Microbe-Mediated Induced Abiotic Stress Tolerance Responses in Plants

5

Neveen B. Talaat and Bahaa T. Shawky

Abstract

Abiotic stresses, including salinity, drought, high temperature, chilling injury, and heavy metal toxicity, have become major limiting factors for the global agricultural production. Moreover, these environmental conditions have increased over time due to change in global climate pattern and human interference. Using a diverse array of microorganisms harbored by plants to improve plant growth and host stress tolerance may benefit in sustaining the increases in food production in many regions of the world. Microbes help in rendering plants tolerant to these unfavorable environmental stresses. This cross-stress protection provided by microbial inoculants plays an important role in maintaining ecological balance and holds promise for generating more tolerant crops. Microorganisms not only provide "non-nutritional" effects in stabilizing soil aggregates, prevent erosion, detoxify pesticides, and suppress plant diseases and soilborne pathogens, but they can also fix atmospheric nitrogen, solubilize mineral phosphate, decompose organic wastes and residues, improve nutrient cycling, produce bioactive compounds, produce phytohormone and siderophore, as well as enhance osmolyte production, plant–water relation, photosynthetic capacity, protein assimilation, plant hormonal status, ionic balance, antioxidant production, and other physiological parameters inside the plant. In addition, using compatible multiple microbial consortia consisting of bacterial symbionts and fungal symbionts acting synergistically, providing various beneficial effects, is also a potential technical tool. Furthermore, intensive selection of stress-tolerant bioinoculants could improve plant abiotic stress tolerance and thus enhance crop productivity under

---

N.B. Talaat (✉)
Department of Plant Physiology, Faculty of Agriculture, Cairo University, Giza, Egypt
e-mail: neveenbt@yahoo.com

B.T. Shawky
Department of Microbial Chemistry, Genetic Engineering and Biotechnology Research Division, National Research Centre, Giza 12622, Egypt

D.P. Singh et al. (eds.), *Plant-Microbe Interactions in Agro-Ecological Perspectives*, https://doi.org/10.1007/978-981-10-6593-4_5

stressful conditions. This chapter documents the potential of microorganisms and highlights insights into the mechanisms underlying improved stress tolerance in plants by microbial colonization.

Keywords
Abiotic stress • Arbuscular mycorrhizal fungi • Microbes • Plant growth-promoting bacteria • Plant microbe interaction • Plant stress tolerance

5.1 Introduction

Plants face several unfavorable abiotic stresses including salinity, drought, heat, chilling injury, and heavy metal toxicity that severely impact plant growth and development and finally decrease their overall yield to about 70% (Saxena et al. 2013). Practical strategies were developed worldwide for mitigating stress toxic effects through the development of tolerant varieties, shifting crop calendars, using chemicals that may be toxic for the environment, resource management practices, etc. (Grover et al. 2011). While most of these practices are time-consuming and costly, microbial inoculation as a safe, low-cost, effective, environment-friendly approach can increase plant stress tolerance and can also maintain ecosystem health (Naveed et al. 2014; Talaat and Shawky 2014a, 2015; Meena et al. 2015; Talaat et al. 2015a). Indeed, microbe's ability to confer plant stress resistance may open a new avenue for alleviating the adverse effect of global climate change on agricultural production (Grover et al. 2011).

Plant roots are colonized by soilborne bacteria and fungi that may have beneficial effects on the agriculture crops by inducing plant adaptation to abiotic stresses (Grover et al. 2011). Arbuscular mycorrhizal fungi (AMF) are microscopic filamentous fungi that colonize cortical tissues and extend hyphae into the rhizosphere (Shokri and Maadi 2009). It has a positive effect on the poorly mobile nutrients such as phosphorus and other nutrients such as N, K, Ca, Mg, Fe, Zn, and Cu of plants subjected to unfavorable environmental stresses (de Andrade et al. 2008; Bagheri et al. 2012; Talaat and Shawky 2011, 2013). AM symbiosis helps plants to cope up with abiotic stresses by defending roots against soilborne pathogens, improving rhizosphere and soil conditions, modifying microbial communities, maintaining membrane integrity, stimulating plant growth regulator production, enhancing/selective nutrient uptake and preventing nutritional disorder, inducing osmoregulator accumulation, controlling reactive oxygen species (ROS) accumulation by enhancing antioxidant enzyme activity and antioxidant molecule content, improving photosynthesis process, enhancing protein synthesis, and changing transcript levels of genes involved in signaling pathway or stress response, as well as structural adaptations (Zhang et al. 2010b; Maya and Matsubara 2013; Talaat and Shawky 2014a, b, 2015; Shabani et al. 2016).

Nitrogen-fixing bacteria which are also called diazotrophic bacteria can fix atmospheric nitrogen for the plant. They can act as free-living bacteria or form a symbiosis with legumes and establish root nodules where biological nitrogen fixation occurs (Gomez-Sagasti and Marino 2015). Rhizobia, a group of associative diazotrophic bacteria, are often used as co-inoculants with other microbes, either bacteria or fungi, to enhance plant growth and productivity under different stressful conditions (Figueiredo et al. 2008; Ahmad et al. 2013; Gomez-Sagasti and Marino 2015).

Other types of beneficial soilborne microbes that are defined as plant growth-promoting bacteria (PGPBs) can colonize the rhizosphere/endorhizosphere of plants, stimulate plant growth, and confer enhanced resistance to biotic and abiotic stresses. Rhizospheric bacteria capable of promoting plant growth under different conditions are known as plant growth-promoting rhizobacteria (PGPRs). They colonize the rhizosphere of many plant species and impart benefit to the plants indirectly by reducing plant pathogens or directly by releasing phytohormones (auxins, cytokinins, gibberellins, and abscisic acid); producing essential enzymes, 1-aminocyclopropane -1-carboxylate (ACC) deaminase, to reduce ethylene level in the root of developing plants; fixing nitrogen; solubilizing and mineralizing nutrients, particularly mineral phosphate; mobilizing nutrients in the rhizosphere; producing siderophores to facilitate root uptake of metal nutrients; emitting volatile organic compounds (VOCs); producing antioxidants; producing exopolysaccharides (EPS); and biofilm formation (Grover et al. 2011). The term induced systemic tolerance (IST) is referred as PGPR-induced physical and chemical changes in plants to respond to changing environmental conditions and mitigate the impacts of stress (Belimov and Wenzel 2009; Cohen et al. 2015; Singh and Jha 2016). Bacteria belonging to different genera including *Achromobacter*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Microbacterium*, *Paenibacillus*, *Pantoea*, *Pseudomonas*, *Serratia*, *Streptomyces*, etc. can improve the host plant growth under abiotic stress conditions (Grover et al. 2011; Nadeem et al. 2016).

Today, sustainable agricultural practices should be productive, profitable, energy-conserving, eco-friendly, conserving of natural resources, and ensuring food safety and quality. Effective microorganism (EM) application can minimize the investment of money and labor, minimize the environmental impact, and support food safety and food security. It consists of naturally occurring beneficial microorganisms: photosynthetic bacteria (*Rhodopseudomonas* spp.), lactic acid bacteria (*Lactobacillus* spp.), yeast (*Saccharomyces* spp.), actinomycetes, and fermenting fungi (*Aspergillus* and *Penicillium*) (Higa 2004). It can enhance crop production and protection by promoting seed germination; enhancing plant growth, root development, flowering, fruiting, and ripening; increasing the efficacy of organic matter as fertilizers; increasing nutrient availability in the rhizosphere of plants; developing resistance of plants to pests and diseases; suppressing soilborne pathogens and pests; and increasing the production of antioxidants that suppress the negative impact of free radicals in plant metabolism (Higa 2004; Talaat 2015a). It can also decrease the damage to plants caused by soil salinization by improving various physiological and biochemical processes inside the plant cell (Talaat 2014, 2015b; Talaat et al. 2015a).

Interestingly, the use of multi-strain microbial inocula is a potential biotechnological approach to ameliorate the deleterious effects of the stressful conditions on plant and enhance its fitness. Co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici* ameliorated the harmful impact of water deficit on *Phaseolus vulgaris* L. (Figueiredo et al. 2008). The combined interaction of *Pseudomonas* and *Rhizobium* protected mung bean from saline soil (Ahmad et al. 2013). Co-inoculation of PGPBs and *Rhizobia* with legume plants also supported the growth of plant during metal phytostabilization and phytoextraction strategies (Gomez-Sagasti and Marino 2015). Furthermore, co-inoculation of PGPR *Dietzia natronolimnaea* strain STR1 and AMF *Glomus intraradices* alleviated the negative impact of salinity on the growth of *Ocimum basilicum* (Bharti et al. 2016a).

The present chapter appraises the crucial role of useful soil microbes in plant tolerance to major abiotic factors, such as salinity, drought, heat, chilling injury, and heavy metal toxicity. Special emphasis is given to the physiological impacts and how the compatible multiple microbial consortia mitigate the abiotic stress symptoms in the plants. Moreover, it explores the beneficial effects of using stress-tolerant bioinoculants to develop plant stress tolerance. Finally, major aspects for future work in the current direction have also been highlighted.

5.2 Salt Stress

Soil salinization is a devastating ecological and agronomical problem that limits agricultural production and land development in many areas on the earth. Approximately 7% of the global land surface is salt-affected. More than 800 million hectares of global land are affected by salinity (Munns and Tester 2008). Plant cells can sense salt stress through membrane disorganization; enzyme damage; metabolic toxicity; inhibition of photosynthesis, respiration, and protein synthesis; disturbance in nutrient accumulation; toxicity of excessive Na^+ and Cl^-; disturbance in water and osmotic potential; reduction in assimilate translocation to sinks; and increasing ROS production in chloroplasts (Talaat and Shawky 2013, 2014a, b; Pedranzani et al. 2016). Indeed, increasing salinization of soils, increasing costs of fertilizers, and increasing need for food to feed the global population are the main factors that stressed the need for full exploitation of soil microbes. Exploitation of soil microbes for utilizing salt-stressed land is an effective tool and may provide a quick-fix solution to this problem. The benefit to mankind and the economic potential make it a worthwhile task.

5.2.1 Plant Growth-Promoting Bacteria in Salt Stress Mitigation

PGPRs can act as elicitors of tolerance to salt stress. They facilitate growth in the saline environment via inducing different physical and biochemical changes in stressed plants, to confer IST. Certain PGPR strains confer salt tolerance by protecting the plants from the negative impact of high Na^+ concentrations in the soil. For example, soil bacterium *Bacillus subtilis* strain GB03 conferred salt tolerance in *A. thaliana* by tissue-specific regulation of *HKT1* (high-affinity K^+ transporter 1).

GB03 under saline condition concurrently downregulates *HKT1* expression in roots and upregulates its expression in shoots, which lowered the accumulation of Na^+ throughout the plant compared with controls (Zhang et al. 2008). Similarly, soil bacterium inoculation with GB03 promoted the growth of white clover under salt stress by decreasing shoot and root Na^+ accumulation, thereby improving K^+/Na^+ ratio. GB03 also regulated chlorophyll content, leaf osmotic potential, cell membrane integrity, and ion accumulation in salt-affected plants (Han et al. 2014). Furthermore, inoculation with *Bacillus* sp. strain L81 and *Arthrobacter oxidans* strain BB1 significantly reduced *A. thaliana* Col 0 mortality under salt stress, which might be due to the induction in the expression of *PR1* that is a gene associated to the SA-dependent pathway (Barriuso et al. 2008). Co-inoculation of *B. subtilis* and *Arthrobacter* sp. alleviated the deleterious effects of salt stress on wheat growth by increasing plant dry biomass and by inducing the accumulation of sugars and proline (Upadhyay et al. 2011). Recently, the multi-strain consortium of three bacterial species *P. fluorescens*, *B. megaterium*, and *V. paradoxus* enhanced the leaf chlorophyll content in cucumber plants subjected to saline conditions (Nadeem et al. 2016). Hence, the multi-strain bacterial inoculum can play a crucial role in protecting the plant from saline soil.

PGPR improves salt stress tolerance in different plant species by producing ACC deaminase, phytohormones, siderophores, exopolysaccharides (EPS), antioxidants, and volatile organic compounds (VOCs) (Grover et al. 2011). PGPB with ACC deaminase activity colonizes the rhizosphere and keeps ethylene levels low that is beneficial for root growth and plant survival under saline conditions. High K^+/Na^+ ratio, relative water content, chlorophyll level, and low proline content were detected in salt-stressed maize inoculated with *Pseudomonas syringae*, *Enterobacter aerogenes*, and *P. fluorescens* containing ACC deaminase activity (Nadeem et al. 2007). Similarly, improved root length, shoot height, as well as fresh and dry weight was observed in salt-stressed wheat plants inoculated with ACC deaminase-producing *Klebsiella* spp. SBP-8 (Singh et al. 2015). Inoculation with *Enterobacter* sp. UPMR18 containing ACC deaminase activity induced antioxidant enzyme activities (SOD, APX, and CAT) and upregulated ROS pathway genes (CAT, APX, GR, and DHAR) of salt-affected okra plants (Habib et al. 2016). PGPB also promotes plant growth and development under soil salinization by enhancing the synthesis of plant hormones. Production of indoleacetic acid, gibberellins, and some unknown determinants by PGPR improved wheat salt tolerance as a result of increasing root length, root surface area, and number of root tips, which increased nutrient uptake (Egamberdieva and Kucharova 2009). Salt-stressed *Medicago* plants infected with IAA-overproducing PGPR *Sinorhizobium meliloti* strain showed high antioxidant enzyme activity (Bianco and Defez 2009). Inoculation with *Streptomyces* producing the PGP activity of an auxin and siderophore significantly improved the germination rate, shoot length, dry weight, and N, P, Fe, and Mn concentrations in salt-stressed wheat plants (Sadeghi et al. 2012). Furthermore, exopolysaccharide-producing bacteria inoculation could restrict Na^+ influx into roots. EPS production by PGP strains helps in binding cations, including Na^+, and thus decreases the content of Na^+ available for uptake by plants, which is especially beneficial for alleviating salt stress in plants. Wheat seedling inoculation with bacteria that produce EPS restricted sodium uptake and stimulated plant growth under salt stress (Grover et al. 2011). PGPR can also enhance salt tolerance via enhancing ROS-scavenging system. Inoculation of paddy with two root-associated bacteria *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* enhanced salt tolerance via regulating lipid peroxidation, SOD activity, caspase-like protease activity, and programmed cell death (Jha and Subramanian 2014). In addition, plant perception of bacterial VOC causes a tissue-specific regulation of HKT1 that controls Na^+ homeostasis under saline conditions. VOCs from PGPB downregulated high-affinity K^+ transporter 1 (HKT1) expression in roots, but upregulated it in shoot tissues and thus reduced the Na^+ levels in the whole plant (Yang et al. 2009). Soybean plants exposed to volatile emissions from *Pseudomonas simiae* strain AU not only decreased root Na^+ levels but also enhanced the proline accumulation, which protect the plant cells from osmotic stress. Consistent with induced systemic tolerance under salt stress, inoculation with AU VOCs resulted in increase in the vegetative storage protein and several other proteins that can help the stressed plants to sustain their growth and development (Vaishnav et al. 2015). Recently, *Herbaspirillum* sp. strain GW103, which is capable of producing plant beneficial factors, such as auxin, siderophore, and ACC deaminase, alleviated salinity stress in Chinese cabbage by increasing the root K^+/Na^+ ratio that generated balance in the ion homeostasis and thus contributed to biomass increase (Lee et al. 2016). Inoculation with *Enterobacter* sp. SBP-6 containing ACC deaminase activity and showing other PGP traits like phosphate solubilization, phytohormone production, and nitrogen fixation to wheat plants ameliorated the negative impact of saline conditions. It significantly improved plant biomass, chlorophyll content, K^+ uptake, and K^+/Na^+ ratio, while it diminished Na^+, proline, and malondialdehyde contents (Singh and Jha 2016).

Co-inoculation of PGPR with symbiotic bacteria under saline conditions is a potential biotechnological approach that improves both the plant productivity and the soil health. Co-inoculation of *Serratia proteamaculans* ATCC 35475 and *Rhizobium leguminosarum* bv. *viciae* 128C56G alleviated the inhibitory effect of salinity on plant growth, antioxidant enzyme activity, photosynthesis process, and mineral content of *Lactuca sativa* (Han and Lee 2005). Inoculation by *Pseudomonas* sp. 54RB and *Rhizobium* sp. Thal-8 decreased the electrolyte leakage, while it increased the proline production, the relative water content, and the K^+ ion uptake of maize plants subjected to salinity stress (Bano and Fatima 2009). Likewise, co-inoculation of *Pseudomonas* and *Rhizobium* enhanced growth, nodulation, and ionic acquisition of mung bean grown under saline conditions (Ahmad et al. 2013).

Halotolerant bacteria isolated from saline environments have potential to improve plant establishment under saline conditions through direct or indirect mechanisms and would be most appropriate as bioinoculants under such conditions. Inoculation with 14 halotolerant bacterial strains ameliorated salt stress in canola plants through the reduction of ethylene production *via* ACC deaminase activity (Siddikee et al. 2010). Inoculation with the salt-tolerant rhizosphere bacteria (*Bacillus pumilus*, *Pseudomonas mendocina*, *Arthrobacter* sp., *Halomonas* sp., and *Nitrinicola lacisaponensis*) enhanced chlorophyll, carotenoids, and protein contents, as well as the accumulation of individual phenolics (gallic, caffeic, syringic, vanillic, ferulic, and cinnamic acids), flavonoid quercetin, and IAA, which induced salt stress tolerance in wheat (Tiwari et al. 2011). Wheat plants inoculated with saline-adapted *Azospirillum* strains had higher shoot dry weight, grain yield, and N concentrations than the uninoculated ones under saline conditions (Nia et al. 2012). Inoculation by halotolerant bacteria *Halobacillus* sp. and *B. halodenitrificans* ameliorated salinity stress in wheat by improving root elongation and root dry weight (Ramadoss et al. 2013). *Bacillus* sp. and *Arthrobacter pascens* sp. isolated from rhizospheric soil of halophyte regions promoted the growth of salt-stressed maize plants by enhancing sugar and proline accumulation as well as increasing SOD, POX, CAT, and APX activities (Ullah and Bano 2015). Another PGPB, *Pseudomonas koreensis* strain AK-1, mitigated salt stress and promoted soybean growth by reducing Na^+ level while increasing K^+ level, stress enzyme activity, and proline content in leaves and roots (Kasotia et al. 2015). Inoculation with ACC deaminase-producing PGPB *Enterobacter cloacae* strain KBPD isolated from salt-affected soil alleviated salt toxicity in *Vigna radiata* L. by increasing shoot length, root length, fresh and dry weights, as well as total chlorophyll content. Salt-affected plants had higher proline content, while inoculation with *E. cloacae* KBPD reduced its content (Bhise et al. 2016). Carotenoid producing halotolerant PGPR *Dietzia natronolimnaea* STR1 promoted growth and protected wheat plants from damage to salt stress via modulating the expression of stress-responsive genes. It modulated ABA-signaling of cascade genes (*TaABARE* and *TaOPR1*), expression of SOS pathway-related genes (*SOS1* and *SOS4*) and ion transporters (*TaNHX1*, *TaHAK*, and *TaHKT1*), expression of *TaST* (a salt stress-induced gene), and gene expression of various antioxidant enzymes (*APX*, *MnSOD*, *CAT*, *POD*, *GPX*, and *GR*), which contributed to increased salt stress tolerance in these plants. Inoculated plants subjected to salinity stress recorded also higher proline and lower MDA levels in comparison to the uninoculated ones (Bharti et al. 2016b).

5.2.2 Arbuscular Mycorrhizal Fungi in Salt Stress Mitigation

Mycorrhizal infection has gained a considerable importance as a shotgun approach to overcome the salt-induced reduction in crop production by altering the physiological and biochemical properties of the host plant. It has been considered a bioameliorator of saline soils. Several mechanisms have been reported behind mycorrhizal elicited plant stress tolerance. It alleviated salinity-induced injuries by regulating water uptake, increasing nutrient acquisition, inducing organic solute accumulation, maintaining photosynthetic capacity, improving protein synthesis, altering plant hormonal status, and enhancing ROS-scavenging activity resulting in higher crop yield (Talaat and Shawky 2015).

The improved salt tolerance of AM plants could be due to a more efficient uptake of nutrients. Symbiosis between AMF and most plant species provides nutrients such as phosphorus and others including N, K, Ca, Mg, Fe, Zn, and Cu (Shokri and Maadi 2009). Arbuscular mycorrhizal colonization and arbuscule formation effectively alleviated salinity-induced injuries by increasing N, P, K^+, Ca^{2+}, and Mg^{2+} uptake and decreasing Na^+ concentration in wheat (Talaat and Shawky 2011). Indeed, AMF may act as a first barrier for ion selection during the fungal uptake of nutrients from the soil or during their transfer to the host plant. For example, *Rhizophagus intraradices* can take up K^+, Mg^{2+}, and Ca^{2+} while avoiding Na^+ uptake, which suggest that AMF can induce a buffering effect on the Na^+ uptake (Hammer et al. 2011). AMF colonization can also improve the water absorption capacity of maize plants grown under saline conditions, by increasing root hydraulic conductivity and by adjusting the osmotic balance (Sheng et al. 2008). Moreover, mycorrhizae can increase the root growth and thus could enhance the plant adaptation to adverse soil conditions (Talaat and Shawky 2012; Pedranzani et al. 2016). Indeed, root growth promotion can lead to a larger root surface and consequently increase the water acquisition and nutrient uptake. Change in polyamine balance is a frequent response of plant metabolism to the mycorrhizal colonization influencing many physiological aspects including stress resistance and resulting in better performance of plants under stressful conditions (Smith and Read 2008). Mycorrhization improved wheat salt stress tolerance by altering polyamine balance; it changed Put, Spd, and Spm content as well as reduced the activities of diamine oxidase and polyamine oxidase. It also improved host plant nutrient status via increasing N, P, K^+, Fe, Zn, and Cu acquisition and diminishing Na^+ uptake and thus increased the fitness of wheat plant to salt stress (Talaat and Shawky 2013).

Mycorrhizal symbiosis can also play as an ecosystem service provider to guarantee plant productivity in saline soils by improving carbon and nitrogen metabolisms. It alleviated the deleterious effect of salinity through improving relative water content and membrane stability index; inducing a better osmotic adjustment via compatible solute accumulation such as soluble sugars, free amino acids, proline, and glycinebetaine; altering ionic balance via increasing N, K^+, and Mg^{2+} acquisition and decreasing Na^+ uptake; enhancing photosynthetic efficiency via improving photochemical reactions of photosynthesis, gas exchange capacity, chlorophyll content, Chl a/b ratio, carbonic anhydrase activity, and carbohydrate content; promoting protein synthesis via enhancing nitrate content and nitrate reductase activity; as well as preventing oxidative stress via alleviating membrane lipid peroxidation and decreasing H_2O_2 content (Talaat and Shawky 2011, 2014a). Inoculation via *Rhizophagus irregularis* to salt-affected *Populus cathayana* plants enhanced plant–water status (relative water content and water-use efficiency), which could increase the capacity of photosynthesis and thus biomass production (Wu et al. 2015). Furthermore, AMF can improve plant adaptation to saline soils by eliminating the ROS. Mycorrhizal symbiosis altered the plant physiology of salt-stressed wheat plants by reducing membrane lipid peroxidation, membrane permeability, and H_2O_2 content as well as by enhancing ROS-scavenging system activity via increasing the antioxidative enzyme (SOD, POX, CAT, and GR) activity and the antioxidant molecules (glutathione, ascorbate, and glycine-betaine) concentration (Talaat and Shawky 2014b). AM *Digitaria eriantha* plants grown under saline conditions had higher CAT, APX, and SOD activity, higher stomatal conductance value, higher endogenous jasmonate level, and lower hydrogen peroxide level than the non-AM ones (Pedranzani et al. 2016).

Influence of AMF on organic acids in maize leaves under salt stress was studied by Sheng et al. (2011), who found that AM symbiosis increased the accumulation of organic acids such as oxalic acid, fumaric acid, acetic acid, malic acid, and citric acid, whereas the concentrations of formic acid and succinic acid decreased, and no significant effect was found on lactic acid concentrations. Mycorrhizal infection can also alter plant hormonal status in salt-stressed plants. Lower ABA levels were detected in *Glomus intraradices*-colonized lettuce plants indicating that AM plants were less strained than non-AM plants by salinity stress imposed; hence, they accumulated less ABA (Jahromi et al. 2008). An increase in strigolactone, a new class of plant hormone, in mycorrhizal-treated plants was demonstrated to overcome salinity effects in lettuce plants (Aroca et al. 2013). Higher cytokinin concentration and higher translocation of photosynthetase were detected in AMF-inoculated plants subjected to salt stress (Hameed et al. 2014).

Potential molecular mechanisms underlying AMF-mediated plant salt stress tolerance were reported. AMF-induced plant salinity tolerance may be influenced by genes encoding Δ1-pyrroline-5-carboxylate synthetase (*LsP5CS*), late embryogenesis-abundant protein (*LsLea*), and ABA (*Lsnced*) (Kapoor et al. 2013). Cyclic nucleotide-gated ion channels (CNGCs) assisted the AM-inoculated plants to survive under saline conditions by supplying the sodium reallocation within the plant tissues (Ruiz-Lozano et al. 2012). Although the Na^+/H^+ antiporters – *LeNHX1* and *LeNHX2* – catalyze the transfer of Na^+ out of the cytoplasm into either vacuole or apoplasm, the AM symbiosis under salt stress did not alter the expression of *LeNHX1* and *LeNHX2* genes (Ouziad et al. 2006). Inoculation of three native AMF from a Mediterranean saline area to salt-stressed maize plants showed significant increase in K^+ and reduction in Na^+ accumulation as compared to salt-stressed non-mycorrhizal ones, concomitantly with higher K^+/Na^+ ratios. This effect correlated with the regulation of *ZmAKT2*, *ZmSOS1*, and *ZmSKOR* genes in their roots (Estrada et al. 2013). Mycorrhizal infection enhanced the rice salt tolerance by decreasing Na^+ root-to-shoot distribution and increasing Na^+ accumulation in rice roots. In aerial plant tissues, the AM symbiosis may favor Na^+ extrusion from cytoplasm, its sequestration into the vacuole, the unloading of Na^+ from the xylem, and its recirculation from photosynthetic organs to roots through regulation of the expression of *OsNHX3*, *OsSOS1*, *OsHKT2;1* and *OsHKT1;5* genes encoding plant transporters involved in ion homeostasis (Porcel et al. 2016).

Mycorrhizal-colonized plants can also interact with several soil microorganisms including PGPR to increase the plant salt tolerance. Inoculation with PGPR *P. mendocina* alone and in combination with an AMF *Glomus intraradices* or *G. mosseae* improved the biomass of salt-stressed *Lactuca sativa* cv. *Tafalla* plants, along with antioxidant enzymes and proline content in foliage (Kohler et al. 2009). The combined application of AMF and PGPB attenuated the negative salinity effects on the plants by producing phytohormone and increasing nutrient uptake (Dodd and Perez-Alfocea 2012). Co-inoculation with a mixture of AMF from the genera *Glomus*, *Gigaspora*, and *Acaulospora* and the rhizobia *Sinorhizobium terangae* resulted in a positive osmotic adjustment that improved salinity tolerance in *Acacia saligna* (Soliman et al. 2012). Co-inoculation of AMF (*Glomus etunicatum*) and PGPB

(*Methylobacterium oryzae* CBMB20) alleviated salt stress and significantly increased dry biomass and nutrient accumulation, while it significantly reduced proline content and Na^+ uptake in maize plants (Lee et al. 2015). Co-inoculation of PGPR *Dietzia natronolimnaea* strain STR1 and AMF *Glomus intraradices* positively influenced the growth of *Ocimum basilicum* plants grown in salt-affected soils (Bharti et al. 2016a).

5.2.3 Effective Microorganisms in Salt Stress Mitigation

Using EM application as a biological strategy to enhance plant salt stress tolerance can increase the saline soil utilization and become an emerging challenge as a promising environmentally friendly method. It provides an inexpensive and viable method for alleviating the effect of soil salinization on crop production (Talaat 2014, 2015b; Talaat et al. 2015a). It protected the plant cell against the oxidative damage and enhanced the plant survival under soil salinization by countering the lipid peroxidation via enhancing the enzymatic activities of antioxidative enzymes involved in the ascorbate–glutathione cycle and a higher redox status of the antioxidants ascorbate and glutathione. Indeed, EM treatment enhanced the H_2O_2-scavenging capacity of the ascorbate–glutathione cycle to attenuate the activation of plant defenses (Talaat 2014). Preventing oxidative stress and eliminating ROS are the most effective mechanisms used by EM-treated plants to cope with salinity stress (Talaat 2015a). EM application can also increase plant salinity tolerance by enhancing the nutrient acquisition and improving the osmotic adjustment via compatible solute accumulation. EM treatment reduced Na^+ uptake, increased N, P, K^+, Ca^{2+}, Mg^{2+}, Fe, Zn, and Cu absorption, and enhanced important osmolytes such as soluble sugar, free amino acid, proline, and glycinebetaine accumulation in *Phaseolus vulgaris* plants subjected to saline conditions (Talaat et al. 2015a). Moreover, the application of EM could improve salt stress tolerance by the regulation of protein synthesis and the modulation of polyamine pool. It activated the nitrate uptake and enhanced the NR activity, which could be a reason for the observed increase in the protein content. It also regulated the ionic homeostasis, modified the biosynthesis of polyamines, decreased the activity of the polyamine catabolizing enzymes, prevented the oxidative stress via decreasing the MDA and H_2O_2 contents, and enhanced the membrane stability index in *Phaseolus vulgaris* plants grown in salty soils (Talaat 2015b).

5.3 Water Stress

Drought is one of the major environmental factors that limit crop production worldwide by altering a series of physiological, biochemical, and molecular responses. It disrupts photosynthesis and protein synthesis, increases photorespiration, affects plant hormone balance, alters the normal homeostasis of cells, and induces high levels of ROS in plant cells (Cohen et al. 2015; Talaat et al. 2015b; Talaat and

Shawky 2016). Therefore, there is a serious need to find new ways to cope with the threat of global water deficiency on agricultural production. Microbial inoculants are a powerful strategic tool in inducing plant drought tolerance.

5.3.1 Plant Growth-Promoting Bacteria in Water Stress Mitigation

Microbial inoculants can alleviate the negative impact of water deficit by inducing different physical and biochemical changes in plants. Probably specific mechanisms are responsible for plant performance under this condition. *Azospirillum*-inoculated wheat seedling showed better phospholipid composition in its root than that in non-inoculated ones when exposed to water-deficit condition, which suggested that bacterial inoculation led to changes in the root cell membrane elasticity and thus improved tolerance to water deficiency (Pereyra et al. 2006). Root colonization with rhizobacteria *Pseudomonas chlororaphis* 06 enhanced water stress tolerance in *Arabidopsis* by reducing water loss and increasing stomatal closure. The volatile metabolite 2,3-butanediol produced by *P. chlororaphis* 06 increased salicylic acid (SA) content and thus induced the stomatal closure and subsequently drought resistance. Hence, induction of drought tolerance in *Arabidopsis* by *P. chlororaphis* 06 is through a SA-dependent mechanism (Cho et al. 2008). Indeed, studies with *Arabidopsis* mutant lines revealed that induced water stress tolerance requires SA, ethylene, and jasmonic acid signaling pathways. Additionally, many bacteria can ameliorate the adverse effect of water deficiency by increasing osmoprotectant accumulation. Both Gram-negative (*Azospirillum* and *Pseudomonas*) and Gram-positive (*Bacillus*) strains promoted water stress resistance of basil plants by inducing the production of proline and soluble carbohydrates in root and leaf tissues. Inoculated plants had also higher chlorophyll content, confirming the positive effect of bacteria under drought conditions (Heidari et al. 2011). Wheat seedlings inoculated by *Azospirillum* under osmotic stress had better water status, which could be attributed to the morphological changes in xylem vessels of the coleoptiles, upregulation of its own indole-3-pyruvate decarboxylase gene, and enhanced bacterial IAA synthesis (Pereyra et al. 2012). As a drought tolerance mechanism, plants overexpress zeatin to delay the leaf senescence. Inoculation by engineered strains of *Sinorhizobium meliloti* with *ipt* gene enhanced the concentration of zeatin and cytokinin and improved the activity of antioxidant enzymes in the leaves of alfalfa plants grown under severe drought conditions (Xu et al. 2012). Furthermore, drought stress amelioration was detected in wheat inoculated with *Burkholderia phytofirmans* strain PsJN by modulation of metabolism and improving the ionic balance (Naveed et al. 2014). *Azospirillum brasilense* Sp 245 strain ameliorated the deleterious effect of drought on *Arabidopsis thaliana* via altering root architecture, stimulating photosynthetic and photoprotective pigments, and retarding water loss in correlation with enhancement of ABA levels (Cohen et al. 2015). Overall, modulating water stress tolerance and minimizing the stress damage could be induced in the plant tissues by the microbial activities irrespective of the microbial origin.

PGPR ameliorates the negative effect of water deficiency on plant cells via a so-called process induced systemic tolerance (IST), which includes:

(a) Production of cytokinins that causes abscisic acid accumulation in leaves and results in the stomatal closure
(b) Production of indoleacetic acid which improves root growth and nutrient uptake
(c) Degradation of the ethylene precursor ACC by bacterial ACC deaminase
(d) Production of antioxidants that causes ROS degradation and reduces damage to cells and biomolecules
(e) Production of volatile organic compounds (VOCs)
(f) Production of exopolysaccharides which tends to improve soil structure by facilitating the formation of macroaggregates
(g) Production of siderophores to facilitate root nutrient uptake (Grover et al. 2011)

PGPR containing ACC deaminase significantly lowered the ACC level in water-stressed plants and thus decreased the ethylene synthesis and the plant damage. Inoculation with rhizobacteria containing ACC deaminase, *Pseudomonas fluorescens* biotype G (ACC-5), increased fresh weight, dry weight, root length, shoot length, number of leaves per plant, and water-use efficiency of water-stressed peas. Longer roots might increase the water uptake from deep soil, thus increasing water-use efficiency (Zahir et al. 2008). PGPB *Pseudomonas* sp., *P. putida*, and *B. megaterium* with IAA-producing abilities alleviated water stress in *Trifolium repens* (Marulanda et al. 2009). Certain PGPBs alleviated plant drought stress via VOC production. Osmotic-stressed *Arabidopsis* plants inoculated by the soil microbe *Bacillus subtilis* GB03 VOCs accumulated higher levels of choline and glycinebetaine, which are important osmoprotectants that confer dehydration tolerance in plants than plants without VOC treatment (Zhang et al. 2010a). PGPR-induced water stress tolerance can also be achieved via enhancing the antioxidant enzyme activity and the antioxidant molecule concentration. *Pseudomonas fluorescens* Pf1 ameliorated drought by increasing catalase and peroxidase activities, as well as proline accumulation in green gram plants (Saravanakumar et al. 2011). Water stress amelioration and plant growth promotion were detected in wheat plants inoculated with *Bacillus safensis* strain W10 and *Ochrobactrum pseudogregnonense* strain IP8. These PGPBs enhanced antioxidant responses via elevating activities of antioxidant enzymes catalase, peroxidase, ascorbate peroxidase, superoxide dismutase, and glutathione reductase as well as increasing accumulation of antioxidants carotenoids and ascorbate (Chakraborty et al. 2013). PGPR-treated potato plants had higher gene expression of ROS-scavenging enzymes as well as higher photosynthetic performance, which displayed increased tolerance to various abiotic stresses (Gururani et al. 2013). Certain PGPR may also indirectly ameliorate drought by enhancing the production of exopolysaccharide. Rhizobacteria *Pseudomonas putida* strain P45 with exopolysaccharide-producing abilities improved sunflower drought resistance. Exopolysaccharides possess unique water-holding and water-cementing properties, thus helping in the formation and stabilization of soil aggregates and regulation of nutrients and water flow across plant roots through biofilm formation (Sandhya et al. 2009). *Pseudomonas aeruginosa* strain Pa2 produce exopolysaccharides that enhanced bacterial ability to maintain soil moisture content and increased maize drought tolerance (Naseem and Bano 2014).

Rhizosphere bacteria also induce plant drought tolerance when applied in combination with rhizobial strains. Co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici* alleviated drought stress in common bean (*Phaseolus vulgaris* L.) by increasing the plant growth, nitrogen content, and nodulation as well as by altering the phytohormone content (Figueiredo et al. 2008).

Moreover, adapted drought-tolerant microorganisms may compensate for the stress effect and can be active in promoting plant establishment. The use of adapted autochthonous microorganisms to regenerate arid soils is an attractive possibility. Inoculation with five drought-tolerant PGP *Pseudomonas* spp. strains, namely, *P. entomophila*, *P. stutzeri*, *P. putida*, *P. syringae*, and *P. montelli*, ameliorated maize drought stress by modifying compatible solute accumulation and antioxidant status (Sandhya et al. 2010). The stress protecting agent *Stenotrophomonas rhizophila* DSM14405T produced spermidine, which is a general, highly efficient stress protectant (Alavi et al. 2013). Autochthonous bacteria strains of *Bacillus megaterium*, *Enterobacter* sp., *Bacillus thuringiensis*, and *Bacillus* sp. alleviated water stress in *Lavandula* and *Salvia* by increasing K content, depressing stomatal conductance, and controlling shoot proline accumulation (Armada et al. 2014). The autochthonous bacteria *Bacillus thuringiensis* and the allochthonous bacteria *Pseudomonas putida* alleviated drought stress impact on wheat plants through improving the content of nutrients and relative water as well as decreasing the stomatal conductance, electrolyte leakage, proline content, and APX activity (Ortiz et al. 2015).

5.3.2 Arbuscular Mycorrhizal Fungi in Water Stress Mitigation

Mycorrhizal soil community is a vital component in the plant–soil system. AM symbiosis facilitates the nutrient transfer from soil to host plants. It also improves drought tolerance through enhancing water uptake by extraradical hyphae, improving gas exchange and water-use efficiency, improving osmotic adjustment as a result of the enhancement in compatible solute accumulation, altering plant hormonal status, regulating antioxidant system, and improving soil structure by glomalin (Gong et al. 2013; Yooyongwech et al. 2013; Ortiz et al. 2015; Pedranzani et al. 2016). AMF enhancing the host plant drought tolerance can also be achieved by proteins with chaperone-like activity, such as that of luminal binding protein (BiP), which prevent intramolecular and intermolecular interactions in endoplasmic reticulum that can result in permanent misfolding or aggregation and thus loss of their function (Porcel et al. 2007).

AMF-induced drought tolerance can be mediated through lowered oxidative burst via increasing antioxidant enzyme activity and antioxidant molecule content. AM associations improved the *C. equisetifolia* drought tolerance via lowering the plasma membrane permeability and malondialdehyde content as well as by enhancing peroxidase activity and P, soluble sugar, and soluble protein concentrations

(Zhang et al. 2010b). Mycorrhization enhanced photosynthetic efficiency, induced glutathione accumulation, as well as reduced hydrogen peroxide accumulation and oxidative damage to lipids in rice plants grown under drought stress conditions (Ruiz-Sanchez et al. 2010). AMF inoculation mitigated the oxidative stress generated in *Poncirus trifoliata* under water deficiency by increasing the mRNA levels of four stress-responsive genes *CSD1* (copper/zinc SOD), *MIOX1* (myo-inositol oxygenase), *GLX1* (glyoxalase), and TTC5 (transparent testa 5), which encode enzymes responsible for elimination of ROS, alleviating oxidative stress and detoxification of cytotoxic compounds (Fan and Liu 2011). Higher shoot and root biomass as well as higher flavonoids as one of the ROS scavengers were observed in *Glomus etunicatum*-colonized pistachio plants as compared to non-colonized ones under drought conditions (Abbaspour et al. 2012). Colonization of pomegranate plants by *Rhizophagus intraradices* resulted in considerably higher shoot superoxide dismutase and catalase activity under water-deficit conditions (Bompadre et al. 2014). AM symbiosis improved plant drought tolerance by elevating the production of isoprenoids, nonvolatile compounds, and antioxidants (Rapparini and Penuelas 2014). In addition to antioxidant concentration and antioxidant enzyme activity, mycorrhizal plants possess a H_2O_2 efflux pathway to prevent oxidative burst being induced under water stress conditions. *Funneliformis mosseae*-colonized trifoliate orange seedlings had lower oxidative burst under drought conditions, which resulted from a combination of higher antioxidant enzyme activity (superoxide dismutase and catalase), lower O_2^- accumulation, higher H_2O_2 effluxes, and higher Ca^{2+} influxes (Zou et al. 2015). Increases in shoot/root biomass ratio; shoot dry matter content; stomatal conductance value; CAT, APX, and SOD activity; and endogenous jasmonate accumulation and decreases in H_2O_2 level were recorded in AM *Digitaria eriantha* plants grown under drought conditions (Pedranzani et al. 2016).

The symbiotic association formed by AMF with higher plants under water-deficit conditions could increase the water uptake from the soil and improve the regulation of stomatal aperture to get higher water-use efficiency. AMF inoculation improved maize drought tolerance by affecting plant–water relation through inducing changes in cytokinin and auxin concentrations, enhancing stele tissue size, increasing soil aggregate stability and soil available water, as well as enhancing stomatal conductance (Boomsma and Vyn 2008). AMF can alter water regulation in water-stressed *Poncirus trifoliata* plants through modulation in hormonal signaling or by stimulating the accumulation of osmolytes (Fan and Liu 2011). Abscisic acid plays an important role as one of the non-nutritional mechanisms by which AM symbiosis influences stomatal conductance in drought-exposed plants (Ludwig-Muller 2010). In addition, improving plant–water status in AM-inoculated *Zea mays* plants played an indirect role in enhancing osmotic adjustment, gas exchange capacity, effectiveness of photochemistry of PSII, and nutrient uptake under water-deficit conditions (Zhu et al. 2012). Greater leaf water potential, gas exchange, stomatal conductance, and photosynthetic rates were detected in mycorrhizal sunflowers grown under drought stress (Gholamhoseini et al. 2013). Furthermore, AM symbiosis can enhance drought tolerance through improving soil structure by glomalin. AM symbiosis increased plant growth under drought stress indirectly via affecting soil moisture retention via glomalin's effect on soil water-stable aggregates (Wu et al. 2008). Extensive hyphal network formation and glomalin secretion by AMF can improve soil structure and enhance water and nutrient uptake, thus improving plant growth under drought conditions (Gong et al. 2013). Mycorrhization has also been known to ameliorate the drought-induced deficiency in nutrients such as P, K, Ca, Mg, Fe, and Zn. Pistachio plants inoculated with two AMF species (*G. mosseae* and *G. intraradices*) under soil water deficit showed significant increases in P, K, Zn, and Mn concentrations (Bagheri et al. 2012). *G. mosseae* inoculation improved P concentration in sunflowers and thus improved plant drought tolerance and seed oil yield (Gholamhoseini et al. 2013). Mycorrhizal inoculation significantly minimizes drought stress-imposed effects on wheat plants by enhancing plant growth, nutrient uptake, and the relative water content (Ortiz et al. 2015).

AMF could also mitigate the adverse effects of drought stress by regulating plant endogenous ABA concentration. Changes in plant ABA concentration caused by AMF have been postulated to induce the expression of many stress-related genes including aquaporin genes encoding membrane intrinsic proteins that facilitate transport of certain small molecules in addition to water across biological membranes. Expression of two aquaporin genes (*GintAQPF1* and *GintAQPF2*) was improved in both root cortical cells holding arbuscules and extraradical mycelia of *Zea mays* plants colonized by *Glomus intraradices* under drought stress. Thus, the fungal AQPs could mediate the AM plant's ability to enhance water uptake under water deficiency (Li et al. 2013). Moreover, in *Rhizophagus intraradices*, 14-3-3 protein and aquaporins (GintAQPF1 and GintAQPF2) could be activated by the simultaneous increase in the expression of plant genes encoding D-*myo*-inositol-3-phosphate synthase (IPS) and 14-3-3-like protein GF14 (14-3GF) that are responsible for ABA signal transduction. These findings suggested that co-expression of *IPS* and *14-3GF* is responsible for the crosstalk between maize and *R. intraradices* under drought stress and potentially induces the synergistic actions of the symbiotic partners in enhancing plant drought tolerance. Hence, mycorrhizal colonization decreased root ABA concentration mainly by downregulating *AO* expression under drought stress. Consequently, *Rhizophagus intraradices* improved plant–water status by modulating ABA-mediated abiotic signaling pathway involving IPS and 14-3-3 proteins (Li et al. 2016).

Compatible solute accumulation is another important mechanism underlying AMF-mediated protection of drought-exposed plants. Inoculated citrus plants by *Glomus versiforme* enhanced the plant osmotic adjustment under drought conditions via improved nonstructural carbohydrates and K^+, Ca^{2+}, and Mg^{2+} levels (Wu and Xia 2006). Sugars and proline accumulation as osmolytes decreased the osmotic potential in *Macadamia tetraphylla* water-stressed mycorrhizal plants, which lead to subsequent plant drought tolerance (Yooyongwech et al. 2013). In contrast, AM-mediated decrease in soluble sugar concentration in *Erythrina variegata* drought-exposed plants (Manoharan et al. 2010) was related to the lower levels of drought injury in these plants. Inoculation of drought-exposed *Poncirus trifoliata* plants with *Funneliformis mosseae* decreased proline accumulation and improved its growth performance and biomass production (Zou et al. 2013). Furthermore, AMF colonization improved free polyamines and soluble nitrogenous compound levels in water-stressed plants (Rapparini and Penuelas 2014).

Higher upregulation of the message levels of phospholipase D delta, calcineurin B-like proteins (CBL 1), and histone acetyltransferase (HAT) was detected in *Arabidopsis thaliana* seedlings colonized by *Piriformospora indica*, an endophytic fungus, under drought conditions. These increases could result from the priming of the expression of a quite diverse set of stress-related genes in the leaves (Sheramati et al. 2008).

Interaction between AMF and PGPR could have beneficial effect on the development of revegetation in water limitation soils. Inoculation with the PGPR *P. mendocina* alone or in combination with an AMF, *G. intraradices* or *G. mosseae*, conferred drought resistance to lettuce plants by stimulating nitrate reductase, phosphatase, and catalase activities in plant roots and proline accumulation in leaves significantly, which support the potential use of dual application of PGPR and AMF as an inoculant to ameliorate the adverse effect of water stress on the plant antioxidant system (Kohler et al. 2008).

5.4 Heat Stress

With the recent advent of global warming, heat stress has become a major area of concern to crop production. Plants react to temperature changes at cellular, tissue, and organ levels. Generation of several toxic ROS in cells, protein denaturation and aggregation, fluidity of membrane lipids, inactivation of enzymes in chloroplast and mitochondria, inhibition of protein synthesis, and loss of membrane integrity are the major types of cellular damage that result from higher temperatures (Ali et al. 2011; Meena et al. 2015). Rhizosphere microbes have positive impact on counteracting the adverse effects of heat stress on plants.

5.4.1 Plant Growth-Promoting Bacteria in Heat Stress Mitigation

PGPB may enhance plant thermotolerance through several mechanisms including biological nitrogen fixation, enhancing the bioavailability of phosphorous, iron, and other mineral nutrients; production of phytohormones including indoleacetic acid, abscisic acid, gibberellic acid, brassinosteroids, jasmonates, and salicylic acid; production of ACC deaminase; as well as generation of antioxidants (Grover et al. 2011). In this respect, three PGPR isolates *P. alcaligenes* PsA15, *Bacillus polymyxa* BcP26, and *Mycobacterium phlei* MbP18 conferred heat and salt stress tolerance by enhancing growth and nutrient acquisition of maize plants and consequently improve their survival under these stressful conditions (Egamberdiyeva 2007). More interestingly, heat tolerance induced by bacteria can be due to reducing the ROS generation and thus less cell damage as well as to inducing changes in the activation of certain heat shock transcription factors (Abd El-Daim et al. 2014).

Pseudomonas aeruginosa strain 2CpS1 showing ACC deaminase activity ameliorated the deleterious impacts of temperature stress on wheat by increasing plant height, root length, leaf area, dry matter, chlorophyll content, relative water content, and decreasing cell membrane injury (Meena et al. 2015).

Furthermore, adapted thermotolerant microorganisms can promote plant establishment and alleviate heat stress effects. Thermotolerant strain of *Pseudomonas* sp. AKM-P6 possessing PGPR activities helped sorghum seedlings to withstand heat stress by inducing heat shock proteins (HSPs) in leaves, reducing membrane injury, and increasing proline, chlorophyll, sugar, amino acid, and protein content (Ali et al. 2009). Inoculation with a PGP-thermotolerant *Pseudomonas putida* strain AKMP7 improved survival and growth of heat-stressed wheat plants via increasing root and shoot length, dry biomass, tiller, spikelet, and grain formation; improving proline, chlorophyll, sugar, starch, amino acid, and protein level; and reducing membrane injury and the activity of several antioxidant enzymes such as SOD, APX, and CAT (Ali et al. 2011).

5.4.2 Arbuscular Mycorrhizal Fungi in Heat Stress Mitigation

Mycorrhizal infection evokes various physiological and biochemical processes to help plants to sustain their development under heat stress. Antioxidant compounds such as polyphenol and ascorbic acid were enhanced in the leaves of mycorrhizal strawberry compared to that in non-mycorrhizal ones under heat stress conditions (Matsubara 2010). Anti-oxidative activity of superoxide dismutase and ascorbate peroxidase, content of ascorbic acid and polyphenol, and scavenging activity of 2,2-diphenyl-1-picrylhydrazyl radical were increased in mycorrhizal cyclamen under heat stress, which suggested that the AM symbiosis can alleviate ROS damage, protect plants against oxidation, and improve heat stress tolerance during plant production (Maya and Matsubara 2013).

Colonization of *Arabidopsis thaliana* plants by *Paraphaeosphaeria quadriseptata* as a rhizosphere fungus improved plant heat stress tolerance by induction of HSP101 and HSP70 proteins, the conserved components of the stress response (McLellan et al. 2007). Endophytic fungus *Paecilomyces formosus* LWL1 mitigated heat damage in japonica rice by improving plant growth attributes (plant height, fresh weight, and dry weight), downregulating the stress-related signaling molecules (abscisic acid and jasmonic acid), as well as increasing the contents of total protein and chlorophyll (Waqas et al. 2015).

5.5 Chilling Injury

Low temperature stress (cold or chilling) is a serious problem that reduces agricultural output potential by influencing cellular metabolism, macromolecule activity, antioxidant–ROS balance, decreasing osmotic potential in the cellular milieu, solidification or rigidification of plasma membrane, and destabilization of protein complexes (Barka et al. 2006; Chen et al. 2013; Pedranzani et al. 2016). Microbial inoculants are potential candidates that can improve plant cold stress tolerance.

5.5.1 Plant Growth-Promoting Bacteria in Chilling Injury Mitigation

PGPR root colonization can improve the plant ability to withstand cold stress. Epiphytic bacterial species with ice-nucleating activity (ice$^+$ bacteria), such as *Pseudomonas syringae*, contribute to the frost injuries of many cold-sensitive plants via reducing the plants' ability to supercool, a process that prevents the formation of membrane-damaging ice crystals (Lindow and Leveau 2002). Inoculation of grapevine (*Vitis vinifera*) with a PGPR, *Burkholderia phytofirmans* strain PsJN, lowered the rate of biomass reduction and electrolyte leakage – an indicator of cell membrane injury – during cold treatment (4°C) and promoted post-chilling recovery. Levels of starch, proline, and phenols and rates of photosynthesis and starch deposition were also enhanced (Barka et al. 2006). *Burkholderia phytofirmans* PsJN acclimated grapevine to cold by improving plant photosynthesis and regulating carbohydrate metabolism (Fernandez et al. 2012). Moreover, *Burkholderia phytofirmans* PsJN primed *Vitis vinifera* L. and conferred cold stress tolerance by modulating stress-related gene expression, carbohydrate metabolism, and metabolite accumulation (Theocharis et al. 2012).

Cold-tolerant PGPB *Pantoea dispersa* strain 1A isolated from a subalpine soil in the North Western Indian Himalayas and cold-tolerant *Serratia marcescens* strain SRM (MTCC 8708) isolated from flowers of summer squash exhibited PGP characteristics like IAA production, P-solubilization, HCN, and siderophore production. Higher biomass and nutrient acquisition were observed in cold-stressed wheat seedlings when their seeds were bacterization with these strains (Selvakumar et al. 2007a, 2007b). *Pseudomonas lurida* M2RH3 (MTCC 9245), a psychrotolerant bacterium, solubilized phosphate; produced siderophores, IAA, and HCN; and promoted the growth of cold-stressed wheat seedling (Selvakumar et al. 2011). Cold-tolerant *Pseudomonas* spp. and *Rhizobium leguminosarum*-PR1 acclimated lentil to cold and improved its iron acquisition, nutrient uptake, and growth (Mishra et al. 2011).

5.5.2 Arbuscular Mycorrhizal Fungi in Chilling Injury Mitigation

The underlying potential mechanisms improved plant cold stress tolerance as a result of AMF inoculation. AM symbiosis enhanced photosynthetic characteristics, chlorophyll synthesis, plant–water status, water-use efficiency, and SOD, CAT, POD, and APX activities in plants grown under cold stress (Zhu et al. 2010; Abdel Latef and Chaoxing 2011). Furthermore, osmotic adjustment is one of the most important mechanisms in plants to achieve low temperature tolerance. Mycorrhization enhanced the accumulation of osmoprotectants such as soluble sugar, soluble protein, and proline in tomato plants under low temperature stress (Abdel Latef and Chaoxing 2011).

AM mediated also increase in the accumulation of phenolics, flavonoids, and lignin accompanied with significant decrease in the H_2O_2 accumulation in cucumber subjected to low temperature stress (Chen et al. 2013). AM symbiosis enhanced shoot dry matter content, photosynthetic efficiency, and CAT, APX, and SOD activities, while it decreased H_2O_2 and MDA contents in *Digitaria eriantha* plants under cold stress condition, which could help plants to cope with stressful conditions (Pedranzani et al. 2016). At the molecular level, Aroca *et al.* (2007) found that AM symbiosis enhanced *Phaseolus vulgaris* tolerance to cold, drought, and salt stress by regulation of root hydraulic properties, which were closely correlated with the regulation of PIP2 protein levels and phosphorylation state.

5.6 Heavy Metal Toxicity

Heavy metal toxicity is an increasingly serious problem worldwide that reduces agricultural output potential and damages the health of ecosystem. Some of these metals are essential plant micronutrients such as Cu, Fe, Mn, Ni, and Zn and are required for beneficial plant growth and development, while others have no known biological function such as Cd, Pb, and Hg. High contents of heavy metals in soils are generally considered a matter of concern as they can accelerate rate of mortality, reduce potential survival, and induce toxicity symptoms. They severely damage plant metabolic activities by altering the structure and function of enzymes, the permeability and function of plasma membrane, the uptake and distribution of macro- and micronutrients, the hormonal balance and water movement, the photosynthetic process, the nitrogen assimilation, as well as the production of ROS (Garg and Singla 2012; Islam et al. 2016). Therefore, interaction between the rhizospheric microorganism and the plant activity related to soil metal toxicity is inevitable. Restoration and remediation of metal-polluted soils through biological remediation is safe, low-cost, effective, eco-friendly, and socially accepted strategy. Microbial inoculants such as PGPRs or mycorrhizae could protect plants from the harmful effects of heavy metal-contaminated areas.

5.6.1 Plant Growth-Promoting Bacteria in Heavy Metal Toxicity Mitigation

PGPB as bioinoculants can improve plant heavy metal stress tolerance via inducing different biochemical changes in stressed plants. PGPR *Pseudomonas aeruginosa* OSG41 enhanced chickpea growth under chromium stress with considerable decrease in proline content (Oves et al. 2013). PGPR inoculation increased SOD, CAT, DHAR, GR, and APX activities in potato under salt, water, and heavy metal stresses, which enhanced photosynthetic efficiency and ultimately plant growth (Gururani et al. 2013).

Furthermore, PGPB was used as a tool for rhizoremediation in contaminated soils. They can reduce the injury effect of heavy metals on plant and enhance its fitness by employing various mechanisms, such as:

(a) Influencing the pH and the redox potential in the rhizosphere through releasing organic acids
(b) Reducing the heavy metal mobilization in contaminated soils
(c) Improving the bacterial migration from the rhizoplane to the rhizosphere, which can reduce Cd plant uptake
(d) Forming the iron–siderophore complexes, which can be taken up by the host plant
(e) Forming the bacterial exopolysaccharides, which can develop the soil sheaths around the plant root, thus reducing the sodium flow into the stele
(f) Production of indoleacetic acid
(g) Production of ACC deaminase (Gadd 2004; Dimkpa et al. 2009)

Inoculation with PGPR strain, *Klebsiella mobilis* CIAM 880, resulted in 120% higher grain yield and twofold decreased in grain Cd content of barley plants grown on Cd-contaminated soil. Here, free Cd ions can be bound by bacteria into complex forms that cannot be taken up by the plant (Pishchik et al. 2002). *Methylobacterium oryzae* and *Burkholderia* sp. reduced nickel and cadmium stress in tomato via reducing their uptake and translocation (Madhaiyan et al. 2007). Moreover, some bacteria can protect plants against nickel, lead, iron, or zinc toxicity by siderophore production. Microbial siderophores were able to alleviate metal-induced oxidative stress in plants. By chelating and reducing toxic metal concentrations in the root zone, siderophores exerted a bioprotective effect by lowering the formation of cell-damaging free radicals, thereby enabling a microbial IAA-mediated plant biomass increase (Dimkpa et al. 2009). Rhizobacteria containing ACC deaminase activity improved plant growth and development as well as enhanced plant heavy metal stress tolerance (Belimov and Wenzel 2009). Several PGPR modulated plant–soil chemistry by mediating the methylation of Pb, Hg, Se, As, Tn, and Sn. These bacteria can transfer a methyl group to the metals, resulting in volatile methylated metal compounds that can easily excavate the soil zone (Bolan et al. 2014).

An extensive range of PGPR has been identified as most efficient candidates in phytoremediation. Significant enhancement of heavy metal phytoremediation by *Alnus firma* with an endophytic strain of *Bacillus thuringiensis* GDB-1 was reported by Babu *et al.* (2013). *Enterobacter* sp. 192 and *Klebsiella* sp. strains inoculated in *Brassica napus* L. improved its growth and resulted in bioaccumulation of Cd, Pb, and Zn (Jing et al. 2014). The recombinant strain KT2440-spPCS, which developed through the cloning of phytochelatin synthase (PCS) genes from *Schizosaccharomyces pombe* expressed in *Pseudomonas putida* KT2440, enhanced resistance to Hg, Cd, and Ag and a three- to fivefold increase in Cd accumulation (Yong et al. 2014). Introducing glutathione synthase gene *gcsgs* into endophytic *Enterobacter* sp. CBSB1 improved phytoremediation efficiency of host plant (Qiu et al. 2014). PGPR increased the phytoextraction ability of plants via enhancing the mobility of heavy metal and improving their bioavailability by releasing chelating agents, acidification, phosphate solubilization, and redox changes. Some others produce organic acids, such as gluconic, oxalic, and citric acids that can mobilize and solubilize the heavy metals (Ullah et al. 2015).

More interestingly, the use of multi-strain inocula could be one of the better strategies to improve plant growth under contaminated soil. Co-inoculation of PGPBs with *Rhizobia* allowed a longer exudation of nod-gene-inducing flavonoids, which improve the performance of symbiotic nitrogen fixation. This co-inoculation with legume plants also supported the seedling vitality and their survival during metal phytostabilization and phytoextraction strategies (Gomez-Sagasti and Marino 2015).

In addition, for effective microbe-assisted bioremediation, metal-resistant PGPB can facilitate the growth and development of plants by restricting their uptake of excess metal and thus prevent its bio-amplification in the ecosystem. Clover-inoculated with a Cd-adapted autochthonous PGPR, *Brevibacillus* and grown in soil contaminated with Cd, resulted in growth-promoting effects and a reduction in Cd transfer from soil to plants. Cd accumulated by PGPR in their cells and, thus, reduced the bioavailable Cd concentrations, thereby reducing its uptake by plants and rhizobia (Vivas et al. 2005). Lupine inoculated with a consortium of metal-resistant PGPR (including *Bradyrhizobium*, *Pseudomonas* sp., and *Ochrobactrum cytisi*), for reclamation of multi-metal-contaminated soil, showed increment in plant growth. This mixture also succeeded to reduce plant toxicity symptoms and metal accumulation in both shoots and roots. This ameliorating impact might also be due to more intimate bacteria–plant relationships such as those ensured by endophytic PGPRs (Dary et al. 2010). Inoculation with copper-resistant bacteria had a positive effect on the upregulation of antioxidative defense mechanism (improved SOD, CAT and APX, and GPX activities) that eliminated the ROS and reduced the MDA content in wheat. They also found that bacterial inoculation prevented the negative impact of copper stress on protein synthesis/production by lowering the metal toxicity, which might be due to the fact that bacterial inoculation activates the gene expression profile of metal detoxifying enzymes to cope with the metal stress (Wang et al. 2013). Cd-tolerant PGP *Bradyrhizobium* sp. exhibit several PGP traits (synthesis of IAA, ACC deaminase, siderophores) increased shoot dry weight and Cd accumulation in roots of *Lolium multiflorum* grown in Cd-contaminated soil. They also detected that *Bradyrhizobium* sp. improved the extractable Cd concentrations in the rhizosphere, as well as it diminished the accumulation of Cd in root and shoot of *Glycine max* by increasing Fe availability (Guo and Chi 2014). Copper-resistant bacteria *Providencia vermicola* with different PGP traits (synthesis of the plant required hormone (IAA), P solubilization, siderophore production, and efficient ACC deaminase activity) protected lentil plants grown in copper-contaminated soil from copper toxicity. It increased root and shoot length, plant dry weight, leaf area, pod number, seed weight, gas exchange characteristics, N and P accumulation, leaf chlorophyll content, and root nodulation. Anti-oxidative defense mechanism also improved by inducing the expression of ROS-scavenging enzymes, such as ascorbate peroxidase, superoxide dismutase, catalase, and guaiacol peroxidase with alternate decrease in malondialdehyde, H_2O_2, proline, and total phenolic contents and electrolyte leakage (Islam et al. 2016). Thus, using multifarious growth-promoting bacteria with metal resistance properties holds a great potential to be used as biofertilizer in metal-contaminated soils.

5.6.2 Arbuscular Mycorrhizal Fungi in Heavy Metal Toxicity Mitigation

AMF play one of the most important ecological roles in phytostabilization of toxic trace elements in soil by sequestration and thus can increase the survival of mycorrhizal plants in polluted soils. AM plant in heavy metal-polluted soil shows higher biomass and more tolerance because of:

1. Metal adsorption to chitin in the cell wall
2. Chelation of metals inside the fungus
3. Metals bound to metallothioneins or PCs inside the fungal or plant cells
4. Sequestration of heavy metals by siderophores, which deposit the heavy metals in root apoplasm or in soil
5. Restriction of metals by compounds secreted by the fungus
6. Immobilizes heavy metal on its hyphae and sequesters it inside the cell, thereby lessening its transfer to shoot
7. Changes in rhizophere pH and microflora, thereby decreasing heavy metal availability
8. Precipitation in polyphosphate granules in the soil
9. Plasma membrane acts as a living and selective barrier of toxic metals
10. Promotes plant growth and thus dilutes metal concentrations in plant tissues
11. Regulation of gene expression (Hossain et al. 2012; Shirmohammadi et al. 2014)

AMF enhanced plant Zn tolerance by absorbing and crystallizing it in AMF hyphae and cortical cells of mycorrhizal root, and thus Zn transfer to shoot was decreased (Khan et al. 2000). AMF enhanced Fe and Mn uptake in plants, at high concentrations, while it decreased Mn translocation in shoots and retain Fe in roots (Leyval et al. 2002). AMF produced glycoprotein (Glomalin), which has a metal chelating function and thus reduces the metal availability and decreases toxicity risk. One gram of glomalin could extract up to 4.3 mg of Cu, 0.08 mg of Cd, and 1.12 mg of Pb from the polluted sites (Gonzalez-Chavez et al. 2004). Furthermore, AMF colonization also enhances nutrient and water uptake, thereby maintaining better nutrient status. Mycorrhizal sunflower plants showed higher P/Cd, N/Cd, and S/Cd ratios in both shoots and roots than non-mycorrhizal ones. Higher N and S uptake in mycorrhizal plants leads to higher production of thiol-rich proteins, while higher P status leads to phosphate complexation with metal ions inside the cells that could have an important role in heavy metal detoxification (de Andrade et al. 2008). AMF in the roots of *Pteris vittata* modulated the activity of two major enzymes, namely, glutamine synthetase (which control the use of nitrogen inside the cells) and S-adenosyl methionine (SAM) synthase (which catalyze the SAM formation from methionine and ATP) under arsenic exposure (Bona et al. 2010). AMF induced a clear protective effect against the high concentration of Mn in the soil which was related to "dilution" of the metal in plant tissues, because of increased growth and, to a varying degree, of mechanisms of exclusion, immobilization, or retention by which uptake and root-to-shoot transport of heavy metals are restricted (Bati et al. 2015).

Four AM fungal genes (*GrosMT1*, *GinZnT1*, *GmarMT1*, *and GintABC1*) play a vital role in maintenance of the cellular homeostasis against metals. Zn transporter *GinZnT1* helps in vacuolar Zn compartmentalization. *GmarMT1* codes for metallothioneins (MTs), the major metal chelators, regulates the fungal redox potential, and protects it against oxidative stress. *GintABC1* codes for a polypeptide of 434 amino acids and participates actively in Cu and Zn detoxification. *GintMT1* contributes to the pool of cytosolic thiols and regulates redox status of the extraradical mycelia of *G. intreradices* through its metal chelation activity or its –SH group (Gonzalez-Guerrero et al. 2010; Azcon et al. 2013). AMF colonization improved plant heavy metal tolerance/detoxification by inducing the expression of several plant genes coding for proteins. Inoculation with AMF *F. mosseae* or *G. intraradices* restored normal growth in a white poplar clone grown on Cu- and Zn-polluted soil, and this was associated with upregulation of foliar metallothionein and polyamine biosynthetic gene expression (Cicatelli et al. 2010). Moreover, *Glomus intraradices* colonization increased transcriptional of a GSH-dependent GST gene in *Medicago truncatula* Zn-stressed plants (Hossain et al. 2012). Inoculation with AMF *Funneliformis mosseae* significantly lowered nickel (Ni) translocation from roots to the aboveground parts of tall fescue plants, which may be due to the activation of mechanisms in mycorrhizal plants roots, viz., chelation of Ni and/or compartmentation within vacuoles. The ATP-binding cassette (ABC) transporter and metallothionein (MT) transcripts accumulated to considerably higher levels in the roots of mycorrhizal plants than in the corresponding non-mycorrhizal ones, which probably made metal levels insufficient for the expression of these genes in the shoots (Shabani et al. 2016).

Furthermore, AMF symbiosis can ameliorate the injury of heavy metal by stimulating or modifying specific physiological mechanisms related to the adaptation to stressful environments. AMF colonization alleviated cadmium stress in *Medicago truncatula* via promoting photosynthesis process through increasing the plant's ability to use light energy, maximizing the area available for CO_2 assimilation, facilitating the electron transport, preventing inhibition of aminolevulinic acid synthesis and protochlorophyllide photoreduction, increasing the density of photosynthetic units, increasing the photosynthesis-related proteins, as well as reducing the gluconeogenesis/glycolysis and the antioxidant processes (Aloui et al. 2011). *Glomus mosseae* colonization promoted the relative water and chlorophyll contents, cellular sucrose and glycinebetaine accumulation, as well as enzymatic components of antioxidant defense system in pea plants subjected to arsenic contaminated soil, which signifying the role of AM colonization in the higher turgor maintenance and lower leaf chlorosis (Garg and Singla 2012). AMF were confirmed to be strong growth stimulants in olive Mn-stressed plants by optimizing P absorption and ensuring a greater supply of macronutrients and micronutrients (Bati et al. 2015). *Funneliformis mosseae* not only improved nutrition and water absorption, but there was also a significant increase in the content of leaf pigments (chlorophyll, carotenoid) under Ni stress. Mycorrhization increased the carotenoids amount in tall fescue nickel-stressed plants. Carotenoids as antioxidants can quench singlet oxygen and can scavenge free radicals (Shabani et al. 2016).

5.7 Conclusion and Future Perspectives

The beginning of the twenty-first century is marked by global scarcity of water resources, global warming, environmental pollution, and increased salinization of soil and water, which cause major reductions in crop productivity and quality. A significant increase in agricultural productivity is required to fulfill the food supply requirements to feed the world's growing population, and that should be based on sustainable practices that minimize the environmental impact but also support food safety and food security. Plant-associated microorganisms are a powerful strategy in this regard. Plants in their natural environment are colonized by both endocellular and intracellular microorganisms. Rhizosphere microorganisms, particularly beneficial bacteria and fungi, can control abiotic stresses and are considered as eco-friendly strategies to improve crop yield. Utilizing microbial inoculation subordinates the plant stresses and is an alternative to traditional remediation methods that involve the addition of synthetic chemicals, which are time-consuming and increase the cost of the final crop. Some PGPR can enhance plant growth and productivity via providing plants with fixed nitrogen, soluble phosphate, iron, and phytohormones. Others can do this indirectly by protecting the plant against soilborne diseases. PGPR can also adapt plants to different abiotic stress factors through the presence of the ACC deaminase enzyme, the production of exopolysaccharides, the enhancement of defense-related enzymes, the production of phenolic compounds, and the eliciting of jasmonic and ethylene pathways in plants.

To help plants to combat abiotic stresses, selection of the appropriate microbial inoculants (mycorrhizae or PGPRs) is one of the most important technical traits. In addition, using compatible multiple microbial consortia consisting of bacterial symbionts and fungal symbionts acting synergistically, providing various beneficial effects, is also a powerful strategic tool. Hence, future research has to be focused on the application of multi-microbial inoculation, which could be an effective approach to reduce harmful impact of stress on plant development, but prerequisites for effective combinations need to be established. Furthermore, the challenge in the twenty-first century lies on developing stable multiple stress tolerance traits, thus improving yields particularly in areas with adverse environmental conditions and contributing to global food security.

Genetic techniques may point out to new insight in the alleviating role of microbial inoculants under abiotic stresses. Therefore, using microorganism application as an elicitor to increase plant abiotic stress tolerance and to incorporate microbial genes into stressed plants is now being addressed and getting the interest of scientists in such studies. Furthermore, special attention should be drawn on isolating bacteria from stressful conditions. Indeed, their use as bioinoculants could help to emerge a new dimension into the microbial inoculant application to plants under abiotic stress conditions. The application of isolated, characterized, and tested stress-tolerant microbial strains can enhance plant stress tolerance and could be used as a feasible strategy for improving crop production under the stressful conditions.

References

Abbaspour H, Saeid-Sar S, Afshari H, Abdel-Wahhab MA (2012) Tolerance of mycorrhiza infected Pistachio (*Pistacia vera* L.) seedlings to drought stress under glasshouse conditions. J Plant Physiol 169:704–709

Abd El-Daim IA, Bejai S, Meijer J (2014) Improved heat stress tolerance of wheat seedlings by bacterial seed treatment. Plant Soil 379:337–350

Abdel Latef A, Chaoxing H (2011) Arbuscular mycorrhizal influence on growth, photosynthetic pigments, osmotic adjustment and oxidative stress in tomato plants subjected to low temperature stress. Acta Physiol Plant 33:1217–1225

Ahmad M, Zahir ZA, Khalid M, Nazli F, Arshad M (2013) Efficacy of *Rhizobium* and *Pseudomonas* strains to improve physiology, ionic balance and quality of mung bean under salt–affected conditions on farmer's fields. Plant Physiol Biochem 63:170–176

Alavi P, Starcher MR, Zachow C et al (2013) Root-microbe systems: the effect and mode of interaction of Stress Protecting Agent (SPA) *Stenotrophomonas rhizophila* DSM14405 T. Front Plant Sci 4:141

Ali SZ, Sandhya V, Grover M, Kishore N, Linga VR, Bandi V (2009) *Pseudomonas* sp. strain AKM-P6 enhances tolerance of sorghum seedlings to elevated temperatures. Biol Fertil Soils 46:45–55

Ali SZ, Sandhya V, Grover M, Linga VR, Bandi V (2011) Effect of inoculation with a thermotolerant plant growth promoting *Pseudomonas putida* strain AKMP7 on growth of wheat (*Triticum* spp.) under heat stress. J Plant Interact 6:239–246

Aloui A, Recorbet G, Robert F, Schoefs B, Bertrand M, Henry C, Gianinazzi-Pearson V, Dumas-Gaudot E, Aschi-Smiti S (2011) Arbuscular mycorrhizal symbiosis elicits shoot proteome changes that are modified during cadmium stress alleviation in *Medicago truncatula*. BMC Plant Biol 11:75

Armada E, Roldán A, Azcon R (2014) Differential activity of autochthonous bacteria in controlling drought stress in native lavandula and salvia plants species under drought conditions in natural arid soil. Microb Ecol 67:410–420

Aroca R, Porcel P, Ruiz-Lozano JM (2007) How does arbuscular mycorrhizal symbiosis regulate root hydraulic properties and plasma membrane aquaporins in *Phaseolus vulgaris* under drought, cold or salinity stresses? New Phytol 173:808–816

Aroca R, Ruiz-Lozano JM, Zamarreno AM, Paz JA, Garcia-Mina JM, Pozo MJ, Lopez-Raez JA (2013) Arbuscular mycorrhizal symbiosis influences strigolactone production under salinity and alleviates salt stress in lettuce plants. J Plant Physiol 170:47–55

Azcon R, Medina A, Aroca R, Ruiz-Lozano JM (2013) Abiotic stress remediation by the arbuscular mycorrhizal symbiosis and rhizosphere bacteria/yeast interactions. In: de Bruijn FJ (ed) Molecular microbial ecology of the rhizosphere, vol 2, 1st edn. Wiley, Hoboken, pp 991–1002

Babu G, Kim JD, BT O (2013) Enhancement of heavy metal phytoremediation by *Alnus firma* with endophytic *Bacillus thuringiensis* GDB-1. J Hazard Mater 250:477–483

Bagheri V, Shamshiri MH, Shirani H, Roosta H (2012) Nutrient uptake and distribution in mycorrhizal pistachio seedlings under drought stress. J Agric Sci Technol 14(Suppl):1591–1604

Bano A, Fatima M (2009) Salt tolerance in *Zea mays* (L.) following inoculation with *Rhizobium* and *Pseudomonas*. Biol Fertil Soils 45:405–413

Barka EA, Nowak J, Clement C (2006) Enhancement of chilling resistance of inoculated grapevine plantlets with a plant growth-promoting rhizobacterium, *Burkholderia phytofirmans* strain PsJN. Appl Environ Microbiol 72:7246–7252

Barriuso J, Ramos Solano B, Gutiérrez Mañero FJ (2008) Protection against pathogen and salt stress by four plant growth-promoting rhizobacteria isolated from *Pinus* sp. on *Arabidopsis thaliana*. Phytopathology 98:666–672

Bati CB, Santilli E, Lombardo L (2015) Effect of arbuscular mycorrhizal fungi on growth and on micronutrient and macronutrient uptake and allocation in olive plantlets growing under high total Mn levels. Mycorrhiza 25:97–108

Belimov AA, Wenzel WW (2009) The role of rhizosphere microorganisms in heavy metal tolerance of higher plants. Asp Appl Biol 98:81–90

Bharti N, Barnawal D, Wasnik K, Tewari SK, Kalra A (2016a) Co-inoculation of *Dietzia natronolimnaea* and *Glomus intraradices* with vermicompost positively influences *Ocimum basilicum* growth and resident microbial community structure in salt affected low fertility soils. Appl Soil Ecol 100:211–225

Bharti N, Pandey SS, Barnawa D, Patel VK, Kalra A (2016b) Plant growth promoting rhizobacteria *Dietzia natronolimnaea* modulates the expression of stress responsive genes providing protection of wheat from salinity stress. Sci Rep 6:34768

Bhise KK, Bhagwat PK, Dandge PB (2016) Plant growth-promoting characteristics of salt tolerant *Enterobacter cloacae* strain KBPD and its efficacy in amelioration of salt stress in *Vigna radiata* L. J Plant Growth Regul. https://doi.org/10.1007/s00344-016-9631-0

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

Bolan N, Kunhikrishnan A, Thangarajan R, Kumpiene J, Park J, Makino T, Kirkham MB, Scheckel K (2014) Remediation of heavy metal (loid)s contaminated soils—to mobilize or to immobilize. J Hazard Mater 266:141–166

Bompadre MJ, Silvani VA, Bidondo LF, Ríos de Molina MC, Colombo RP, Pardo AG, Godeas AM (2014) Arbuscular mycorrhizal fungi alleviate oxidative stress in pomegranate plants growing under different irrigation conditions. Botany 92:187–193

Bona E, Cattaneo C, Cesaro P, Marsano F, Lingua G, Cavaletto M, Berta G (2010) Proteomic analysis of *Pteris vittata* fronds: two arbuscular mycorrhizal fungi differentially modulate protein expression under arsenic contamination. Proteomics 10:3811–3834

Boomsma CR, Vyn TJ (2008) Maize drought tolerance: Potential improvements through arbuscular mycorrhizal symbiosis? Field Crops Res 108:14–31

Chakraborty U, Chakraborty BN, Chakraborty AP, Dey PL (2013) Water stress amelioration and plant growth promotion in wheat plants by osmotic stress tolerant bacteria. World J Microbiol Biotechnol 29:789–803

Chen S, Jin W, Liu A, Zhang S, Liu D, Wang F, Lin X, He C (2013) Arbuscular mycorrhizal fungi (AMF) increase growth and secondary metabolism in cucumber subjected to low temperature stress. Sci Hortic 160:222–229

Cho SM, Kang BR, Han SH, Anderson AJ, Park JY, Lee YH, Cho BH, Yang KY, Ryu CM, Kim YC (2008) 2R, 3R-Butanediol, a bacterial volatile produced by *Pseudomonas chlororaphis* O6, is involved in induction of systemic tolerance to drought in *Arabidopsis thaliana*. Mol Plant Microbe Interact 21(8):1067–1075

Cicatelli A, Lingua G, Todeschini V, Biondi S, Torrigiani P, Castiglione S (2010) Arbuscular mycorrhizal fungi restore normal growth in a white poplar clone grown on heavy metal-contaminated soil, and this is associated with upregulation of foliar metallothionein and polyamine biosynthetic gene expression. Ann Bot 106:791–802

Cohen AC, Bottini R, Pontin M, Berli FJ, Moreno D, Boccanlandro H, Piccoli PN (2015) *Azospirillum brasilense* ameliorates the response of *Arabidopsis thaliana* to drought mainly via enhancement of ABA levels. Physiol Plant 153:79–90

Dary M, Chamber-Pérez MA, Palomares AJ, Pajuelo E (2010) “In situ” phytostabilisation of heavy metal polluted soils using *Lupinus luteus* inoculated with metal resistant plant-growth promoting rhizobacteria. J Hazard Mater 177:323–330 de Andrade SA, de Silviera AP, Jorge RA, de Abreu MF (2008) Cadmium accumulation in sunflower plants influenced by arbuscular mycorrhiza. Inter J Phytorem 10:1–13

Dimkpa CO, Merten D, Svatoš A, Büchel G, Kothe E (2009) Metal-induced oxidative stress impacting plant growth in contaminated soil is alleviated by microbial siderophores. Soil Biol Biochem 41:154–162

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

Egamberdieva D, Kucharova Z (2009) Selection for root colonizing bacteria stimulating wheat growth in saline soils. Biol Fert Soils 45:563–571

Egamberdiyeva D (2007) The effect of plant growth promoting bacteria on growth and nutrient uptake of maize in two different soils. Appl Soil Ecol 36:184–189

Estrada B, Aroca R, Maathuis FJM, Barea JM, Ruiz-Lozano JM (2013) Arbuscular mycorrhizal fungi native from a Mediterranean saline area enhance maize tolerance to salinity through improved ion homeostasis. Plant Cell Environ 36:1771–1782

Fan QJ, Liu JH (2011) Colonization with arbuscular mycorrhizal fungus affects growth, drought tolerance and expression of stress-responsive genes in *Poncirus trifoliate*. Acta Physiol Plant 33:1533–1542

Fernandez O, Theocharis A, Bordiec S, Feil R, Jasquens L, Clement C, Fontaine F, Ait Barka E (2012) *Burkholderia phytofirmans* PsJN acclimates grapevine to cold by modulating carbohydrate metabolism. Mol Plant Microbe Interact 25:496–504

Figueiredo MVB, Burity HA, Martinez CR, Chanway CP (2008) Alleviation of drought stress in the common bean (*Phaseolus vulgaris* L.) by co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. Appl Soil Ecol 40:182–188

Gadd GM (2004) Microbial influence on metal mobility and application for bioremediation. *Geoderma* 122:109–119

Garg N, Singla P (2012) The role of *Glomus mosseae* on key physiological and biochemical parameters of pea plants grown in arsenic contaminated soil. Sci Hortic 143:92–101

Gholamhoseini M, Ghalavand A, Dolatabadian A, Jamshidi E, Khodaei-Joghan A (2013) Effects of arbuscular mycorrhizal inoculation on growth, yield, nutrient uptake and irrigation water productivity of sunflowers grown under drought stress. Agric Water Manag 117:106–114

Gomez-Sagasti M, Marino D (2015) PGPRs and nitrogen fixing legumes: a perfect team for efficient Cd phytoremediation? Front Plant Sci 81:1–9

Gong M, Tang M, Chen H, Zhang Q, Feng X (2013) Effects of two Glomus species on the growth and physiological performance of *Sophora davidii* seedlings under water stress. New Forest 44:399–408

Gonzalez-Chavez MC, Carrillo-Gonzalez R, Wright SF, Nichols KA (2004) The role of glomalin, a protein produced by arbuscular mycorrhizal fungi, in sequestering potentially toxic elements. Environ Pollut 130:317–323

Gonzalez-Guerrero M, Benabdellah K, Valderas A, Azcon-Aguilar C, Ferrol N (2010) *GintABC1* encodes a putative ABC transprter of the MRP subfamily induced by Cu, Cd, and oxidative stress in *Glomus intraradices*. Mycorrhiza 20:137–146

Grover M, Ali SZ, Sandhya V, Rasul A, Venkateswarlu B (2011) Role of microorganisms in adaptation of agriculture crops to abiotic stresses. World J Microbiol Biotechnol 27:1231–1240

Guo J, Chi J (2014) Effect of Cd-tolerant plant growth promoting *Rhizobium* on plant growth and Cd uptake by *Lolium multiflorum* Lam. and *Glycine max* (L.) Merr. in Cd-contaminated soil. Plant Soil 375:205–214

Gururani MA, Upadhyaya CP, Baskar V, Venkatesh J, Nookaraju A, Park SW (2013) Plant growth-promoting rhizobacteria enhance abiotic stress tolerance in *Solanum tuberosum* through inducing changes in the expression of ROS-scavenging enzymes and improved photosynthetic performance. J Plant Growth Regul 32:245–258

Habib SH, Kausar H, Saud HM (2016) Plant growth-promoting rhizobacteria enhance salinity stress tolerance in Okra through ROS-scavenging enzymes. BioMed Res Int 2016, Article ID 6284547., 10 pages

Hameed A, Dilfuza E, Abd-Allah EF, Hashem A, Kumar A, Ahmad P (2014) Salinity stress and arbuscular mycorrhizal symbiosis in Plants. In: Miransari M (ed) Use of microbes for the alleviation of soil stresses, vol 1. Springer, New York, pp 139–159

Hammer E, Nasr H, Pallon J, Olsson P, Wallander H (2011) Elemental composition of arbuscular mycorrhizal fungi at high salinity. Mycorrhiza 21:117–129

Han HS, Lee KD (2005) Plant growth promoting rhizobacteria effect on antioxidant status, photosynthesis, mineral uptake and growth of lettuce under soil salinity. Res J Agric Biol Sci 1:210–215

Han Q, Lü X, Bai J, Qiao Y, Paré PW, Wang S, Zhang J, Wu Y, Pang X, Xu W, Wang Z (2014) Beneficial soil bacterium *Bacillus subtilis* (GB03) augments salt tolerance of white clover. Front Plant Sci 5:1–8

Heidari M, Mousavinik SM, Golpayegani A (2011) Plant growth promoting rhizobacteria (PGPR) effect on physiological paramters and mineral uptake in basil (*Ociumum basilicum* L.) under water stress. ARPN J Agric Biol Sci 6:6–11

Higa T (2004) Effective microorganisms – a new dimension for nature farming. In: Parr JF, Hornick SB, Simpson ME (eds) Proceedings of the second international nature farming conference on U.S. Department of Agriculture, Washington, DC, USA, pp 20–22

Hossain MA, Piyatida P, da Silva JAT, Fujita M (2012) Molecular mechanism of heavy metal toxicity and tolerance in plants: central role of glutathione in detoxification of reactive oxygen species and methylglyoxal and in heavy metal chelation. J Botany 2:1–37

Islam F, Yasmeen T, Ali Q, Mubin M, Ali S, Arif MS, Hussain S, Riaz M, Abbas F (2016) Copper-resistant bacteria reduces oxidative stress and uptake of copper in lentil plants: potential for bacterial bioremediation. Environ Sci Pollut Res 23:220–233

Jahromi F, Aroca R, Porcel R, Ruiz-Lozano JM (2008) Influence of salinity on the *in vitro* development of *Glomus intraradices* and on the *in vivo* physiological and molecular responses of mycorrhizal lettuce plants. Microb Ecol 55:45–53

Jha Y, Subramanian RB (2014) PGPR regulate caspase-like activity, programmed cell death, and antioxidant enzyme activity in paddy under salinity. Physiol Mol Biol Plant 20:201–207

Jing YX, Yan JL, He HD, Yang DJ, Xiao L, Zhong T, Yuan M, Cai XD, Li SB (2014) Characterization of bacteria in the rhizosphere soils of *polygonum pubescens* and their potential in promoting growth and Cd, Pb, Zn uptake by *Brassica napus*. Int J Phytoremed 16:321–333

Kapoor R, Evelin H, Mathur P, Giri B (2013) Arbuscular mycorrhiza: Approaches for abiotic stress tolerance in crop plants for sustainable agriculture. In: Tuteja N, Gill SS (eds) Plant acclimation to environmental stress, Springer Science+Business Media, LLC, pp 359–401

Kasotia A, Varma A, Choudhary DK (2015) Pseudomonas mediated mitigation of salt stress and growth promotion in *Glycine max*. Agric Res 4:31–41

Khan AG, Kuek C, Chaudhary TM, Khoo CS, Hayes WJ (2000) Role of plants, mycorrhizae and phytochelators in heavy metal contaminated land remediation. Chemosphere 41:197–207

Kohler A, Hernandez JA, Caravaca F, Roldan A (2008) Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plant. Funct Plant Biol 35:141–151

Kohler J, Hernandez JA, Caravaca F, Roldan A (2009) Induction of antioxidant enzymes is involved in the greater effectiveness of a PGPR versus AM fungi with respect to increasing the tolerance of lettuce to severe salt stress. Environ Exp Bot 65:245–252

Lee Y, Krishnamoorthy R, Selvakumar G, Kim K, Sa T (2015) Alleviation of salt stress in maize plant by co-inoculation of arbuscular mycorrhizal fungi and *Methylobacterium oryzae* CBMB20. J Korean Soc Appl Biol Chem 58:533–540

Lee GW, Lee K, Chae J (2016) *Herbaspirillum* sp. strain GW103 alleviates salt stress in *Brassica rapa* L. ssp. *pekinensis*. Protoplasma 253:655–661

Leyval C, Joner EJ, del Val C, Haselwandter K (2002) Potential of arbuscular mycorrhizal fungi for bioremediation. In: Gianinazzi S, Schuepp H, Barea JM, Haselwandter K (eds) Mycorrhizal technology in agriculture. Birkhauser Verlag, Basel, pp 175–186

Li T, Hu Y, Hao Z, Li H, Wang Y, Chen B (2013) First cloning and characterization of two functional aquaporin genes from an Arbuscular mycorrhizal fungus *Glomus intraradices*. New Phytol 197:617–630

Li T, Sun Y, Ruan Y, Xu L, Hu Y, Hao Z, Zhang X, Li H, Wang Y, Yang L, Chen B (2016) Potential role of D-*myo*-inositol-3-phosphate synthase and 14-3-3 genes in the crosstalk between *Zea mays* and *Rhizophagus intraradices* under drought stress. Mycorrhiza 26:879–893

Lindow SE, Leveau JHJ (2002) Phyllosphere microbiology. Curr Opin Biotechnol 13:238–243

Ludwig-Muller J (2010) Hormonal responses in host plants triggered by arbuscular mycorrhizal fungi. In: Koltai H, Kapulnik Y (eds) Arbuscular mycorrhizas: physiology and function. Springer, New York, pp 169–190

Madhaiyan M, Poonguzhali S, Sa T (2007) Metal tolerating methylotrophic bacteria reduces nickel and cadmium toxicity and promotes plant growth of tomato (*Lycopersicon esculentum* L.) Chemosphere 69:220–228

Manoharan PT, Shanmugaiah V, Balasubramanian N, Gomathinayagam S, Sharma MP, Muthuchelian K (2010) Influence of AM fungi on the growth and physiological status of *Erythrina variegate* Linn. grown under different water stress conditions. Eur J Soil Biol 46:151–156

Marulanda A, Barea J-M, Azcón R (2009) Stimulation of plant growth and drought tolerance by native microorganisms (AM fungi and bacteria) from dry environments: mechanisms related to bacterial effectiveness. J Plant Growth Regul 28:115–124

Matsubara Y (2010) High temperature stress tolerance and the changes in antioxidative ability in mycorrhizal strawberry plants. In: Sampson AN (ed) Horticulture in the 21st century. Nova Science, New York, pp 179–192

Maya MA, Matsubara Y (2013) Influence of arbuscular mycorrhiza on the growth and antioxidative activity in cyclamen under heat stress. Mycorrhiza 23:381–390

McLellan CA, Turbyville TJ, Wijeratne K, Kerschen A, Vierling E, Queitsch C, Whiteshell L, Gunatilaka AAL (2007) A rhizosphere fungus enhances *Arabidopsis* thermotolerance through production of an HSP90 inhibitor. Plant Physiol 145:174–182

Meena H, Ahmed MA, Prakash P (2015) Amelioration of heat stress in wheat, *Triticum aestivum* by PGPR (*Pseudomonas aeruginosa* strain 2CpS1). Biosci Biotech Res Comm 8:171–174

Mishra PK, Bisht SC, Ruwari P, Joshi GK, Singh G, Bisht JK, Bhatt JC (2011) Bioassociative effect of cold tolerant Pseudomonas spp. and *Rhizobium leguminosarum* -PR1 on iron acquisition, nutrient uptake and growth of lentil (*Lens culinaris* L.) Eur J Soil Biol 47:35–43

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

Nadeem SM, Zahir ZA, Naveed M, Arshad M (2007) Preliminary investigations on inducing salt tolerance in maize through inoculation with rhizobacteria containing ACC deaminase activity. Can J Microbiol 53:1141–1149

Nadeem SM, Ahmad M, Naveed M, Imran M, Zahir ZA, Crowley DE (2016) Relationship between in vitro characterization and comparative efficacy of plant growth-promoting rhizobacteria for improving cucumber salt tolerance. Arch Microbiol 198:1–9

Naseem H, Bano A (2014) Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. J Plant Interact 9:689–701

Naveed M, Hussain MB, Zahir ZA, Mitter B, Sessitsch A (2014) Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. Plant Growth Regul 73:121–131

Nia SH, Zarea MJ, Rejali F, Varma A (2012) Yield and yield components of wheat as affected by salinity and inoculation with *Azospirillum* strains from saline or non-saline soil. J Saudi Soc Agric Sci 11:113–121

Ortiz N, Armada E, Duque E, Roldán A, Azcón R (2015) Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: effectiveness of autochthonous or allochthonous strains. J Plant Physiol 174:87–96

Ouziad F, Wilde P, Schmelzer E, Hilderbrandt U, Bothe H (2006) Analysis of expression of aquaporins and Na^+ /H^+ transporters in tomato colonized by arbuscular mycorrhizal fungi and affected by salt stress. Environ Exp Bot 57:177–186

Oves M, Khan M, Zaidi A (2013) Chromium reducing and plant growth promoting novel strain *Pseudomonas aeruginosa* OSG41 enhance chickpea growth in chromium amended soils. Eur J Soil Biol 56:72–83

Pedranzani H, Rodríguez-Rivera M, Gutiérrez M, Porcel R, Hause B, Ruiz-Lozano JM (2016) Arbuscular mycorrhizal symbiosis regulates physiology and performance of *Digitaria eriantha* plants subjected to abiotic stresses by modulating antioxidant and jasmonate levels. Mycorrhiza 26:141–152

Pereyra MA, Zalazar CA, Barassi CA (2006) Root phospholipids in *Azospirillum*-inoculated wheat seedlings exposed to water stress. Plant Physiol Biochem 44:873–879

Pereyra MA, Garcia P, Colabelli MN, Barassi CA, Creus CM (2012) A better water status in wheat seedlings induced by *Azospirillum* under osmotic stress is related to morphological changes in xylem vessels of the coleoptile. Appl Soil Ecol 53:94–97

Pishchik VN, Vorobyev NI, Chernyaeva II, Timofeeva SV, Kozhemyakov AP, Alexeev YV, Lukin SM (2002) Experimental and mathematical simulation of plant growth promoting rhizobacteria and plant interaction under cadmium stress. Plant Soil 243:173–186

Porcel R, Aroca R, Cano C, Bago A, Ruiz-Lozano JM (2007) A gene from the arbuscular mycorrhizal fungus *Glomus intraradices* encoding a binding protein is up-regulated by drought stress in some mycorrhizal plants. Environ Exp Bot 60:251–256

Porcel R, Aroca R, Azcon R, Ruiz-Lozano JM (2016) Regulation of cation transporter genes by the arbuscular mycorrhizal symbiosis in rice plants subjected to salinity suggests improved salt tolerance due to reduced Na^+ root-to-shoot distribution. Mycorrhiza 26:673–684

Qiu Z, Tan H, Zhou S, Cao L (2014) Enhanced phytoremediation of toxic metals by inoculating endophytic *Enterobacter* sp. CBSB1 expressing bifunctional glutathione synthase. J Hazard Mater 267:17–20

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. SpringerPlus 2(6):1–7

Rapparini F, Penuelas J (2014) Mycorrhizal fungi to alleviate drought stress on plant growth. In: Miransari M (ed) Use of microbes for the alleviation of soil stresses, vol 1. Springer, New York, pp 21–42

Ruiz-Lozano JM, Porcel R, Azcon C, Aroca R (2012) Regulation by Arbuscular mycorrhizae of the integrated physiological response to salinity in plants: new challenges in physiological and molecular studies. J Exp Bot 63(11):4033–4044

Ruiz-Sanchez M, Aroca R, Munoz Y, Armada E, Polon R, Ruiz- Lozano JM (2010) The arbuscular mycorrhizal symbiosis enhances the photosynthetic efficiency and the antioxidative response of rice plants subjected to drought stress. J Plant Physiol 167:862–869

Sadeghi A, Karimi E, Dahaji PA, Javid MG, Dalvand Y, Askari H (2012) Plant growth promoting activity of an auxin and siderophore producing isolate of Streptomyces under saline soil conditions. World J Microbiol Biotechnol 28:1503–1509

Sandhya V, Ali SZ, Grover M, Reddy G, Venkateswarlu B (2009) Alleviation of drought stress effects in sunflower seedlings by exopolysaccharides producing *Pseudomonas putida* strain P45. Biol Fert Soil 46:17–26

Sandhya V, Ali SZ, Grover M, Reddy G, Venkateswarlu B (2010) Effect of plant growth promoting *Pseudomonas* spp. on compatible solutes, antioxidant status and plant growth of maize under drought stress. Plant Growth Regul 62:21–30

Saravanakumar D, Kavino M, Raguchander T, Subbian P, Samiyappan R (2011) Plant growth promoting bacteria enhance water stress resistance in green gram plants. Acta Physiol Plant 33:203–209

Saxena S, Kaur H, Verma P, Petla BP, Andugula VR, Majee M (2013) Osmoprotectants: Potential for crop improvement under adverse conditions. In: Tuteja N, Gill SS (eds) Plant acclimation to environmental stress. Springer, New York, pp 197–232

Selvakumar G, Kundu S, Joshi P, Nazim S, Gupta AD, Mishra PK, Gupta HS (2007a) Characterization of a cold tolerant plant growth promoting bacterium *Pantoea dispersa* 1A isolated from a sub-alpine soil in the North Western Indian Himalayas. World J Microbiol Biotechnol 24:955–960

Selvakumar G, Mohan M, Kundu S, Gupta AD, Joshi P, Nazim S, Gupta HS (2007b) Cold tolerance and plant growth promotional potential of *Serratia marcescens* strain SRM (MTCC 8708) isolated from flowers of summer squash. Lett Appl Microbiol 46(2):171–175

Selvakumar G, Joshi P, Suyal P, Mishra PK, Joshi GK, Bisht JK, Bhatt JC, Gupta HS (2011) *Pseudomonas lurida* M2RH3 (MTCC 9245), a psychrotolerant bacterium from the Uttarakhand Himalayas, solubilizes phosphate and promotes wheat seedling growth. World J Microbiol Biotechnol 27:1129–1135

Shabani L, Sabzalian MR, pour SM (2016) Arbuscular mycorrhiza affects nickel translocation and expression of ABC transporter and metallothionein genes in *Festuca arundinacea*. Mycorrhiza 26:67–76

Sheng M, Tang M, Chen H, Yang B, Zhang F, Huang Y (2008) Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. Mycorrhiza 18:287–296

Sheng M, Tang M, Zhang F, Huang Y (2011) Influence of arbuscular mycorrhiza on organic solutes in maize leaves under salt stress. Mycorrhiza 21:423–430

Sheramati I, Tripathi S, Varma A, Oelmuller R (2008) The rotcolonizing endophyte *Piriformaspora indica* confers drought tolerance in *Arabidopsis* by stimulating the expression of drought stress-related genes in leaves. Mol Plsnt Microbe Interact 21:799–807

Shirmohammadi E, Khaje M, Shirdali M, Hosein GT, Shahgholi H (2014) Microorganism's application strategy for bio-phytoremediation of heavy metal: a review. J Biodiv Environ Sci (JBES) 5(3):289–298

Shokri S, Maadi B (2009) Effects of arbuscular mycorrhizal fungus on the mineral nutrition and yield of *Trifolium alexandrium* plants under salinity stress. J Agron 8:79–83

Siddikee MA, Chauhan PS, Anandham R, Han GH, Sa T (2010) Isolation, characterization and use for plant growth promotion under salt stress, of ACC deaminase-producing halotolerant bacteria derived from coastal soil. J Microbiol Biotechnol 20:1577–1584

Singh RP, Jha PN (2016) Mitigation of salt stress in wheat plant (*Triticum aestivum*) by ACC deaminase bacterium *Enterobacter* sp. SBP-6 isolated from *Sorghum bicolor*. Acta Physiol Plant 38:110

Singh RP, Jha P, Jha PN (2015) The plant-growth-promoting bacterium *Klebsiella* sp. SBP-8 confers induced systemic tolerance in wheat (*Triticum aestivum*) under salt stress. J Plant Physiol 184:57–67

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic, London

Soliman AS, Shanan NT, Massoud ON, Swelim DM (2012) Improving salinity tolerance of *Acacia saligna* (Labill.) plant by arbuscular mycorrhizal fungi and *Rhizobium* inoculation. Afr J Biotechnol 11:1259–1266

Talaat NB (2014) Effective microorganisms enhance the scavenging capacity of the ascorbate-glutathione cycle in common bean (*Phaseolus vulgaris* L.) plants grown in salty soils. Plant Physiol Biochem 80:136–143

Talaat NB (2015a) Effective microorganisms improve growth performance and modulate the ROS-scavenging system in common bean (*Phaseolus vulgaris* L.) plants exposed to salinity stress. J Plant Growth Regul 34:35–46

Talaat NB (2015b) Effective microorganisms modify protein and polyamine pools in common bean (*Phaseolus vulgaris* L.) plants grown under saline conditions. Sci Hortic 190:1–10

Talaat NB, Shawky BT (2011) Influence of arbuscular mycorrhizae on yield, nutrients, organic solutes, and antioxidant enzymes of two wheat cultivars under salt stress. J Plant Nutr Soil Sci 174:283–291

Talaat NB, Shawky BT (2012) Influence of arbuscular mycorrhizae on root colonization, growth and productivity of two wheat cultivars under salt stress. Arch Agron Soil Sci 58:85–100

Talaat NB, Shawky BT (2013) Modulation of nutrient acquisition and polyamine pool in salt-stressed wheat (*Triticum aestivum* L.) plants inoculated with arbuscular mycorrhizal fungi. Acta Physiol Plant 35:2601–2610

Talaat NB, Shawky BT (2014a) Protective effects of arbuscular mycorrhizal fungi on wheat (*Triticum aestivum* L.) plants exposed to salinity. Environ Exp Bot 98:20–31

Talaat NB, Shawky BT (2014b) Modulation of the ROS-scavenging system in salt-stressed wheat plants inoculated with arbuscular mycorrhizal fungi. J Plant Nutr Soil Sci 177:199–207

Talaat NB, Shawky BT (2015) Plant-microbe interaction and salt stress tolerance in plants. In: Wani SH, Hossain MA (eds) Managing salt tolerance in plants: molecular and genomic perspectives. CRC Press/Taylor & Francis Group, Boca Raton, pp 267–289

Talaat NB, Shawky BT (2016) Dual application of 24-epibrassinolide and spermine confers drought stress tolerance in maize (*Zea mays* L.) by modulating polyamine and protein metabolism. J Plant Growth Regul 35:518–533

Talaat NB, Ghoniem AE, Abdelhamid MT, Shawky BT (2015a) Effective microorganisms improve growth performance, alter nutrients acquisition and induce compatible solutes accumulation in common bean (*Phaseolus vulgaris* L.) plants subjected to salinity stress. Plant Growth Regul 75:281–295

Talaat NB, Shawky BT, Ibrahim AS (2015b) Alleviation of drought induced oxidative stress in maize (*Zea mays* L.) plants by dual application of 24-epibrassinolide and spermine. Environ Exp Bot 113:47–58

Theocharis A, Bordiec S, Fernandez O, Paquis S, Dhondt- Cordelier S, Baillieul F, Clement C, Barka EA (2012) *Burkholderia phytofirmans* PsJN primes *Vitis vinifera* L. and confers a better tolerance to low nonfreezing temperatures. Mol Plant Microbe Interact 25:241–249

Tiwari S, Singh P, Tiwari R, Meena KK, Yandigeri M, Singh DP, Arora DK (2011) Salt-tolerant rhizobacteria-mediated induced tolerance in wheat (*Triticum aestivum*) and chemical diversity in rhizosphere enhance plant growth. Biol Fertil Soils 47:907–916

Ullah S, Bano A (2015) Isolation of PGPRs from rhizospheric soil of halophytes and its impact on maize (*Zea mays* L.) under induced soil salinity. Can J Microbiol 11:1–7

Ullah A, Mushtaq H, Ali H, Munis MFH, Javed MT, Chaudhary HJ (2015) Diazotrophs- assisted phytoremediation of heavy metals: a novel approach. Environ Sci Pollut Res 22:2505–2514

Upadhyay SK, Singh JS, Saxena AK, Singh DP (2011) Impact of PGPR inoculation on growth and antioxidant status of wheat under saline conditions. Plant Biol 14:605–611

Vaishnav A, Kumari S, Jain S, Varma A, Choudhary DK (2015) Putative bacterial volatile-mediated growth in soybean (*Glycine max* L. Merrill) and expression of induced proteins under salt stress. J Appl Microbiol 119:539–551

Vivas A, Barea JM, Azcon R (2005) Interactive effect of *Brevibacillus brevis* and *Glomus mosseae*, both isolated from Cd contaminated soil, on plant growth, physiological mycorrhizal fungal characteristics and soil enzymatic activities in Cd polluted soil. Environ Pollut 134:257–266

Wang H, Xu R, You L, Zhong G (2013) Characterization of Cu-tolerant bacteria and definition of their role in promotion of growth, Cu accumulation and reduction of Cu toxicity in *Triticum aestivum* L. Ecotoxicol Environ Safety 94:1–7

Waqas M, Khan AL, Shahzad R, Ullah I, Khan AR, Lee I (2015) Mutualistic fungal endophytes produce phytohormones and organic acids that promote japonica rice plant growth under prolonged heat stress. J Zhejiang Univ-Sci B (Biomed Biotechnol) 16(12):1011–1018

Wu QS, Xia RX (2006) Arbuscular mycorrhizal fungi influence growth, osmotic adjustment and photosynthesis of citrus under well-watered and water stress conditions. J Plant Physiol 163:417–425

Wu QS, Xia RX, Zou YN (2008) Improved soil structure and citrus growth after inoculation with three arbuscular mycorrhizal fungi under drought stress. Eur J Soil Biol 44:122–128

Wu N, Li Z, Liu H, Tang M (2015) Influence of arbuscular mycorrhiza on photosynthesis and water status of *Populus cathayana* Rehder males and females under salt stress. Acta Physiol Plant 37:183

Xu J, Li XL, 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

Yang J, Kloepper JW, Ryu CM (2009) Rhizosphere bacteria help plants tolerate abiotic stress. Trends Plant Sci 14:1–4

Yong X, Chen Y, Liu W, Xu L, Zhou J, Wang S, Chen P, Ouyang P, Zheng T (2014) Enhanced cadmium resistance and accumulation in *Pseudomonas putida* KT2440 expressing the phytochelatin synthase gene of *Schizosaccharomyces pombe*. Lett Appl Microbiol 58:255–261

Yooyongwech S, Phaukinsang N, Cha-Um S, Supaibulwatana K (2013) Arbuscular mycorrhiza improved growth performance in *Macadamia tetraphylla* L. grown under water deficit stress involves soluble sugar and proline accumulation. Plant Growth Regul 69:285–293

Zahir ZA, Munir A, Asghar HN, Arshad M, Shaharoona B (2008) Effectiveness of rhizobacteria containing ACC-deaminase for growth promotion of peas (*Pisum sativum*) under drought conditions. J Microbiol Biotechnol 18:958–963

Zhang H, Kim MS, Sun Y, Dowd SE, Shi H, Paré PW (2008) Soil bacteria confer plant salt tolerance by tissue-specific regulation of the sodium transporter HKT1. Mol Plant Microbe Interact 21:737–744

Zhang H, Murzello C, Kim MS, Xie X, Jeter RM, Zak JC et al (2010a) Choline and osmotic-stress tolerance induced in *Arabidopsis* by the soil microbe *Bacillus subtilis* (GB03). Mol Plant Microbe Interact 23:1097–1104

Zhang Y, Zhong CL, Chen Y, Chen Z, Jiang QB, Wu C, Pinyopusarerk K (2010b) Improving drought tolerance of *Casuarina equisetifolia* seedlings by arbuscular mycorrhizas under glasshouse conditions. New For 40:261–271

Zhu XC, Song FB, HW X (2010) Effects of arbuscular mycorrhizal fungi on photosynthetic characteristics of maize under low temperature stress. Acta Ecol Sin 21:470–475

Zhu XC, Song FB, Liu SQ, Liu TD, Zhou X (2012) Arbuscular mycorrhizae improves photosynthesis and water status of *Zea mays* L. under drought stress. Plant Soil Environ 58:186–191

Zou YN, QS W, Huang YM, Ni QD, He XH (2013) Mycorrhizal-mediated lower proline accumulation in *Poncirus trifoliate* under water deficit derives from the integration of inhibition of proline synthesis with increase of proline degradation. PLOS One 8:1–8

Zou Y, Huang Y, Wu Q, He X (2015) Mycorrhiza-induced lower oxidative burst is related with higher antioxidant enzyme activities, net H_2O_2 effluxes, and Ca^{2+} influxes in trifoliate orange roots under drought stress. Mycorrhiza 25:143–152