

Role of microorganisms in adaptation of agriculture crops to abiotic stresses

Minakshi Grover · Sk. Z. Ali · V. Sandhya ·
Abdul Rasul · B. Venkateswarlu

Received: 26 July 2010/Accepted: 16 September 2010/Published online: 5 October 2010
© Springer Science+Business Media B.V. 2010

Abstract Increased incidences of abiotic and biotic stresses impacting productivity in principal crops are being witnessed all over the world. Extreme events like prolonged droughts, intense rains and flooding, heat waves and frost damages are likely to further increase in future due to climate change. A wide range of adaptations and mitigation strategies are required to cope with such impacts. Efficient resource management and crop/livestock improvement for evolving better breeds can help to overcome abiotic stresses to some extent. However, such 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 could play a significant role in this respect, if we can exploit their unique properties of tolerance to extremities, their ubiquity, genetic diversity, their interaction with crop plants and develop methods for their successful deployment in agriculture production. Besides influencing the physico-chemical properties of rhizospheric soil through production of exopolysaccharides and formation of biofilm, microorganisms can also influence higher plants response to abiotic stresses like drought, chilling injury, salinity, metal toxicity and high temperature, through different mechanisms like induction of osmo-protectants and heat shock proteins etc. in plant cells. Use of these microorganisms per se can alleviate stresses in crop plants thus opening a new and emerging application in agriculture. These microbes also provide excellent models for understanding the stress tolerance, adaptation and response

mechanisms that can be subsequently engineered into crop plants to cope with climate change induced stresses.

Keywords Abiotic stress tolerance · Microorganisms · Crop production · Climate change

Introduction

Agriculture is considered to be one of the most vulnerable sectors to climate-change. Crop production, particularly in tropical regions is facing increasing stresses caused due to natural and anthropogenic factors. Increased incidence of abiotic and biotic stresses has become major cause for stagnation of productivity in principal crops. There are evidences of yield declines in wheat and paddy crops in many parts of South Asia due to increasing water stress, reduction in number of rainy days and increased air temperature. The average temperature in the Indian sub-continent has risen by 0.57°C in the last 100 years and models project that it is likely to rise further to a maximum of 2.5°C by 2050 and 5.8°C by 2100 (Kumar et al. 2006). Irrigation requirement in arid and semi-arid regions is estimated to increase by 10% with every 1°C rise in temperature. Besides high temperature, droughts, elevated CO₂, extreme rainfall events, more floods, cold waves, heat waves, and cyclones are the other important natural disasters that cause serious economic losses, are likely to be witnessed as a result of global warming. These factors are likely to cause serious negative impacts on crop growth and yields and impose severe pressure on our land and water resources.

The principal abiotic stresses in India are drought or soil moisture stress that affect nearly two-thirds area forming parts of the arid and semi arid eco systems, high

M. Grover · Sk. Z. Ali · V. Sandhya · A. Rasul ·
B. Venkateswarlu (✉)
Central Research Institute for Dryland Agriculture, Hyderabad
500059, India
e-mail: vbandi_1953@yahoo.com

temperatures, soil salinity/alkalinity, low pH and metal toxicity. Nearly 11 m ha area is affected by salinity, a chemical stress and another 16 m ha by water logging, a physical stress.

Evolving efficient, low cost, easily adaptable methods for the abiotic stress management is a major challenge. Worldwide, extensive research is being carried out, to develop strategies to cope with abiotic stresses, through development of heat and drought tolerant varieties, shifting the crop calendars, resource management practices etc. (Venkateswarlu and Shanker 2009). While most of these technologies are cost-intensive, recent studies indicate that microorganisms can also help crops cope with abiotic stresses. The role of microorganisms in plant growth promotion, nutrient management and disease control is well known. These beneficial microorganisms colonize the rhizosphere/endorhizosphere of plants and promote growth of the plants through various direct and indirect mechanisms (Saxena et al. 2005). However, of late, the role of microbes in management of biotic and abiotic stresses is gaining importance. The subject of PGPR elicited tolerance to abiotic stresses has been reviewed recently (Venkateswarlu et al. 2008; Yang et al. 2009). The term Induced Systemic Tolerance (IST) has been proposed for PGPR-induced physical and chemical changes that result in enhanced tolerance to abiotic stress.

The present review captures the recent work on the role of microorganisms in helping crops cope with various abiotic stresses like heat stress, salt stress, drought, chilling injury and water-logging, the most common stresses caused due to climate change.

Abiotic stresses: adaptation of microorganisms at cellular level

The different stress factors have a significant influence on the performance of microorganisms. The selection and deployment of microorganisms in stressed ecosystems therefore requires concerted research and technology development. Extensive research has been carried out on occurrence and functional diversity of agriculturally important microbes in stressed environments as reviewed by several authors (Grahm 1992; Zahran 1999; Venkateswarlu et al. 2008). The occurrence of *Rhizobium*, *Bradyrhizobium*, *Azotobacter*, *Azospirillum*, *Pseudomonas* and *Bacillus* has been reported from desert ecosystems, acid soils, saline and alkaline areas and highly eroded hill slopes of India (Tilak et al. 2005, Selvakumar et al. 2009, Upadhyay et al. 2009).

Adaptation of microorganisms to stress is a complex multilevel regulatory process in which many genes may be involved (Srivastava et al. 2008). In certain species living under extreme environments (thermophiles and

halophiles), optimum metabolic process like enzymatic activities and membrane stability occur at high temperature or salinity respectively (Madigen 1999), whereas other microorganisms develop different adaptation mechanisms to combat the stress.

Under stress, most of the rhizobacteria produce osmoprotectants (K^+ , glutamate, trehalose, proline, glycine betaine, proline betaine and ectoine etc.) to modulate their cytoplasmic osmolarity (Blanco and Bernard 1994; Magdy et al. 1990). The periplasmic space of bacteria contains large quantities of highly anionic polysaccharides known as membrane derived oligosaccharides, which are too large to diffuse through the porin proteins and probably function to maintain the turgor pressure of the periplasm of these organisms. Several reviews have focused on the response of bacteria to variations in the solute content of their aqueous environment (Chang et al. 1996, 2007, Sandhya et al. 2009a, b). Vriezen et al. (2006) studied the physiological factors that determine the survival of rhizobia during desiccation and found that survival of *Sinorhizobium meliloti* USDA 1021 during desiccation was enhanced, when cells were dried in stationary phase with an increasing drying temperature and availability of chloride and sulphate. Such studies may help in development of improved strains for stress conditions.

Certain bacteria like *Pseudomonas* survive under stress conditions due to the production of exopolysaccharides (EPS), which protects microorganisms from hydric stress and fluctuations in water potential by enhancing water retention and regulating the diffusion of carbon sources in microbial environment (Sandhya et al. 2009a, b). Exopolysaccharides possess unique water holding and cementing properties, thus play a vital role in the formation and stabilization of soil aggregates and regulation of nutrients and water flow across plant roots through biofilm formation (Roberson and Firestone 1992; Tisdall and Oadea 1982).

High soil temperatures in tropical and subtropical areas, is a major problem for crop production and microbial colonization. Protein denaturation and aggregation are the major types of cellular damage that result from higher temperatures. All organisms respond to a sudden increase in temperature by inducing the synthesis of specific group of polypeptides known as heat shock proteins (HSPs). HSPs consist of chaperons (such as GroEL, DnaK, DnaJ, GroES, ClpB, ClpA, ClpX, small heat shock proteins (sHSP) and proteases). Chaperons are involved in the proper folding of denatured proteins and proteases are required for the degradation of irreversibly damaged proteins (Munchbach et al. 1999). A thermotolerant *P. aeruginosa* strain AMK-P6 isolated from semi-arid location showed induction of HSPs when exposed to high temperature (Ali et al. 2009). The activity of such chaperones is essential for cell survival during heat shock and for

subsequent recovery. Similarly cold tolerant bacteria respond to a decrease in temperature by induction of cryoprotective protein (Koda et al. 2001).

Microorganisms could play a significant role in stress management, once their unique properties of tolerance to extremities, their ubiquity, genetic diversity are understood and methods for their successful deployment in agriculture production are developed. These organisms also provide excellent models for understanding stress tolerance mechanisms that can be subsequently engineered into crop plants.

Alleviation of abiotic stress in plants by rhizosphere and endophytic bacteria

Besides developing mechanisms for stress tolerance, microorganisms can also impart some degree of tolerance to plants towards abiotic stresses like drought, chilling injury, salinity, metal toxicity and high temperature. In the last decade, bacteria belonging to different genera including *Rhizobium*, *Bacillus*, *Pseudomonas*, *Pantoea*, *Paenibacillus*, *Burkholderia*, *Achromobacter*, *Azospirillum*, *Microbacterium*, *Methylobacterium*, *variovorax*, *Enterobacter* etc. have been reported to provide tolerance to host plants under different abiotic stress environments (Table 1). Use of these microorganisms per se can alleviate stresses in agriculture thus opening a new and emerging application of microorganisms.

A variety of mechanisms have been proposed behind microbial elicited stress tolerance in plants (Fig. 1). Production of indole acetic acid, gibberellins and some unknown determinants by PGPR, result in increased root length, root surface area and number of root tips, leading to enhanced uptake of nutrients thereby improving plant health under stress conditions (Egamberdieva and Kucharova 2009). Plant growth promoting bacteria have been found to improve growth of tomato, pepper, canola, bean and lettuce under saline conditions (Barassi et al. 2006; Glick et al. 1997; Yildirim and Taylor 2005). Some PGPR strains produce cytokinin and antioxidants, which result in abscisic acid (ABA) accumulation and degradation of reactive oxygen species. High activities of antioxidant enzymes are linked with oxidative stress tolerance (Stajner et al. 1997). Timmusk and Wagner (1999) were among the firsts to show that inoculation of *Paenibacillus polymyxa* confers drought tolerance in *A. thaliana* through the induction of drought responsive gene, *ERD15* (EARLY RESPONSE TO DEHYDRATION 15). Inoculation of *Azospirillum brasilense* Sp245 in wheat (*Triticum aestivum*) under drought stress resulted in a better water status and an additional “elastic adjustment” resulting in better grain yield and mineral quality (Mg, K and Ca) at harvest.

Another PGPR starin, *Achromobacter piechaudii* ARV8 which produced 1-aminocyclopropane-1-carboxylate (ACC) deaminase, conferred IST against drought and salt in pepper and tomato (Mayak et al. 2004). Many aspects of plant life are regulated by ethylene levels and the biosynthesis of ethylene is subjected to tight regulation, involving transcriptional and post-transcriptional factors regulated by environmental cues, including biotic and abiotic stresses (Hardoim et al. 2008). In the biosynthetic pathway of ethylene, S-adenosylmethionine (S-AdoMet) is converted by 1-aminocyclopropane-1-carboxylate synthase (ACS) to 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene. Under stress conditions, the plant hormone ethylene endogenously regulates plant homoeostasis and results in reduced root and shoot growth. In the presence of ACC deaminase producing bacteria, plant ACC is sequestered and degraded by bacterial cells to supply nitrogen and energy. Furthermore, by removing ACC, the bacteria reduce the deleterious effect of ethylene, ameliorating plant stress and promoting plant growth (Glick 2007). Saleem et al. (2007) have reviewed the role of PGPR containing ACC deaminase, in stress agriculture. Inoculation with ACC deaminase containing bacteria induce longer roots which might be helpful in the uptake of relatively more water from deep soil under drought stress conditions, thus increasing water use efficiency of the plants under drought conditions (Zahir et al. 2008).

The complex and dynamic interactions among microorganisms, roots, soil and water in the rhizosphere induce changes in physicochemical and structural properties of the soil (Haynes and Swift 1990). Microbial polysaccharides can bind soil particles to form microaggregates and macroaggregates. Plant roots and fungal hyphae fit in the pores between microaggregates and thus stabilize macroaggregates. Plants treated with EPS producing bacteria display increased resistance to water stress due to improved soil structure (Sandhya et al. 2009b). EPS can also bind to cations including Na^+ thus making it unavailable to plants under saline conditions. Chen et al. (2007) correlated proline accumulation with drought and salt tolerance in plants. Introduction of *proBA* genes derived from *Bacillus subtilis* into *A. thaliana* resulted in production of higher levels of free proline resulting in increased tolerance to osmotic stress in the transgenic plants. Increased production of proline along with decreased electrolyte leakage, maintenance of relative water content of leaves and selective uptake of K^+ ions resulted in salt tolerance in *Zea mays* coinoculated with *Rhizobium* and *Pseudomonas* (Bano and Fatima 2009). Proline protects membranes and proteins against the adverse effects of high concentration of inorganic ions and temperature extremes. It also functions as a protein-compatible hydrophobe, and as a hydroxyl radical scavenger (Smirnoff and Cumbes 1989).

Table 1 Microorganisms conferring abiotic stress tolerance in crop plants

Organism	Crop	Type of stress	Mechanism	References
<i>Pantoea agglomerans</i>	Wheat	Drought	<i>Rhizosphere</i> soil aggregation through EPS	Amellal et al. (1998)
<i>Paenibacillus polymyxa</i>	Arabiodopsis	Drought	Induction of stress resistant gene ERD 15	Timmusk and Wagner (1999)
<i>Rhizobium</i> sp.	Sunflower	Drought	Soil aggregation through EPS	Alami et al. (2000)
<i>Pseudomonas putida</i> , <i>Enterobacter cloacae</i> , <i>P. putida</i>	Tomato	Flooding	Synthesis of ACC-deaminase	Grichko and Glick (2001)
PGPR	Chickpea	Metal toxicity	Sequestration of metal ions	Gupta et al. (2004)
<i>Azospirillum</i> sp.	Wheat	Drought	Improved Water relations	Creus et al. (2004)
<i>Achromobacter piechaudii</i>	Tomato	Salt, drought	Synthesis of ACC-deaminase	Mayak et al. (2004)
<i>Variovorax paradoxus</i>	Pea	Drought	Synthesis of ACC-deaminase	Dodd et al. (2005)
<i>Piriformaspora indica</i>	Barley	Salinity	Elevated antioxidative capacity	Waller et al. (2005)
AM Fungi	Sorghum	Drought, salinity	Improved Water relation	Cho et al. (2006)
<i>B. amylolequifaciens</i>	Wheat	Salinity	Restricted Na ⁺ influx	Ashraf et al. (2004)
<i>B. insolitus</i>				
<i>Microbacterium</i> sp.				
<i>P. syringae</i>				
<i>Paraphaeosphaeria quadriseptata</i> (A rhizospheric fungi)	Arabiodopsis	Drought	Induction of HSP	McLellan et al. (2007)
<i>Scyttonema</i>	Rice	Coastal Salinity	Gibberellic acid & extra cellular products	Rodriguez et al. (2006)
<i>Burkholderia phytofirmans</i> PsJN	Grapevine	Low temperature	Synthesis of ACC-deaminase	Ait Bakra et al. (2006)
AM fungi & <i>Bradyrhizobium</i>	Dragonblood (<i>Pterocarpus officinalis</i>)	Flooding	Development of adv. roots, aerenchyma and hyper trophied lenticels	Fougnies et al. (2007)
<i>Brome mosaic virus</i>	Rice	Drought	Unknown	Marquez et al. (2007)
<i>Methylobacterium oryzae</i> , <i>Burkholderia</i> sp.	Tomato	Ni & Cd Toxicity	Reduced uptake and translocation	Madhaiyan et al. (2007)
<i>Pseudomonas fluorescens</i>	Groundnut	Salinity	Synthesis of ACC-deaminase	Saravanakumar and Samiyappan (2007)
<i>P. putida</i>	Canola	Low temperature	Synthesis of ACC-deaminase	Chang et al. (2007)
<i>P. polymyxa</i> and <i>Rhizobium tropici</i>	Common bean	Drought	Change in hormone balance and stomatal conductance	Figueiredo et al. (2008)
<i>Pseudomonas</i> sp.	Pea	Drought	Decreased ethylene production	Arshad et al. (2008)
<i>Pseudomonas mendocina</i> and <i>Glomus intraradices</i>	Lettuce	Drought	Improved antioxidant status	Kohler et al. (2008)
<i>Pseudomonas</i> sp. AMK-P6	Sorghum	Heat	Induction of heat shock proteins and improved plant biochemical status	Ali et al. (2009)
<i>Pseudomonas putida</i> P45	Sunflower	Drought	Improved soil aggregation due to EPS production	Sandhya et al. (2009a, 2009b)
<i>Bacillus megaterium</i> and <i>Glomus</i> sp.	Trifolium	Drought	IAA and proline production	Marulanda et al. (2007)

Accumulation of proline buffers cellular redox potential under environmental stresses (Jain et al. 2001; Wahid and Close 2007).

Trehalose metabolism in rhizobia is key for signaling plant growth, yield and adaptation to abiotic stress and its manipulation had a major agronomical impact on

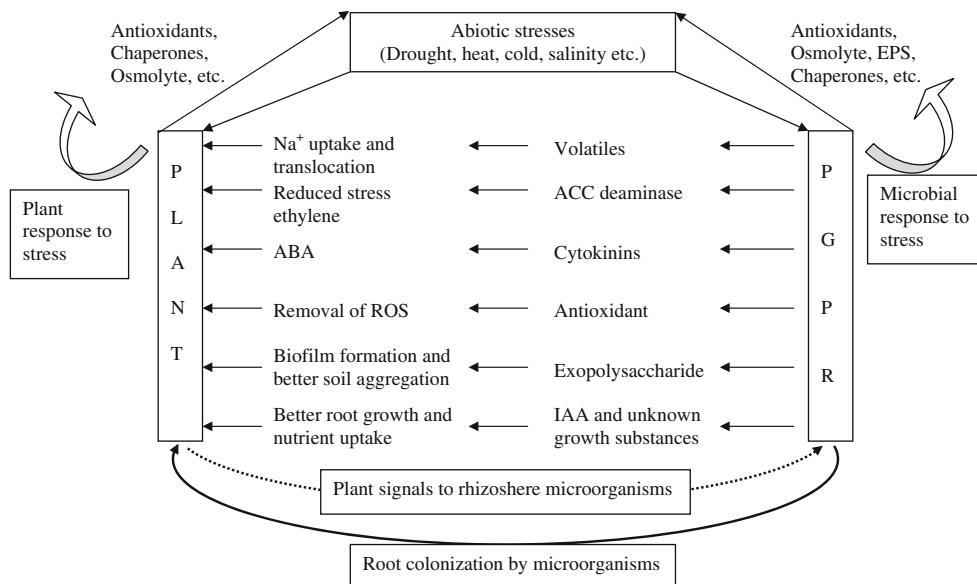


Fig. 1 Conceptual diagram, on the plant–microbe interactions under abiotic stress

leguminous plants (Suarez et al. 2008). Figueiredo et al. (2008) reported increased plant growth, N content and nodulation of *Phaseolus vulgaris* L. under drought stress due to coinoculation of *Rhizobium tropici* and *P. polymyxia*. *Phaseolus vulgaris* (common bean) plants inoculated with *Rhizobium etli* overexpressing trehalose-6-phosphate synthase gene had more nodules with increased nitrogenase activity and high biomass compared with plants inoculated with wild type *R. etli*. Three weeks old plants subjected to drought stress fully recovered whereas plants inoculated with a wild type *Rhizobium etli* died. Microarray analysis of 7,200 expressed sequence tags from nodules of plants inoculated with strain over expressing trehalose-6-phosphate synthase gene revealed upregulation of genes involved in stress tolerance, suggesting a signaling mechanism for trehalose.

Some of the volatiles organic compounds (VOCs) emitted from *Bacillus* (Ryu 2004) are bacterial determinants involved in IST. The volatiles emitted by PGPR down regulate *hkt1* (*HIGH AFFINITY K⁺ TRANSPORTER 1*) expression in roots but upregulates it in shoots, orchestrating lower Na⁺ levels and recirculation of Na⁺ in the whole plant under salt conditions (Zhang et al. 2008). Root colonization of *Arabidopsis thaliana* by *Pseudomonas chlororaphis* O6 induced tolerance in the plants against biotic and abiotic stresses due to the production of a volatile metabolite, 2R, 3R-butanediol. Studies with *Arabidopsis* mutant lines indicated that induced drought tolerance requires salicylic acid (SA), ethylene and jasmonic acid-signalling pathways (Cho et al. 2008).

Higher temperatures influence photosynthetic rate, plant water relations, flowering and fruit set in tropical and

temperate crops. Similarly low temperature is a major factor limiting the productivity and geographical distribution of many species, including important agricultural crops. Srivastava et al. (2008) isolated a thermotolerant *Psseudomonas putida* NBRI0987 from drought affected rhizosphere of chickpea. Over production of stress sigma (S) (*RpoS*) was observed by this microorganism when grown under high temperature stress at 40°C compared with 30°C. A thermotolerant *Pseudomonas* sp. strain AMK-P6 induced thermotolerance in sorghum seedlings due to synthesis of high molecular weight protein in leaves and improved plant biomass as well as biochemical status in terms of proline, sugar, amino acid and chlorophyll content (Ali et al. 2009). A plant growth promoting bacterium *Burkholderia phytofirmans* PsJN, capable of epiphytic and endophytic colonization of grapevine tissue and organs (Compan et al. 2005) could protect the plants against heat as well as chilling stress (Bensalim et al. 1998; Ait Bakra et al. 2006). The bacterized plantlets showed significantly increased levels of starch, proline and phenolics. These increases correlated with the enhancement of cold tolerance of the grapevine plantlets. Cold tolerant *Serratia marscescens* strain SRM and *Pantoea dispersa* strain 1A exhibited PGP characteristics like IAA production, P-solubilization, HCN and siderophores production at 15 and 4°C. Seed bacterization with the strains significantly enhanced biomass and nutrient uptake of wheat seedlings grown in cold temperature (Selvakumar et al. 2007a, b).

In bacteria, cold shock proteins (CSP) proteins are 7 to 10 kD in size and contain the nucleic acid binding activity, sufficient for their function as RNA chaperones. The chaperone function of CSP is thought to be important for

stimulating growth following stress acclimation and during periods of high metabolic activity. The expression of bacterial CSPs (Csp A and Csp B) was shown to improve tolerance of transgenic rice, maize and arabidopsis plants to a number of abiotic stresses including cold, heat and water deficit resulting in improved yields under field conditions (Castiglioni et al. 2008). These studies confirmed that the family of proteins is capable of delivering broad stress tolerance, which also translates to improved grain yields under both managed stress and natural environment.

Rhizobacteria inhabiting the sites exposed to frequent stress conditions, are likely to be more adaptive or tolerant and may serve as better plant growth promoters under stressful conditions (Lifshitz et al. 1986). It has been reported that *P. polymyxa* inoculation is more effective in relatively harsh and poor quality conditions (Chanway and Holl 1994). Drought-exposed barley plants when inoculated with *P. polymyxa* could tolerate stress, 2 weeks longer than uninoculated control plants (Timmusk 2003). The isolation of indigenous microorganisms from the stress affected soils and screening on the basis of their stress tolerance and PGP traits may be useful in the rapid selection of efficient strains that could be used as bioinoculants for stressed crops.

Symbiotic fungi for alleviation of abiotic stress in plants

Arbuscular mycorrhizal (AM) symbiosis is often alleged to improve plant resistance to water deficit and drought stress through the alteration of plant physiology and the expression of plant genes (Subramanian and Charest 1998; Ruiz-Lozano and Azcon 2000). There are reports of AM-induced increases in drought tolerance, involving both increased dehydration and dehydration tolerance (Allen and Boosalis 1983). AM fungi inoculation could decrease the leaf content of malondialdehyde and soluble protein and enhance activities of superoxide dismutases (SOD), peroxidase (POD) and catalase (CAT) resulting in improved osmotic adjustment and drought tolerance of mycorrhized citrus grafting seedlings (Wu and Xia 2005). Inoculation of *Glomus versiforme* in citrus plants improved the osmotic adjustment of the plant under drought stress through enhanced levels of non-structural carbohydrates, K(+), Ca(+) and Mg(2+) resulting in the enhancement of drought tolerance (Wu and Xia. 2006).

The role of abscisic acid (ABA) had been suggested behind AM mediated stress response of plants (Aroca et al. 2008). The addition of exogenous ABA considerably enhanced the ABA content in shoots of non-AM plants, concomitant with the expression of the stress marker genes *Lsp5cs* and *Ls1ea* and the gene *Lsnced*. By contrast, the addition of exogenous ABA decreased the

content of ABA in shoots of AM plants and did not produce any further enhancement of the expression. Co-inoculation 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). A 14-3-3 protein encoding gene from *Glomus intraradices* growing in vitro and subjected to drought stress was identified (Porcel et al. 2006). Role of these proteins that regulate both signaling pathways and also effector proteins was suggested in imparting protection to the host plants against drought stress. Glutathione and ascorbate have an important role in conferring protection and maintain metabolic function of plants under water deficit conditions. Low accumulation of these compounds in the lavender plants colonized by autochthonous drought tolerant *Glomus intraradices* and *Glomus* sp. strain indicated high drought tolerance in plants (Marulanda et al. 2007). Mycorrhized lavender plants showed improved water content, root biomass and N and K content.

AM symbiosis has frequently increased resilience of host plants to salinity stress, perhaps with greater consistency than to drought stress. Growth in saline soils was increased by inoculation with *Glomus* spp., with AM plants having increased phosphate and decreased Na⁺ concentrations in shoots compared to uninoculated controls (Pfeiffer and Bloss 1987; Giri and Mukerji 2004). 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. AM inoculation also improved NaCl resistance in tomato, with extent of improvement related to salt sensitivity of the cultivar (Al-Karaki et al. 2001). AM improvement of salt resistance has usually been associated with AM-induced increases in P acquisition and plant growth in cucumber (Rosendahl and Rosendahl 1991). *Gigaspora margarita* colonization promoted stomatal conductance in sorghum on exposure to drought stress in salinized soils and also improved the survival dual stress.

Occurrence of AM fungi in wetlands is well documented (Saint-Etienne et al. 2006). Accumulation of acetaldehyde, a highly toxic intermediate in ethanol formation, in roots has been suggested as the main factor responsible for flooding injury in sensitive species (Osundina 1998). AM colonization by *Glomus intraradices* contributed substantially to the flood tolerance of *Pterocarpus officinalis* seedlings by improving plant growth and P acquisition in leaves. Flooding induced nodules both on adventitious roots and submerged parts of the stem (Fougnies et al. 2007). Mycorrhized *Casuarina equisetifolia* seedlings could better adapt to flooding than noninoculated seedlings. This

could be due to increased O₂ diffusion and removal of ethanol through greater development of adventitious roots, aerenchymatous tissue and hypertrophies lenticels on the root zone and submerged part of the stem (Rutto et al. 2002). The better tolerance of AM inoculated *A. trifolium* plants to flooding was mediated through an improvement of osmotic adjustment and proline in plant tissue (Neto et al. 2006).

Besides AMF, Endophytic symbiont dark septate fungi (DSF) found in plants growing under stressed environments such as alpine habitats and arid grasslands have been reported to increase their resistance to drought and heat and facilitate the acquisition of nutrients (Porras-Alfaro et al. 2008). *Piriformaspora indica* an endophytic fungus confers drought tolerance in *Arabidopsis thaliana* through priming of the expression of a quite diverse set of stress related genes in the leaves, resulting in stronger upregulation of the message levels for phospholipase Ddelta, calcineurin B-like proteins (CBL 1) and histone acetyltransferase (HAT) in *P. indica* colonized seedlings (Sheramati et al. 2008). Rhizosphere fungus *Paraphaeosphaeria quadri-septata* enhanced plant heat stress tolerance of *Arabidopsis thaliana* through induction of HSP101 and HSP70 the conserved components of the stress response (McLellan et al. 2007).

Dual symbiotic systems for alleviation of abiotic stress in plants

Besides rhizosphere and endophytic bacteria and symbiotic fungi, role of virus in conferring tolerance to host plant against abiotic stress has also been reported. An endophytic fungi *Curvularia* sp. isolated from the *Dichanthelium lanuginosum* grown under geothermal soils could impart thermo-tolerance (constant 50°C soil temperature for 3 days and intermittent soil temperature as high as 65°C for 10 days) (Redman et al. 2002). Neither the fungus nor the plant could grow at temperature above 38°C, when grown separately. The ability of *Curvularia protuberata* to confer heat tolerance to the host plant was related to the presence of a virus named as *Curvularia* thermotolerance virus (CatahTV). Plants inoculated with the virus-infected wild type isolate of fungus tolerated intermittent soil temperatures as high as 65°C for 2 weeks (10 h of heat per day) whereas both non-symbiotic plants and plants inoculated with the virus free isolate of the fungus became shriveled, chlorotic and died. The ability of *C. protuberata* isolated from a monocot, to confer heat tolerance to tomato (a dicot) was tested and similar results to those obtained with *D. lanuginosum* were observed (Marquez et al. 1996). Several possible mechanisms could confer thermotolerance. In plants, the fungal endophytes produce cell wall

melanin that may dissipate heat along the hyphae and/or complex with oxygen radicals generated during heat stress (Davidson et al. 1996). Alternatively, the endophyte may act as a biological “trigger” allowing symbiotic plants to activate stress response systems more rapidly and strongly than non-symbiotic plants (Redman et al. 1999).

Conclusion

Plant-associated microorganisms can play an important role in conferring resistance to abiotic stresses. These organisms could include rhizoplane and endophytic bacteria and symbiotic fungi and 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. Taking the current leads available, concerted future research is needed in this area, particularly on field evaluation and application of potential organisms.

References

- Ait bakra E, 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(11):7246–7252
- Alami Y, Achouak W, Marol C, Heulin T (2000) Rhizosphere soil aggregation and plant growth promotion of sunflowers by exopolysaccharide producing *Rhizobium* sp. strain isolated from sunflower roots. *Appl Environ Microbiol* 66:3393–3398
- Ali Sk Z, Sandhya V, Grover M, Kishore N, Rao LV, Venkateswarlu B (2009) *Pseudomonas* sp. strain AKM-P6 enhances tolerance of sorghum seedlings to elevated temperatures. *Biol Fert Soil* 46:45–55
- Al-Karaki GN, Ahmad R, Rusan M (2001) Response of two tomato cultivars differing in salt tolerance to inoculation with mycorrhizal fungi under salt stress. *Mycorrhiza* 11:43–47
- Allen MF, Boosalis MG (1983) Effects of two species of VA mycorrhizal fungi on drought tolerance of winter wheat. *New Phytol* 93:67–76
- Amella N, Burtin G, Bartoli F, Heulin T (1998) Colonization of wheat rhizosphere by EPS producing *Pantoea agglomerans* and its effect on soil aggregation. *Appl Environ Microbiol* 64:3740–3747
- Aroca R, Vernieri P, Ruiz-Lozano JM (2008) Mycorrhizal and non-mycorrhizal *Lactuca sativa* plants exhibit contrasting responses to exogenous ABA during drought stress and recovery. *J Exp Bot* 59(8):2029–2041
- Arshad M, Sharona B, Mahmood T (2008) Inoculation with *Pseudomonas* spp. containing ACC deaminase partially eliminate the effects of drought stress on growth, yield and ripening of pea (*Pisum sativum* L.). *Pedosphere* 18:611–620

- Ashraf M, Berge SH, Mahmood OT (2004) Inoculating wheat seedling with exopolysaccharide-producing bacteria restricts sodium uptake and stimulates plant growth under salt stress. *Biol Fert Soils* 40:157–162
- Bano A, Fatima M (2009) Salt tolerance in *Zea mays* (L.) following inoculation with *Rhizobium* and *Pseudomonas*. *Biol Fert Soils* 45:405–413
- Barassi CA, Ayrault G, Creus CM, Suelo RJ, Sobero MT (2006) Seed inoculation with *Azospirillum* mitigates NaCl effects on lettuce. *Sci Hortic* (Amsterdam) 109:8–14
- 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
- Bensalim S, Nowak J, Asiedu S (1998) A plant growth promoting rhizobacterium and temperature effects on performance of 18 clones of potato. *A. Potato J* 75:145–152
- Blanco, Bernard T (1994) Osmoadaptation in rhizobia: ectoine-induced salt tolerance. *J Bacteriol* 176:5210–5217
- Castiglioni P, Warner D, Benson RJ, Anstrom DC, Harrison J, Stoecker M, Abad M, Kumar G, Salvador S, D'Ordine R, Navarro S, Back S, Fernandes M, Targolli J, Dasgupta S, Bonin C, Luethy MH, Heard JE (2008) Bacterial RNA chaperones confer abiotic stress tolerance to plants and improved grain yield in maize under water-limited conditions. *Plant Physiol* 147:446–455
- Chang WS, van de Mortel M, Nielsen L, de Guzman GN, Li X, Halverson LJ (2007) Alginic production by *Pseudomonas putida* creates a hydrated microenvironment and contributes to biofilm architecture and stress tolerance under water-limiting conditions. *J Bacteriol* 189:8290–8299
- Chanway CP, Holl FB (1994) Growth of outplanted lodepole pine seedlings one year after inoculation with plant growth promoting rhizobacteria. *Forest Sci* 40:238–246
- Chen M, Wei H, Cao J, Liu R, Wang Y, Zheng C (2007) Expression of *Bacillus subtilis* proAB genes and reduction of feedback inhibition of proline synthesis increases proline production and confers osmotolerance in transgenic *Arabidopsis*. *J Biochem Mol Biol* 40(3):396–403
- Cho K, Toler H, Lee J, Ownley B, Stutz JC, Moore JL, Auge RM (2006) Mycorrhizal symbiosis and response of sorghum plants to combined drought and salinity stresses. *J Plant Physiol* 163:517–528
- 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
- Compant S, Reiter B, Sessitsch A, Nowak J, Clement C, Ait Bakra E (2005) Endophytic colonization of *Vitis vinifera* L. by plant growth promoting bacterium *Burkholderia* sp. strain PsJN. *Appl Environ Microbiol* 71:1685–1693
- Creus CM, Suelo RJ, Barassi CA (2004) Water relations and yield in *Azospirillum*-inoculated wheat exposed to drought in the field. *Can J Bot* 82(2):273–281
- Davidson JF, Whyte B, Bissinger PH, Schiestl RH (1996) Oxidative stress is involved in heat-induced cell death in *Saccharomyces cerevisiae*. *Proc Natl Acad Sci* 93:5116–5121
- Dodd IC, Belimov AA, Sobeih WY, Safronova VI, Grierson D, Davies WJ (2005) Will modifying plant ethylene status improve plant productivity in water-limited environments? 4th international crop science congress. http://www.cropscience.org.au/icsc2004/poster/1/3/4/510_doddicref.htm. Accessed 17 June 2007
- 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*
- 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
- 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
- Fougues L, Renciot S, Muller F, Plenquette C, Prin Y, de Faria SM, Bouvet JM, Sylla SND, Dreyfus B, Ba AM (2007) Arbuscular mycorrhizal colonization and nodulation improve tolerance in *Pterocarpus officinalis* Jacq. seedlings. *Mycorrhiza* 17:159–166
- Giri B, Mukerji KG (2004) Mycorrhizal inoculant alleviate salt stress in *Sesbania aegyptiaca* and *Sesbania grandiflora* under field conditions: evidence for reduced sodium and improved magnesium uptake. *Mycorrhiza* 14:307–312
- Glick BR (2007) Promotion of plant growth by bacterial ACC deaminase. *Crit Rev Plant Sci* 26:227–242
- Glick BR, Liu C, Ghosh S, Dumroff EB (1997) Early development of canola seedlings in the presence of plant growth promoting rhizobacterium *Pseudomonas putida* GR 12–2. *Soil Biol Biochem* 29:1233–1239
- Graham PH (1992) Stress tolerance in *Rhizobium*, *Bradyrhizobium* and nodulation under adverse soil conditions. *Can J Microbiol* 38:475–484
- Grichko VP, Glick BR (2001) Amelioration of flooding stress by ACC deaminase containing plant growth promoting bacteria. *Can J Microbiol* 47:77–80
- Gupta DK, Rai UN, Sinha S, Tripathi RD, Nautiyal BD, Rai P, Inouhe M (2004) Role of *Rhizobium* (CA-1) inoculation in increasing growth and metal accumulation in *Cicer arietinum* L. growing under fly-ash stress condition. *Bull Environ Contam Toxicol* 73:424–431
- Harold PR, van Overbeek SV, van Elsas JD (2008) Properties of bacterial endophytes and their proposed role in plant growth. *Trends Microbiol* 16:463–471
- Haynes RJ, Swift RS (1990) Stability of soil aggregates in relation to organic constituents and soil water content. *J Soil Sci* 41:73–83
- Jain M, Mathur G, Koul S, Sarin NB (2001) Ameliorative effects of proline on salt stress induced lipid peroxidation in cell lines of groundnuts (*Arachis hypogaea*). *Plant Cell Rep* 20:463–468
- 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
- Koda N, Asaeda Y, Yamada K, Kawahara H, Obata H (2001) A novel cryoprotective protein (CRP) with high activity from the ice-nucleating bacterium, *Pantoea agglomerans* IFO12686. *Biosci Biotechnol Biochem* 65(4):888–894
- Kohler J et al (2008) Plant growth promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water stressed plants. *Funct Plant Biol* 35:141–151
- Lifshitz R, Kloepper JW, Scher FM, Tipping EM, Laliberte M (1986) Nitrogen-fixing pseudomonads isolated from roots of plants grown in the Canadian high arctic. *Appl Environ Microbiol* 51:251–255
- Madhaiyan M, Poonguzhalai 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
- Madigen Oren (1999) Thermophilic and halophilic extremophiles. *Curr Opin Microbiol* 2:265–269
- Marquez LM, Redman RS, Rodriguez RJ, Roosinck MJ (2007) A virus in a fungus in a plant: Three-way symbiosis required for thermal tolerance. *Science* 315(5811):513–515

- Marulanda A, Porcel R, Barea JM, Azcon R (2007) Drought tolerance and antioxidant activities in lavender plants colonized by native drought tolerant or drought sensitive *Glomus* species. *Microb Ecol* 54(3):543–552
- Mayak S, Tirosh T, Glick BR (2004) Plant growth promoting bacteria that confer resistance to water stress in tomato and pepper. *Plant Sci* 166:525–530
- 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
- Munchbach M, Nocker A, Narberhaus F (1999) Multiple small heat shock proteins in rhizobia. *J Bacteriol* 181:83–90
- Neto D, Carvalho LM, Cruz C, Martin-Loucao MA (2006) How do mycorrhizas affect C and N relationships in flooded *Aster trifolium* plants? *Plant Soil* 279:51–63
- Osundina MA (1998) Nodulation and growth of mycorrhizal *Casuarina equisetifolia* J R and G. First in response to flooding. *Biol Fert Soil* 26:95–99
- Pfeiffer CM, Bloss HE (1987) Growth and nutrition of guayule (*Parthenium argentatum*) in a saline soil as influenced by vesicular-arbuscular mycorrhiza and phosphorous fertilization. *New Phytol* 108:315–343
- Porcel R, Aroca R, Cano C, Bago A, Ruiz-Lozano JM (2006) Identification of a gene from the arbuscular mycorrhizal fungus *Glomus intraradices* encoding for a 14–3–3 protein that is up-regulated by drought stress during the AM symbiosis. *Microb Ecol* 52(3):575–582
- Porras-Alfaro A, Herrera J, Sinsabaugh RL, Odenbach KJ, Lowrey T, Natvig DO (2008) Novel root fungal consortium associated with a dominant desert grass. *Appl Environ Microbiol* 74(4):2805–2813
- Redman RS, Freeman S, Clifton DR, Morrel J, Brown G, Rodriguez RJ (1999) Biochemical analysis of plant protection afforded by a nonpathogenic endophytic mutant of *Colletotrichum magna*. *Plant Physiol* 119:795–804
- Redman RS, Sheehan KB, Stout RG, Rodriguez RJ, Henson JM (2002) Thermotolerance generated by plant/fungal symbiosis. *Science* 298:1581
- Roberson E, Firestone M (1992) Relationship between desiccation and exopolysaccharide production in soil *Pseudomonas* sp. *Appl Environ Microbiol* 58:1284–1291
- Rodriguez AA, Stella AM, Storni MM, Zulpa G, Zaccaro MC (2006) Effect of cyanobacterial extracellular products and gibberellic acid on salinity tolerance in *Oryza sativa* L. *Saline Sys* 2:7. doi: 10.1186/1746-1448-2-7
- Rosendahl CN, Rosendahl S (1991) Influence of vesicular-arbuscular mycorrhiza (*Glomus* sp.) on the response of cucumber (*Cucumis sativus* L.) to salt stress. *Environ Exp Bot* 31:313–318
- Ruiz-Lozano JM, Azcon R (2000) Symbiotic efficiency and infectivity of an autochthonous arbuscular mycorrhizal *Glomus* sp. from saline soils and *Glomus deserticola* under salinity. *Mycorrhiza* 10:137–143
- Rutto KL, Mizutani F, Kadoya K (2002) Effect of root-zone flooding on mycorrhizal and non-mycorrhizal peach (*Prunus persica* Batsch) seedlings. *Sci Hortic* 94:285–295
- Ryu CM (2004) Bacterial volatiles induce systemic resistance in *Arabidopsis*. *Plant Physiol* 134:1017–1026
- Saint-Etienne S, Paul S, Imbert D, Dulorme M, Muller F, Toribio A, Plenquette C, Ba AM (2006) Arbuscular mycorrhizal soil infectivity in a stand of the wetland tree *Pterocarpus officinalis* along asalinity gradient. *For Ecol Manag* 232:86–89
- 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
- Sandhya V, Ali SZ, Grover M, Kishore N, Venkateswarlu B (2009a) *Pseudomonas* sp. strain P45 protects sunflowers seedlings from drought stress through improved soil structure. *J Oilseed Res* 26:600–601
- Sandhya V, Ali SkZ, Grover M, Reddy G, Venkateswarlu B (2009b) Alleviation of drought stress effects in sunflower seedlings by exopolysaccharides producing *Pseudomonas putida* strain P45. *Biol Fert Soil* 46:17–26
- Saravanakumar D, Samiyappan R (2007) Effects of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase from *Pseudomonas fluorescens* against saline stress under in vitro and field conditions in groundnut (*Arachis hypogaea*) plants. *J Appl Microbiol* 102:1283–1292
- 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
- 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, Mishra PK, Bisht JP, Gupta HS (2009) Mountain aspects influence the genetic clustering of psychrotolerant phosphate solubilizing *Pseudomonads* in the Uttarkhand Himalayas. *Curr Microbiol* 59:432–438
- Sheramati I, Tripathi S, Varma A, Oelmuller R (2008) The root-colonizing endophyte *Piriformaspora indica* confers drought tolerance in *Arabidopsis* by stimulating the expression of drought stress-related genes in leaves. *Mol Plnt Microbe Interact* 21(6):799–807
- Smirnoff N, Cumbe QJ (1989) Hydroxyl radical scavenging activity of compatible solutes. *Phytochemistry* 28:1057–1060
- Srivastava S, Yadav A, Seem K, Mishra S, Chaudhary V, Srivastava CS (2008) Effect of high temperature on *Pseudomonas putida* NBRI0987 biofilm formation and expression of stress sigma factor RpoS. *Curr Microbiol* 56(4):453–457
- 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
- Suarez R, Wong A, Ramirez M, Barraza A, OrozcoMdel C, Cevallos MA, Lara M, Hernandez G, Iturriaga G (2008) Improvement of drought tolerance and grain yield in common bean by over-expressing trehalose-6-phosphate synthase in rhizobia. *Mol Plant Microbe Interact* 21(7):958–966
- Subramanian KS, Charest C (1998) Arbuscular mycorrhizae and nitrogen assimilation in maize after drought and recovery. *Physiol Plant* 102:285–296
- Tilak KVBR, Ranganayaki N, Pal KK, De R, Saxena AK, Nautiyal CS, Mittal S, Tripathi AK, Johri BN (2005) Diversity of plant growth and soil health supporting bacteria. *Curr Sci* 89(1):135–150
- Timmusk S (2003) Mechanism of action of the plant growth promoting Bacterium *Paenibacillus polymyxa*. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 908. Acta Univ Upsaliensis Uppsala, Sweden, pp 40
- 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

- Tisdall JM, Oadea JM (1982) Organic matter and water stable aggregates in soils. *J Soil Sci* 33:141–163
- Upadhyay SK, Singh DP, Saikia R (2009) Genetic diversity of plant growth promoting rhizobacteria from rhizospheric soil of wheat under saline conditions. *Curr Microbiol* 59(5):489–496
- Venkateswarlu B, Shanker AK (2009) Climate change and agriculture: adaptation and mitigation strategies. *Indian J Agron* 54:226–230
- Venkateswarlu B, Desai S, Prasad YG (2008) Agriculturally important microorganisms for stressed ecosystems: Challenges in technology development and application". In: Khachatourians GG, Arora DK, Rajendran TP, Srivastava AK (eds) Agriculturally important Microorganisms, vol 1. Academic World, Bhopal, pp 225–246
- Vriezen JAC, Bruijn de FJ, Nusslein K (2006) Desiccation responses and survival of *Sinorhizobium meliloti* USDA 1021 in relation to growth phase, temperature, chloride and sulfate availability. *Letters Appl Microbiol* 42:17178
- Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, Fischer M, Heier T, Huckelhoven R, Neumann C, Von Wettstein D, Franken P, Kogel KH (2005) The endophytic fungus *Piriformis indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proc Natl Acad Sci* 102:13386–13391
- Wahid A, Close TJ (2007) Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. *Biol Plant* 51:104–109
- Wu QS, Xia RX (2005) Effects of AM fungi on drought tolerance of citrus grafting seedling trifoliolate orange/cara cara. *Ying Yong Shen Tai Xue Bao* 16(5):865–869
- 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
- Yang J, Kloepper JW, Ryu CM (2009) Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci* 14:1–4
- Yildirim E, Taylor AG (2005) Effect of biological treatments on growth of bean plans under salt stress. *Ann Rep Bean Improv Coop* 48:176–177
- Zahir ZA, Munir A, Asghar HN, Arshad M, Shahroona B (2008) Effectiveness of rhizobacteria containing ACC-deaminase for growth promotion of peas (*Pisum sativum*) under drought conditions. *J Microbiol Biotech* (in press)
- Zahran HH (1999) *Rhizobium*-Legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. *Microbiol Molec Biol Rev* 3(4):968–989
- Zhang H et al (2008) Soil bacteria confer plant salt tolerance by tissue-specific regulation of sodium transporter HKT1. *Mol Plant Microbe Interact* 21:737–744