates drought stress in chickpea (*Cicer arietinum* L.). Plant Signal Behav. doi:10.1080/15592324.2015.1071004

Lee GW, Lee K-J, Chae J-C (2015) *Herbaspirillum* sp. strain GW103 alleviates salt stress *Brassica rapa* L. ssp. *pekinensis*. Protoplasma. doi:10.1007/s00709-015-0872-8

Li C, Ng CK-Y, Fan L-M (2015) MYB transcription factors, active players in abiotic stress signaling. Environ Exper Bot 114: 80–91

Lim J-J, Kim S-D (2013) Induction of drought stress resistance by multi-functional PGPR *Bacillus licheniformis* K11 in pepper. Plant Pathol J 29:201–208

Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, Yamaguchi Shinozaki K, Shinozaki K (1998) Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought- and 1308 the plant cell low-temperature-responsive gene expression, respectively, in *Arabidopsis*. Plant Cell 10: 1391–1406

Liu X, Meng FX, Zhang SQ, Lou CH (2003) Ca^{2+} is involved in the signal transduction during stomatal movement induced by salicylic acid in *Vicia faba*. J Plant Physiol Mol Biol 1:59–64

Liu Y, Shi Z, Yao L, Yue H, Li H, Li C (2013) Effect of IAA produced by *Klebsiella oxytoca* Rs-5 on cotton growth under salt stress. J Gen Appl Microbiol 59:59–65

Liu W, Li R-J, Han T-T, Cai W, Z-W F, Y-T L (2015) Salt stress reduces root meristem size by nitric oxide-mediated modulation of auxin accumulation and signaling in *Arabidopsis*. Plant Physiol 168:343–356

Luo ZB, Janz D, Jiang X, Göbel C, Wildhagen H, Tan Y, Rennenberg H, Feussner I, Polle A (2009) Upgrading root physiology for stress tolerance by ectomycorrhizas: insights from metabolite and transcriptional profiling into reprogramming for stress anticipation. Plant Physiol 151: 1902–1917

Mahajan S, Tuteja N (2005) Cold, salinity and drought stresses: an overview. Arch Biochem Biophys 444:139–158

Mayak S, Tirosh T, Glick BR (2004a) Plant growth-promoting bacteria that confer resistance to water stress in tomato and pepper. Plant Sci 166:525–530

Mayak S, Tirosh T, Glick BR (2004b) Plant growth-promoting bacteria that confer resistance in tomato to salt stress. Plant Physiol Biochem 42:565–572

McNutt M (2014) The drought you can't see. Science 345:1543

Melotto M, Underwood W, Koczan J, Nomura K, He SY (2006) Plant stomata function in innate immunity against bacterial invasion. Cell 126:969–980

Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R (2010) Reactive oxygen species homeostasis and signaling during drought and salinity stresses. Plant Cell Environ 33:453–467

Miura K, Tada Y (2014) Regulation of water, salinity, and cold stress responses by salicylic acid. Front Plant Sci 5:1–12

Moons A, Prinsen E, Bauw G, Montagu MV (1997) Antagonistic effects of abscisic acid and jasmonates on salt stress-inducible transcripts in rice roots. Plant Cell 9:2243–2259

Morgan PW, He CJ, De Greef JA, De Proft MP (1990) Does water deficit stress promote ethylene synthesis by intact plants? Plant Physiol 94:1616–1624

Moya JL, Primo-Millo E, Talon M (1999) Morphological factors determining salt tolerance in citrus seedling: the shoot-to-root ratio modulates passive root uptake of chloride ions and their accumulation in leaves. Plant Cell Environ 22:1425–1433

Munne-Bosch S, Penuelas J (2003) Photo-and antioxidative protection, and a role for salicylic acid during drought and recovery in field-grown. *Phillyrea angustifolia* plants. Planta 217:758–766

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681

Nakashima K, Ito Y, Yamaguchi-Shinozaki K (2009) Transcriptional regulatory networks in response to abiotic stresses in *Arabidopsis* and grasses. Plant Physiol 149:88–95

Nakbanpote W, Panitlurtumpai N, Sangdee A, Sakulpone N, Sirisom P, Pimthong A (2014) Salt-tolerant and plant growth-promoting bacteria isolated from Zn/Cd contaminated soil: identification and effect on rice under saline conditions. J Plant Interact 9:379–387

Narayana I, Lalonde S, Saini HS (1991) Water-stress-induced ethylene production in wheat: a fact or artifact? Plant Physiol 96:406–410

Nautiyal CS, Srivastava S, Chauhan PS, Seem K, Mishra A, Sopory SK (2013) Plant growth-promoting bacteria *Bacillus amyloliquefaciens* NBRISN13 modulates gene expression profile of leaf and rhizosphere community in rice during salt stress. Plant Physiol Biochem 66:1–9

Nawaz K, Ashraf M (2010) Exogenous application of glycine betaine modulates activities of antioxidants in maize plants subjected to salt stress. J Agron Crop Sci 196:28–37

Nichols SN, Hofmann RW, Williams WM (2015) Physiological drought resistance and accumulation of leaf phenolics in white clover interspecific hybrids. Environ Exp Botany 119:40–47

Nishiyama R, Watanabe Y, Fujita Y, Le DT, Kojima M, Werner T, Vankova R, Yamaguchi-Shinozaki K, Shinozaki K, Kakimoto T (2011) Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid

responses, and abscisic acid biosynthesis. Plant Cell 23: 2169–2183

Nishiyama R, Le DT, Watanabe Y, Matsui A, Tanaka M, Seki M, Yamaguchi-Shinozaki K, Shinozaki K, Tran LS (2012) Transcriptome analyses of a salt-tolerant cytokinin-deficient mutant reveal differential regulation of salt stress response by cytokinin deficiency. PLoS One 7: e32124

Noctor G, Foyer CH (1998) Ascorbate and glutathione: keeping active oxygen under control. Ann Rev Plant Physiol Plant Mol Biol 49:249–279

Nonami H, Boyer JS (1990) Primary events regulating stem growth at low water potentials. Plant Physiol 94:1601–1609

Nuruzzaman M, Sharoni AM, Kikuchi S (2013) Roles of NAC transcription factors in the regulation of biotic and abiotic stress responses in plants. Front Microbiol 4, art 428:1–16

Pandolfi C, Pottosin I, Cuin T, Mancuso S, Shabala S (2010) Specificity of polyamine effects on NaCl-induced ion flux kinetics and salt stress amelioration in plants. Plant Cell Physiol 51(3):422–434

Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf 60:324–349

Peleg Z, Blumwald E (2011) Hormone balance and abiotic stress tolerance in crop plants. Curr Opin Plant Biol 14:1–6

Petrusa LM, Winicov I (1997) Proline status in salt tolerant and salt sensitive alfalfa cell lines and plants in response to NaCl. Plant Physiol Biochem 35:303–310

Qin S, Zhang Y-J, Yuan B, P-Y X, Xing K, Wang J, Jiang J-H (2014) Isolation of ACC deaminase-producing habitat-adapted symbiotic bacteria associated with halophyte Limonium sinense (Girard) Kuntze and evaluating their plant growth-promoting activity under salt stress. Plant Soil 374: 753–766

Qiu Z, Guo J, Zhu A, Zhang L, Zhang M (2014) Exogenous jasmonic acid can enhance tolerance of wheat seedlings to salt stress. Ecotoxicol Environ Saf 104:202–208

Ramadoss D, Lakkineni VK, Bose P, Ali S, Annapurna K (2013) Mitigation of salt stress in wheat seedlings by halotolerant bacteria isolated from saline habitats. Springer Plus 2:6

Redillas MCFR, Park S-H, Lee JW, Kim YS, Jeong JS, Jung H, Bang SW, Hahn T-R, Kim J-K (2012) Accumulation of trehalose increases soluble sugar contents in rice plants conferring tolerance to drought and salt stress. Plant Biotechnol Rep 6:89–96

Reina-Bueno M, Argandoña M, Nieto JJ, Hidalgo-García A, Iglesias-Guerra F, Delgado MJ, Vargas C (2012) Role of trehalose in heat and desiccation tolerance in the soil bacterium Rhizobium etli. BMC Microbiol 12:207

Rodriguez-Salazar J, Suarez R, Caballero-Mellado J, Iturriaga G (2009) Trehalose accumulation in Azospirillum brasilense improves drought tolerance and biomass in maize plants. FEMS Microbiol Lett 296:52–59

Ryu H, Cho Y-C (2015) Plant hormones in salt stress tolerance. J Plant Biol 58:147–155

Sadrnia M, Maksimava N, Khromsova E, Stanislavich S, Owlia P, Arjomandzadegan M (2011) Study of the effect of bacterial 1-aminocyclopropane-1-carboxylte deaminase (ACC) deaminase on resistance to salt stress in tomato plant. Anal Univ Oradea Fas. Biol 18:120–123

Saghafi K, Ahmadi J, Asgharzadeh A, Bakhtiari S (2013) The effect of microbial inoculants on physiological responses of two wheat cultivars under salt stress. Int J Adv Biol. Biomed Res 1:421–431

Sakuma Y, Maruyama K, Qin F, Osakabe Y, Shinozaki K, Yamaguchi-Shinozaki K (2006a) Dual function of an Arabidopsis transcription factor DREB2A in water-stress-responsive and heat-stress-responsive gene expression. Proc Natl Acad Sci U S A 103:18822–18827

Sakuma Y, Maruyama K, Osakabe Y, Qin F, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2006b) Functional analysis of an Arabidopsis transcription factor, DREB2A, involved in drought-responsive gene expression. Plant Cell 18:1292–1309

Sakuraba Y, Kim Y-S, Han S-H, Lee B-D, Paek N-C (2015) The Arabidopsis transcription factor NAC016 promotes drought stress responses by repressing AREB1 transcription through a trifurcate feed-forward regulatory loop involving NAP. Plant Cell 27(6):1771–1787. doi:10.1105/tpc.15.00222; www.plantcell.org/cgi/

Salamone IEG, Hynes RK, Nelson LM (2001) Cytokinin production by plant growth promoting rhizobacteria and selected mutants. Can J Microbiol 47:404–411

Saleem AR, Bangash N, Mahmood T, Khalid A, Centritto M, Siddique MT (2015) Rhizobacteria capable of producing ACC deaminase promote growth of velvet bean (Mucuna pruriens) under water stress conditions. Int J Agri. Biol 17: 663–667

Saravanakumar D, Samiyappan R (2007) ACC deaminase from Pseudomonas fluorescens mediated saline resistance in groundnut (Arachis hypogea) plants. J Appl Microbiol 102: 1283–1292

Schoenborn L, Yates PS, Grinton BE, Hugenholtz P, Janssen PH (2004) Liquid serial dilution is inferior to solid media for isolation of cultures representative of the phylum-level diversity of soil bacteria. Appl Environ Microbiol 70:4363–4366

Seki M, Narusaka M, Ishida J, Nanjo T, Fujita M, Oono Y, Kamiya A, Nakajima M, Enju A, Sakurai T, Satou M, Akiyama K, Taji T, Yamaguchi-Shinozaki K, Carninci P, Kawai J, Hayashizaki Y, Shinozaki K (2002) Monitoring the expression profiles of 7000 Arabidopsis genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. Plant J 31:279–292

Serraj R, Sinclair TR (2002) Osmolyte accumulation: can it really help increase crop yield under drought conditions? Plant Cell Environ 25:333–341

Sharma P, Dubey RS (2005) Drought induces oxidative stress and enhances the activities of antioxidant enzymes in growing rice seedlings. Plant Growth Regulat 46:209–221

Sharp RE, Hsiao TC, Silk WK (1988) Growth of the maize primary root at low water potentials. I spatial distribution of expansive growth. Plant Physiol 87:50–57

Shinozaki K, Yamaguchi-Shinozaki K (1997) Gene expression and signal transduction in water-stress response. Plant Physiol 115:327–334

Siddikee MA, Glick BR, Chauhan PS, Yim W-J, Sa T (2011) Enhancement of growth and salt tolerance of red pepper seedlings (Capsicum annuum L.) by regulating stress ethylene synthesis with halotolerant bacteria containing ACC deaminase activity. Plant Physiol Biochem 49:427–434

Siddikee MA, Sunderem S, Chandrasekaran M, Kim K, Selvakumar G, Sa T (2015) Halotolerant bacteria with ACC

deaminase activity alleviate salt stress in canola seed germination. J Korean Soc Appl Biol Chem 58:237–241

Slavikova S, Ufaz S, Avin-Wittenberg T, Levanony H, Galili G (2008) An autophagy-associated Atg8 protein is involved in the responses of *Arabidopsis* seedlings to hormonal controls and abiotic stresses. J Exp Bot 59:4029–4043

Spaepen S, Vanderleyden J (2011) Auxin and plant-microbe interactions. Cold spring Harb Persp. Biol 3:#4

Suarez R, Wong A, Ramirez M, Barraza A, Orozco MC, Cevallos MA, Lara M, Hernandez G, Iturriaga G (2008) Improvement of drought tolerance and grain yield in common bean by overexpressing trehalose-6-phosphate synthase in rhizobia. Mol Plant-Microbe Interact 21:958–966

Suarez C, Cardinale M, Ratering S, Steffens D, Jung S, Montoya AMZ, Geissler-Plaum R, Schnell S (2015) Plant growth-promoting effects of *Hartmannibacter diazotrophicus* on summer barley (*Hordeum vulgare* L.) under salt stress. Appl Soil Ecol 95:23–30

Sukweenadhi J, Kim Y-J, Choi E-S, Koh S-CLee S-W, Kim Y-J, Yang DC (2015) *Paenibacillusyonginensis* DCY84T induces changes in *Arabidopsis thaliana* gene expression against aluminum, drought, and salt stress. Microbiol Res 172:7–15

Sun J, Chen S-L, Dai S-X, Wang R-G, Li N-Y, Shen X, Zhou X-Y, C–F L, Zheng X-J, Z-M H, Zhang Z-K, Song J, Xu Y (2009) Ion flux profiles and plant ion homeostasis control under salt stress. Plant Signal Behav 4:261–264

Takahashi S, Seki M, Ishida J, Satou M, Sakurai T, Narusaka M, Kamiya A, Nakajima M, Enju A, Akiyama K (2004) Monitoring the expression profiles of genes induced by hyperosmotic, high salinity, and oxidative stress and abscisic acid treatment in *Arabidopsis* cell culture using a full-length cDNA microarray. Plant Mol Biol 56:29–55

Tardieu F (2005) Plant tolerance to water deficit: physical limits and possibilities for progress. C R Geosci 337:57–67

Tavakkoli E, Rengasamy P, McDonald GK (2010) High concentrations of Na^+ and Cl^- ions in soil solution have simultaneous detrimental effects on growth of fava bean under salinity stress. J Exp Bot 61:4449–4459

Tewari S, Arora NK (2014) Multifunctional exopolysaccharides from *Pseudomonas aeruginosa* PF23 involved in plant growth stimulation, biocontrol and stress amelioration in sunflower under saline conditions. Curr Microbiol 69:484–494

Timmusk S, Paalme V, Pavlicek T, Bergquist J, Vangala A, Danilas T, Nevo E (2011) Bacterial distribution in the rhizosphere of wild barley under contrasting microclimates. PLoS One 6:e17968

Timmusk S, Abd El-Daim IA, Copolovici L, Tanilas T, Kännaste A, Behers L, Nevo E, Seisenbaeva G, Stenström E, Niinemets U (2014) Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: enhanced biomass production and reduced emissions of stress volatiles. PLoS ONE 9:e96086

Tittabutr P, Piromyou P, Longtonglang A, Noisa-Ngiam R, Boonkerd N, Teaumroong N (2013) Alleviation of the effect of environmental stresses using co-inoculation of mungbean by *Bradyrhizobium* and rhizobacteria containing stress-induced ACC deaminase enzyme. Soil Sci Plant Nutr 59:559–571

Tran LS, Shinozaki K, Yamaguchi-Shinozaki K (2010) Role of cytokinin responsive two-component system in ABA and osmotic stress signaling. Plant Signal Behav 5:148–150

Türkan I, Demiral T (2009) Recent development in understanding salinity tolerance. Environ Experim. Botany 67:2–9

Tuteja N, Mahajan S (2007) Calcium signaling network in plants. An overview. Plant Signaling Behav 2: 79–85

Tuteja N, Banu SA, Huda KMK, Gill SS, Jain P, Pham XH, Tuteja R (2014a) A) pea p68, a DEAD-box helicase, provides salinity stress tolerance in transgenic tobacco by reducing oxidative stress and improving photosynthesis machinery. PLoS One 9:e98287. doi:10.1371/journal.pone.0098287

Tuteja N, Tarique M, Banu MS, Ahmad M, Tuteja R (2014b) *Pisum sativum* p68 DEAD-box protein is ATP-dependent RNA helicase and unique bipolar DNA helicase. Plant Mol Biol 85:639–651

Ulmasov T, Murfett J, Hagen G, Guilfoyle TJ (1997) Aux/IAA proteins repress expression of reporter genes containing natural and highly active synthetic auxin response elements. Plant Cell 9:1963–1971

Vacheron J, Desbrosses G, Bouffaud M-L, Touraine B, Moenne-Loccoz Y, Muller D, Legendre L, Wisniewski-Dye F, Prigent-Combaret C (2013) Plant growth-promoting rhizobacteria and root system functioning. Front Plant Sci 4:article 356. doi:10.3389/fpls.2013.00356

Verslues PE, Agarwal M, Katiyar-Agarwal S, Zhu J, Zhu J-K (2006) Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. Plant J 45:523–539

Wang Y, Li K, Li X (2009) Auxin redistribution modulates plastic development of root system architecture under salt stress in *Arabidopsis thaliana*. J Plant Physiol 166:1637–1645

Wang Q, Dodd IC, Belimov AA, Jiang F (2016) Rhizosphere bacteria containing 1-aminocyclopropane-1-carboxylate deaminase increase growth and photosynthesis of pea plants under salt stress by limiting Na + accumulation. Function. Plant Biol 43:161–172

Xu J, Li X-L, Luo L (2012) Effects of engineered *Sinorhizobium meliloti* on cytokinin synthesis and tolerance of alfalfa to extreme drought stress. Appl Environ Microbiol 78:8056–8061

Yamaguchi-Shinozaki K, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. Annu rev. Plant Biol 57:781–803

Yan J, Smith MD, Glick BR, Liang Y (2014) Effects of ACC deaminase-containing rhizobacteria on plant growth and expression of toc GTPases in tomato (*Solanum lycopersicum*) under salt stress. Botany 92:775–781

Yoshida T, Fujita Y, Sayama H, Kidokoro S, Maruyama K, Mizoi J, Shinozaki K, Yamaguchi-Shinozaki K (2010) AREB1, AREB2, and ABF3 are master transcription factors that cooperatively regulate ABRE-dependent ABA signaling involved in drought stress tolerance and required ABA for full activation. Plant J 61:672–685

Yoshida T, Mogami J, Yamaguchi-Sninozaki K (2014) ABA-dependent and ABA-independent signaling in response to osmotic stress in plants. Curr Opin Plant Biol 21:133–139

Yue H, Mo W, Li C, Zheng Y, Li H (2007) The salt stress relief and growth promotion effect of Rs-5 on cotton. Plant Soil 297:139–145

Zafar-ul-Hye M, Farooq HM, Zahir ZA, Hussain M, Hussain A (2014) Application of ACC-deaminase containing rhizobacteria with fertilizer improves maize production under drought and salinity stress. Int J Agric Biol 16:591–596

Zapata PJ, Serrano MPretel MT, Amoros A, Botella MA (2004) Polyamines and ethylene changes during germination of different plant species under salinity. Plant Sci 167:781–788

Zhao Y, Dong W, Zhang N, Al X, Wang M, Huang Z, Xiao L, Xia G (2014) A wheat allene oxide cyclase gene enhances salinity tolerance via jasmonate signaling. Plant Physiol 164: 1068–1076

Zhou S, Hu W, Deng X, Ma Z, Chen L, Huang C, Wang C, Wnag J, He Y, Yang G, He G (2012) Overexpression of the wheat aquaporin gene, TaAQP7, enhances drought tolerance in transgenic tobacco. PLOS ONE 7(12):e52439. doi:10.1371/journal.pone.0052439

Zhu JK (2001) Plant salt tolerance. Trends Plant Sci 6:66–71

Zhu JK (2002) Salt and drought stress signal transduction in plants. Annu Rev Plant Physiol Plant Mol Biol 53:247–273

Zhu JK, Liu J, Xiong L (1998) Genetic analysis of salt tolerance in *Arabidopsis*. Evidence for a critical role of potassium nutrition. Plant Cell 10:1181–1191