

Review Article

ROLE OF MICROORGANISMS IN ABIOTIC STRESS MANAGEMENT

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Abstract: The productivity of major crops has been deteriorated due to increased intensity of biotic and abiotic stresses in all over the world. To overcome this, efficient resource management can mitigate the adverse effect of biotic and abiotic stress. However, these strategies being long drawn and cost intensive, there is a need to develop simple and low cost biological methods for the management of abiotic stress, which can be used on short term basis. Microorganisms are the most effective tool which could play a vital role in adaptation strategies and increased the tolerance to abiotic stresses in agricultural plants. Plant-growth-promoting rhizobacteria (PGPR) mitigate most effectively the impact of abiotic stresses (drought, low temperature, salinity, and high temperatures) on plants through the production of exopolysaccharides and bio film formation. PGPR mitigate the impact of drought on plants through a process so-called *induced systemic tolerance* (IST), which includes: a) bacterial production of cytokinins, b) production of antioxidants and c) degradation of the ethylene precursor ACC by bacterial ACC deaminase. Arbuscular mycorrhizal fungi and endophytic rhizospheric bacteria also tend to mitigate the abiotic stress in plants.

Keywords: Abiotic stress, Plant growth promoting rhizobacteria (PGPR), Induced systemic tolerance, arbuscular mycorrhizal fungi.

Introduction

Increased incidences of biotic and abiotic stress are the most important factor for deterioration of agricultural productivity of crops particularly in tropical regions due to natural and anthropogenic factors. In South-East Asia there are evidence of yield reduction due to increased water and temperature stress. In Indian sub-continent the average temperature has risen by 0.57°C in the last 100 years and it is expected that it is likely to increase a maximum of 2.5°C by 2050 and 5.8°C by 2100. Besides high temperature, drought, elevated CO₂, extreme rainfall events, more floods, cold waves, heat waves, and cyclones are the other most important natural disasters that cause serious economic losses. Nearly two-third of arid and semiarid areas is highly affected by soil moisture stresses. In India, 11 m ha area is also affected by salinity. To combat this stresses the beneficial microbes colonizes the rhizosphere of the plant and promote growth through various direct and indirect mechanism (Saxena et al., 2005). A purposeful use of plant growth promoting

rhizobacteria in agriculture is an attractive technology to address this problem. The additional understanding of the fundamental mechanisms employed by these bacteria will likely hasten the acceptance of these organisms as suitable and effective adjuncts to agricultural practice (Reed and Glick 2004). Therefore it is very important how PGPR behaves in the rhizosphere combating biotic and abiotic stress. This review aims to evaluate the beneficial effects of soil biota on the plant response to abiotic stress, with key physiological mechanisms that improves plant growth.

Alleviation of abiotic stress in plants by microorganisms

Microorganisms belonging to different genera such as *Rhizobium*, *Bacillus*, *Pseudomonas*, *Pantoea*, *Paenibacillus*, *Burkholderia*, *Achromobacter*, *Azospirillum*, *Microbacterium*, *Methylobacterium*, *Enterobacter* etc. have been reported to provide tolerance to host plants under different abiotic stress environments. Among these, rhizospheric microbes have some promising effect. Some strains of plant growth promoting rhizobacteria (PGPR) produce cytokinin and antioxidants, which result in abscisic acid (ABA) accumulation and degradation of reactive oxygen species. In 1997 Stajner et al. reported that high activities of antioxidant enzymes are linked with oxidative stress tolerance. PGPR produces various growth promoting substances such as gibberalins, IAA which increase the area of the total root and nutrient uptake of plant. Saleemet al. (2007) viewed that the role of PGPR containing ACC deaminase in stress agriculture. Under drought conditions, inoculation with ACC deaminase containing bacteria induce longer roots which might be helpful in the uptake of relatively more water from deep soil layer. (Zahir et al., 2008). The ability of plant growth-promoting bacteria that produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase to lower plant ethylene levels, often a result of various stresses, is a key component in the efficacious functioning of these bacteria. The optimal functioning of these bacteria includes the synergistic interaction between ACC deaminase and both plant and bacterial auxin, indole-3-acetic acid (IAA). This enzyme is responsible for the cleavage of the plant ethylene precursor, ACC, into ammonia and α -ketobutyrate (Honma and Shimomura 1978).

The net result of the cleavage of exuded ACC by bacterial ACC deaminase is that the bacterium acts as a sink for ACC. Moreover, as a result of lowering either the endogenous or the IAA-stimulated ACC level, the amount of ethylene that could potentially form in the plant is reduced. Subsequently, as a consequence of lowering plant ethylene levels, ACC deaminase-containing plant growth-promoting bacteria can reduce a portion of the ethylene inhibition of plant growth following a wide range of abiotic and biotic stresses. Immediately

following an abiotic or biotic stress, the pool of ACC in the plant is low as the level of ACC deaminase in the associated bacterium. Stress induces the induction of ACC oxidase in the plant so that there is an increased flux through ACC oxidase resulting in the first (small) peak of ethylene that in turn induces the transcription of protective/defensive genes in the plant. At the same time, bacterial ACC deaminase is induced by the increasing amounts of ACC that ensue from the induction of ACC synthase in the plant so that the magnitude of the second, deleterious, ethylene peak is decreased significantly (typically by 50–90%). With plant growth-promoting bacteria that both secrete IAA and synthesize ACC deaminase, plant ethylene levels do not become elevated to the same extent as when plants interact with bacteria that secrete IAA but do not synthesize ACC deaminase. In the presence of ACC deaminase, there is much less ethylene and subsequent ethylene feedback inhibition of IAA signal transduction so that the bacterial IAA can continue to both promote plant growth and increase ACC synthase transcription. However in this case, a large portion of the additional ACC that is synthesized is cleaved by the bacterial ACC deaminase. The net result of this cross-talk between IAA and ACC deaminase is that by lowering plant ethylene levels, ACC deaminase facilitates the stimulation of plant growth by IAA.

Role of microbes to mitigate drought stresses

The mechanisms have been proposed in the drought avoidance mediated by mycorrhiza, such as an improved exploitation of soil water due to the hyphal contribution to water uptake and/or induced changes in root morphology and soil structure. Indeed, the mycorrhizal maintenance of root turgor during drought was apparently not related to osmotic adjustment, despite fungal alteration of concentrations of several key solutes (Auge´ et al., 1992), but to changed apoplastic/symplastic water partitioning. While these local changes contribute to root growth maintenance, soil microbes also affect the ability of the roots to take up water under both drought and saline stresses. It has been postulated that ABA could be the signal that differentially regulates the behaviour of aquaporins in AMF and non-AMF plants under drought and saline stress conditions (Porcel et al., 2006).

Induced systemic tolerance is a mechanism by which PGPR can alleviate drought by production of cytokinins, antioxidants and degradation of ethylene precursor ACC by ACC deaminase. The production of cytokinins causes the accumulation of abscisic acid (ABA) in leaves, which in its turn results in the closing of stomata (Figueiredo et al., 2008; cit. Yang et al., 2009). The production of antioxidants (e.g., the enzyme catalase) causes the degradation of reactive forms of oxygen. The bacterial-produced ACC deaminase degrades the ethylene

precursor 1-aminocyclopropane-1-carboxylate (ACC) (Yang et al., 2009). Certain microbes produces exopolysaccharides, induces resistance genes, increases water circulation in plant and helps in proline synthesis to overcome drought. He also reported that, under drought condition some rhizobacteria neutralizes the toxic effect of reactive oxygen species in plant. Some microbes produce biofilm under drought condition to protect plant from desiccation.

Table 1. Increase in ACC deaminase activity and IAA production by inoculating *Pseudomonas sp.* in wheat crop under water stress condition:-

ISOLATE	SPECIES	ACC deaminase Activity (nmol NH ₃ /g biomass/h)	IAA production (mg/l)
ACC-50	<i>Ps. fluorescens</i>	302±5	15.3±0.8
ACC-73	<i>Ps. fluorescens</i> biotype F	393±7	8.1±0.4

Source- Shaharoon et al. 2007a

TYPE	GRAIN YIELD(g/plant)	STRAW YIELD(g/plant)
Uninoculated	5.0	7.3
<i>Ps. fluorescens</i>	5.7	8.5
<i>Ps. fluorescens</i> biotype F	5.5	8.0

Role of microbes to alleviate temperature and salinity stress:-

The microbial cannot form colony and the yield of crop is affected due to high temperature. All organisms respond to a sudden increase in temperature by inducing synthesis of specific group of polypeptides known as heat shock proteins. A thermo tolerant *P aeruginosa* strain AMK-6 isolated from semi-arid location showed induction of heat shock proteins when exposed to high temperature (Ali et al., 2009). Similarly cold tolerant bacteria response to decrease in temperature by induction of cryoprotective protein (Koda et al., 2001).

Pseudomonas spp. and other rhizobacteria are well known for their ability to colonize the root tissues of wide crop plants and promote the plant growth by the production of phytohormones, antagonistic substances and enzymes (Hong et al., 1991). It has been suggested that bacterial inoculation alleviated abiotic stresses like drought, chilling, salinity,

metal toxicity and elevated temperature. Despite the ability of plants to adapt partially to temperature stress in temperate climates, plant growth and overall productivity generally decline under stress (Haldiman 1998). In the recent study it reveals that, plant growth promoting thermotolerant *P. putida* strain AKMP7 colonizing wheat roots can significantly influence the plant's resistance to heat stress by influencing its metabolism. Seed inoculation with strain AKMP7 had a pronounced effect on growth, development and response to heat stress. The strain AKMP7 could grow and survive at 50°C, which was the maximum survival temperature for the strain and possessed plant growth promoting traits (IAA, GA, P-solubilization, siderophore, HCN and ammonia production). As successful plant growth promoting inoculants, bacteria must be able to rapidly colonize the root system during the growth of plant. Successful colonization of plant roots by the introduced strain suggested a close bacterial-plant association that may be beneficial to plants, probably because inoculation triggers some stress responsive mechanisms that enable the plants to tolerate high temperatures (Timmusk and Wagner 1999). The bacterium *Burkholderia phytofirmans* PSJN colonizes grapevine residues and protects the plant against heat and frost through increases in the levels of starch, and proline and phenols. Seedlings biomass and nutrients uptake increases at low temperatures by inoculation of *Serratia marscescens*, strain SRM and *Pantoeadispea*, strain 1A in wheat seeds. These strains also exhibited plant growth promoting characteristics like IAA production, P-solubilization, HCN and siderophores production at 15° C and 4°C.

Maintaining water homeostasis and the functioning of photosynthetic structures are essential for alleviating the impact of salinity on plant growth and crop yield. There is an evidence that soil microbes alter ion homeostasis and improve plant nutrition in salinized crops is considered. Furthermore, as plant growth under saline stress may be regulated via changes in phytohormone concentrations. Microorganisms use different mechanisms to alleviate the salinity stress in agricultural crops. In high saline condition, exopolysaccharides stimulates plant growth by restricting sodium uptake. AM fungi improve salinity resistance in corn, beans and clover by production of some osmoprotectants which have osmoregulatory mechanisms. In some cases, free auxin sufficiently provides a protective effect against salt stress (Junghans et al., 2006). Siddikee et al. (2010) have also confirmed that inoculation with 14 halotolerant bacterial strains ameliorate salt stress in canola plants through the reduction of ethylene production *via* ACC deaminase activity. Inoculation of maize plants with *Pseudomonas fluorescens* containing ACC deaminase boosted root elongation and fresh

weight significantly under saline conditions.

PGPR (Dodd et al., 2010) can have multiple impacts on phytohormone status, the possibilities that these changes can attenuate the effects of salinity are considered. However, the beneficial effect of PGPR under salinity has been also related to the alleviation of osmotic stress by maintaining higher stomatal conductance and photosynthetic activities. In turn, this could lower accumulation of toxic ions (Na^+ and Cl^-) and improve leaf $\text{K}^+:\text{Na}^+$ ratio, thus delaying toxic effects through both growth and/ or energetic maintenance of ion-exclusion mechanisms. Soil microbes may also modulate other indirect and novel mechanisms to increase plant salt tolerance. Silicon improves plant salt tolerance by limiting Na^+ uptake through an unknown mechanism, improving photochemical efficiency, protecting cell membrane integrity, increasing antioxidant enzyme activity, and decreasing water loss (Romero-Aranda et al., 2006).

Symbiotic fungi in alleviation of abiotic stress management:-

AM fungi play a beneficial role to mitigate abiotic stress by improving plant resistance to water deficit. Incitrus grafted seedlings, inoculation of arbuscular mycorrhizal fungi enhances the activity of superoxide dismutases (SOD), peroxidase (POD) and catalase (CAT) resulting in improved osmotic adjustment and decreases the leaf content of malondialdehyde and soluble protein. (Wu and Xia 2005). Coinoculation of lettuce with PGPR *Pseudomonas mendocina* and *G. intraradices* or *G. mosseae* augmented an antioxidative catalase under severe drought conditions, suggesting that they could be used in inoculants to alleviate the oxidative damage (Kohler et al., 2008). Salt resistance was improved by AM colonization in maize (Feng et al., 2002), mung bean (Jindal et al., 1993) and clover (Ben Khaled et al., 2003) with AM effect correlated with improved osmoregulation or proline accumulation. Root colonization by AMFs can induce major changes in the relative abundance of the major groups of organic solutes such as modifying the composition of carbohydrates and inducing accumulation of specific osmolytes such as proline. However, better growth of AM-inoculated *Jatropha curcas* compared with non-inoculated plants when exposed to salinity (1.7–8.5 dS m^{-1} NaCl for 60 days) may result from increased soluble sugars and proline in the leaves of inoculated plants, allowing maintenance of leaf water status (Kumar et al., 2010).

Table 2. Proline accumulation under drought stress by inoculating *Pseudomonas sp.*

CONDITION	Proline ($\mu\text{mol gFW}^{-1}$)
Normal without inoculation	3.83
Normal with inoculation	3.98
Stress without inoculation	8.66
Stress with inoculation	10.68

Strain AKM-6 on sorghum seedlings:-

Source- Bates LS, Waldren RD, Teare ID 1973

On the other hand, mycorrhizal sink strength influences the whole-plant carbon balance, and fungal colonization can stimulate the rate of photosynthesis sufficiently to compensate for fungal carbon requirements and to eliminate growth reduction of the autotroph. It has been also proposed that sugar accumulation may also be due to the hydrolysis of starch in inoculated seedlings, as mycelium growth requirements mobilize carbon reserves (Heinemeyer et al., 2006), which could help decrease salinity-induced starch accumulation as a consequence of the inhibition of sink activity in growing tissues (Balibrea et al., 2000). Thus maintenance of an active carbohydrate sink in symbiotic roots, when assimilate transport and use in other sink tissues is impaired, could help maintain the source activity of mature leaves for longer, thereby improving salt tolerance.

In support of this idea, the improved salt tolerance of mycorrhizal (*Glomus mosseae*) maize plants was related to higher accumulation of soluble sugars in the roots as a specific response, independent of plant nutritional (P) status (Feng et al., 2002). This effect could be responsible for improved plant water status, chlorophyll concentration, and photosynthetic capacity by increasing photochemical efficiency. Beneficial effects of AM symbiosis under salinity may be due to alterations in basal energetic metabolism (Giri and Mukerji, 2004). Thus, changes in plant metabolism have been also reported in mycorrhizal (*Glomus mosseae*) maize plants grown at different salt levels (Sheng et al., 2011). The AM symbiosis raised the leaf concentrations of soluble sugars, reducing sugars, soluble protein, total organic acids, oxalic acid, fumaric acid, acetic acid, malic acid, and citric acid, and decreased the concentrations of total free amino acids, proline, formic acid, and succinic acid. These results suggest that the symbiosis affects the metabolic regulation of organic acids under saline conditions, involving enzymes from the tricarboxylic acid cycle, glyoxylate cycle, or glycolysis, thus improving the

energetic status of the plant and helping to mitigate the stress (Sheng et al., 2011)

Accumulation of protective compounds:-

Several studies revealed that accumulation of nitrogen-containing compounds (NCC) can overcome drought and salt stress in plants (Parida & Das, 2005). Several comprehensive studies using transgenic plants or mutants to demonstrate that proline metabolism has a complex effect on development and stress responses. Proline acts as a compatible osmolyte and has the capacity to store carbon and nitrogen. Proline may have an antioxidant activity acting as a ROS scavenger. Proline may also function as molecular chaperones which able to stabilize the structures of proteins and enhance the activity of different enzymes.

Table 3. Effect of microbes to mitigate abiotic stress in plant:-

Stress type	Microorganism	Crop	References
Drought	<i>Pantoea agglomerans</i>	Wheat	Grover et al., 2010
Drought	<i>Rhizobium</i> sp.	Sunflower	Grover et al., 2010
Drought	<i>Azospirillum</i> sp.	Wheat	Grover et al., 2010
Salinity	<i>Achromobacter piechaudii</i>	Tomato	Grover et al., 2010
Salinity	<i>Piriforma sporaindica</i>	Barley	Grover et al., 2010
Salinity	<i>Bacillus amylolequifaciens</i>	Wheat	Grover et al., 2010
Temperature	<i>B. phytofirmans</i>	Potato	Bensalim et al. (1998)
Temperature	<i>Pseudomonas fluorescens</i>	Wheat	Egamberdiyeva et al., 2009
Temperature	<i>Serratia liquefaciens</i> ,	Soybean	Zhang et al. (1997)
Heavy metals	<i>Pseudomonas</i> sp.	Tobacco	Mastretta et al. (2009)
Heavy metals	<i>Pseudomonas fluorescens</i>	Rape	Sheng et al. (2008)
Heavy metals	<i>Bacillus subtilis</i>	Rice	Asch & Padham (2005)

Rhizosphere management to alleviate abiotic stress:

Successful commercial application of microbial inoculants to improve crop growth and yield implies that the inoculants are also salt tolerant, which highlights the potential of using microorganisms from salinity, temperature and drought tolerant. In India, resource conservation technologies involving zero or minimum tillage with direct seeding and bed planting with residue mulch are being advocated as the alternative to conventional extensive systems for improving soil quality and sustainability. Potential benefits of resource

conservative technologies through conservation agriculture include improve soil structure, reduced nutrient loss and improve soil fertility which increases the number of microorganisms in rhizosphere zone. Different crops are cultivated in crop diversification results in different deposition of crop exudates increases rhizosphere microorganisms. Application of various stress tolerant microorganisms discussed earlier also improves to mitigate abiotic stress in plant.

Table 4- Different insitu and exsitu management practices practiced:-

In-situ management	Ex-situ management
Tailoring cropping system	Application of critical nutrients like molybdenum and potassium
Crop diversification	Conservation agriculture
Selection of stress tolerant varieties	Mulching

Conclusion

Plant-associated microorganisms can play an important role in conferring resistance to abiotic stresses. These organisms such as rhizobacteria and symbiotic fungi operate through a variety of mechanisms like triggering osmotic response and induction of novel genes in plants. The development of stress tolerant crop varieties through genetic engineering and plant breeding is essential but a long drawn process, whereas microbial inoculation to alleviate stresses in plants could be a more cost effective environmental friendly option which could be available in a shorter time frame. Some microbial species and strains could play an important role for understanding plant tolerance to stress, adaptation to stress, and mechanisms that develop in plants under stress conditions. Selection of microorganisms from stressed ecosystems may contribute to the concept of biotechnology application in agriculture.

References

- [1] Ali Sk Z, Sandhya V, Grover M, Kishore N, Rao LV, Venkateswarlu B. (2009). *Pseudomonas sp.* Strain AKM-6 enhances tolerance of sorghum seedlings to elevated temperatures. *Biol Fert Soil* 46: 45-55.
- [2] Asch F, & Padham JL. (2005). Root associated bacteria suppress symptom of iron toxicity in lowland rice. In *The Global Food & Product Chain - Dynamics, Innovations, Conflicts, Strategies* (eds Tielkes, E., Hulsebusch, Hauser, I., Deininger, A. & Becker, K.), p. 276. MDD GmbH, Stuttgart, Germany.
- [3] Augé RM. (2001). Water relations, drought and VA mycorrhizal symbiosis. *Mycorrhiza*

11, 3–42.

[4] Balibrea ME, Dell'Amico J, Bolari'n MC, Pe'rez-Alfocea F. (2000). Carbon partitioning and sucrose metabolism in tomato plants growing under salinity. *Physiologia Plantarum* 110, 503–511.

[5] Bates LS, Waldren RD, Teare ID. (1973). Rapid determination of free proline for water stress studies. *Plant and Soil* 39, 205–207.

[6] Ben Khaled L, Gomez AM, Ourraqi EM, Oihabi A. (2003). Physiological and biochemical responses to salt stress of mycorrhized and/or nodulated clover seedlings (*Trifolium alexandrinum* L.). *Agronomie* 23:571–580 *Canadian Journal of Microbiology* 50, 521-577.

[7] Bensalim S, Nowak J & Asiedu SK. (1998). A plant growth promoting rhizobacterium and temperatures effects on performance of 18 clones of potato. *American Journal of Potato Research* 75, 145-152.

[8] Dodd IC, Zinovkina NY, Safronova VI, Belimov AA. (2010). Rhizobacterial mediation of plant hormone status. *Annals of Applied Biology* 157, 361–379.

[9] Egamberdieva D, Kucharova Z. (2009). Selection for root colonizing bacteria stimulating wheat growth in saline soils. *Biol Fert Soil* doi:10.1007/s00374-009-0366-y.

[10] Feng G, Zhang FS, Li XL, Tian CY, Tang C, Renegal Z. (2002). Improved tolerance of maize plants to salt stress by arbuscular mycorrhiza is related to higher accumulation of leaf P-concentration of soluble sugars in roots. *Mycorrhiza* 12:185–190.

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

[12] Giri B, Kapoor R, Mukherji KG. (2007). Improved tolerance of *Acacia nilotica* to salt stress by arbuscular mycorrhiza, *Glomus fasciculatum* may be partly related to elevated K/Na ratios in root and shoot tissues. *Microbial Ecology* 54, 753–760.

[13] Grover M, Ali SZ, Sandhya V, Rasul A, Venkateswarlu B. (2010). Role of microorganisms in adaptation of agriculture crops to abiotic stress. *World J. Microbiol. Biotechnol.*

[14] M. Honma, T. Shimomura. (1978). Metabolism of 1-aminocyclopropane-1-carboxylic acid. *Agric Biol Chem*, 43 (1978), pp. 1825-1831

[15] Hong Y, Glick BR, Pasternak JJ. (1991). Plant-microbial interaction under xenobiotic condition: a scanning microscope study. *Curr Microbiol* 23:111-114.

- [16] Jindal V, Atwal A, Sekhon BS, Rattan S, Singh R. (1993). Effect of vesicular-arbuscular mycorrhiza on metabolism of moong plants under salinity. *Plant Physiol Biochem* 31:475–481.
- [17] Junghans U, Polee A, Duchting P, Weiler E, Kuhlman B, Grubber F, Teichmann, T. (2006). Adaptation to high salinity in poplar involves changes in xylemanatomy and auxin physiology. *Plant, Cell and Environment* 29, 1519-1531.
- [18] Koda N, Asaeda, Yamade K, Kawahara H, Obata H. (2001). A novel cryoprotective protein with high activity from the ice nucleating bacterium. *Pantoea agglomerans* IFO12686. *Biosci Biocontrol Biochem* 65(4): 888-894.
- [19] Kohler J, Hernandez JA, Caravaca F, & Roldán A. (2008). Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plants. *Functional Plant Biology* 35, 141-151.
- [20] Kumar A, Sharma S, Mishra S. (2010). Influence of arbuscular mycorrhizal (AM) fungi and salinity on seedling growth, solute accumulation, and mycorrhizal dependency of *Jatropha curcas* L. *Journal of Plant Growth Regulation* 29: 297–306.
- [21] Mastretta C, Taghavi S, Van der Lelie D, Mengoni A, Galardi F, Gonnelli C, Barac T, Boulet J, Weyens N, Vangronsveld, J. (2009). Endophytic bacteria from seeds of *Nicotiana tabacum* can reduce cadmium phytotoxicity. *International Journal of Phytoremediation* 11, 251-267.
- [22] Parida AK, Das AB. (2005). Salt tolerance and salinity effects on plants: a review. *Ecotoxicology and Environmental Safety* 60, 324-349.
- [23] Porcel R, Aroca R, Azco´ n R, Ruiz-Lozano JM. (2006). PIP aquaporin gene expression in arbuscular mycorrhizal Glycine max and Lactuca sativa plants in relation to drought stress tolerance. *Plant Molecular Biology* 60, 389–404.
- [24] Romero-Aranda MR, Jurado O, Cuartero J. (2006). Silicon alleviates the deleterious salt effect on tomato plant growth by improving plant water status. *Journal of Plant Physiology* 163, 847–855.
- [25] MLE Reed, BR Glick. (2004). Applications of free living plant growth-promoting rhizobacteria. *Anton Leeuw* 86 (2004), pp. 1-25
- [26] Saleem M, Arshad M, Hussain S, Bhatti AS. (2007). Perspective of plant growth promoting rhizobacteria (PGPR) containing AC deaminase in stress agriculture. *J. Ind. Microbiol. Biotechnol* 34: 635–648.
- [27] Saxena AK, Lata Shende R, Pandey AK. (2005). Culturing of plant growth promoting

rhizobacteria. In: Gopi KP, Varma A (eds) Basic research applications of mycorrhizae. I K International Pvt Ltd, New Delhi, pp 453–474.

[28] Shaharoon B, Arshad M, Khalid A. (2007a). Differential response of etiolated pea seedling to 1-aminocyclopropane-1-carboxylate and/or L-methionine utilizing rhizobacteria. *Journal of Microbiology* 45: 15-20.

[29] Sheng XF, Xia JJ, Jiang CY, He LY, Qian M. (2008). Characterization of heavy metal-resistant endophytic bacteria from rape (*Brassica napus*) roots and their potential in promoting the growth and lead accumulation of rape. *Environmental pollution* 15, 1164-1170.

[30] 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.

[31] 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. *Journal of Microbiology and Biotechnology* 20, 1577-1584.

[32] Stajner D, Kevresan S, Gasic O, Mimica-Dukic N, Zongli H. (1997). Nitrogen and *Azotobacter chroococcum* enhance oxidative stress tolerance in sugar beet. *Biol Plantarum* 39(3): 441–445.

[33] Timmusk S, Wagner EGH. (1999). The plant growth promoting rhizobacterium *Paenibacillus polymyxa* induces changes in *Arabidopsis thaliana* gene expression: a possible connection between biotic and abiotic stress responses. *Mol Plant-Microbe Inter* 12:951-959

[34] 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(4):417–425.

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

[36] Zahir ZA, Munir A, Asghar HN, Arshad M, Shaharoon B. (2008). Effectiveness of rhizobacteria containing ACC-deaminase for growth promotion of peas (*Pisum sativum*) under drought conditions. *J Microbiol Biotech* (in press).

[37] Zhang F, Dashti N, Hynes RK, Smith DL. (1997). Plant growth-promoting rhizobacteria and soybean [*Glycine max* (L.) Merr] growth and physiology at suboptimal root zone temperatures. *Annals of Botany* 79, 243-249.