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Soil Bacteria Support and Protect Plants Against Abiotic Stresses

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1. Introduction

Numerous stresses caused by complex environmental conditions, e.g. bright light, UV, too high and low temperatures, freezing, drought, salinity, heavy metals and hypoxia, lead to substantial crop losses worldwide (Boyer, 1982; Mahajan & Tuteja, 2005; Mittler, 2006;). These abiotic stresses might increase in the near future even because of global climate change (http://www.ipcc.ch). Among the abiotic factors that are shaping plant evolution, water availability is the most important (Kijne, 2006). Water stress in its broadest sense encompasses both drought and salt stress. Soil salinity affects extensive areas of land in both developed and developing countries. The agricultural intensification, together with unfavourable natural conditions, has accelerated soil salinity in many part of the world. According to the FAO Land and Plant Nutrition Management Service, over 6% of the world's land is *salt-affected* (Table 1).

Regions	Total area (Mha)	Saline soils		Sodic soil	
		Mha	%	Mha	%
Africa	1,899	39	2.0	34	1.8
Asia, the Pacific and Australia	3,107	195	6.3	249	8.0
Europe	2,011	7	0.3	73	3.6
Latin America	2,039	61	3.0	51	2.5
Near East	1,802	92	5.1	14	0.8
North America	1,924	5	0.2	15	0.8
Total	**12,781**	**397**	**3.1**	**434**	**3.4**

Source: FAO Land and Plant Nutrition Management Service.

Table 1. Regional distribution of salt-affected soils, in million hectares

The term *salt-affected* refers to soil that are saline or sodic (Szabolcs, 1989). Saline soil has an excess of soluble salt in the soil solution, the liquid located between aggregates of soil. A sodic soil has too much sodium associated with the negatively charged clay particles. Salinity occur thought natural or human-induced processes that result in the accumulation of dissolved salts in the soil water to an extent that inhibits plant growth. Natural salinity

results from the accumulation of salts over long period of time and is caused by two natural processes. The first is the weathering process that breaks down rock and release soluble salts of various type, mainly chloride of sodium, calcium and magnesium, and to a lesser extent, sulphates and carbonates. Sodium chloride is the most soluble salt. The second is the deposition of oceanic salt carried in wind and rain. Human-induced salinity results from human activity that change the hydrologic balance of the soil between water applied (irrigation or rainfall) and water used by crops (transpiration). The most common causes are (i) land clearing and the replacement of perennial vegetation with annual crops, and (ii) irrigation schemes using salt-rich irrigation water or having insufficient drainage (Munns & Tester, 2008).

Compared to salt stress, the problem of drought is even more pervasive and economically damaging. Nevertheless, most studies on water stress signalling have focused on salt stress primarily because plant responses to salt and drought are closely related and the mechanisms overlap. Salt and drought stresses affect virtually every aspect of plant physiology and metabolism. Although some of the changes observed under these stresses are adaptive, many may be consequences of stress injury (Mahajan & Tuteja, 2005).

Water deficit and salinity disrupt photosynthesis and increase photorespiration, altering the normal homeostasis of cells and cause an increased production of Reactive Oxygen Species (ROS) such as the super oxide radical, hydrogen peroxide and hydroxyl radical (Miller et al., 2010). Under optimal growth conditions, ROS are mainly produced at low level in organelles such as chloroplasts, mitochondria and peroxisomes (Apel & Hirt, 2004). The enhanced production of ROS during stress can pose a threat to cells but it is though that ROS also act as signals for the activation of stress-response and defence pathways (Pitzschke et al., 2006).

The direct effects of salt on plant growth also involve nutrient imbalance caused by the loss of control on nutrient uptake and/or transport to the shoot leading to ion deficiencies (Munns, 2002).

The main reason for these nutrient deficiencies can be related to the abundant presence of ions, like Na^+ and Cl^-, in the soil solution. Abundance of these soluble ions can decrease the activity of other essential elements in the soil and can lead to reduction in accessibility and uptake of some elements by the plants. Several studies show that plants exposed to environmental stresses require additional supplies of mineral nutrients to minimize the adverse effects of stress (Endris & Mohammed, 2007; Heidari & Jamshid, 2010; Kaya et al., 2002; Khayyat et al., 2007;). In particular, it is known that salt stress causes reduction in P accumulation in plants, which developed P-deficiency symptoms. The addition of soluble P to saline growth medium increased crop growth and yield (Awad et al., 1990; Grattan and Grieve, 1999; Mohammad et al., 1998; Naheed et al., 2008; Satti & Al-Yahyai, 1995).

To deal with saline soil and minimize crop loss, scientists have searched for salt-tolerant cultivars, and have attempted to develop salt-tolerant crops through breeding (Araus et al., 2008; Dwivedi et al., 2010; Sreenivasulu et al., 2007; Witcombe et al., 2008). However, gaps in understanding the complex physiological, biochemical, developmental, and genetic mechanisms that underlie environmental stress tolerance, and the subsequent difficulty in combining favourable alleles to create improved high yielding genotypes, are the major constraint to improve crop yield under abiotic stress. Furthermore, it appears certain that domestication has narrowed the genetic diversity within crops for stress tolerance, and thus limited options in traditional crop breeding.

To overcome salinity effects, scientists are also using transgenic approaches to obtain genetically modified plants (Ashraf & Akram, 2009; Mittler & Blumwald, 2010; Valliyodan & Nguyen, 2006; Vinocur & Altman, 2005; Zhang et al., 2000). These approaches are time consuming and costly due to the impressive charges required to validate the consumption or cultivation of genetically modified plants. Indeed, the development of transgenic plants with increased stress tolerance is primarily based on the performance of transgenic lines produced and tested under controlled conditions as greenhouse, and can be found only few reports where the performance of transgenic cultivars was tested under field conditions. Several factors limit the success of producing salt-tolerant cultivars through genetic engineering. 1) In most cases only a single gene has been transformed, although salt stress resistance is polygenic. If, for example, osmoprotectant-producing, transcription factor-expressing, ion homeostasis-maintaining, and antioxidant enzymatic activities are all incorporated into a single species, there is a strong possibility that all these activities could work in concert to overcome concurrently present abiotic stresses. Transforming recipient plants with many genes or crossing plants containing different stress tolerance genes is very time consuming. 2) Transformation of agronomic important crops and identification of uncovered tolerance determinants or stress inducible promoters that direct the expression at proper time and place must be further explored to maximize salt tolerance.

Plants in their natural environment are colonized both by endocellular and intracellular microorganisms (Gray & Smith, 2005). Rhizosphere microorganisms, particularly beneficial bacteria and fungi, can improve plant performance under stress environments and, consequently, enhance yield both directly and indirectly (Dimkpa et al., 2009a). Some plant growth-promoting rhizobacteria (PGPR) may exert a direct stimulation on plant growth and development by providing plants with fixed nitrogen, phytohormones, iron that has been sequestered by bacterial siderophores, and soluble phosphate (Hayat et al., 2010; Rodriguez & Fraga, 1999). Others do this indirectly by protecting the plant against soil-borne diseases, most of which are caused by pathogenic fungi (Lugtenberg & Kamolova, 2009). Common adaptation mechanisms of plants exposed to environmental stresses, such as temperature extremes, high salinity, drought and nutrient deficiency, or heavy metal toxicity, include changes in root morphology (Potters et al., 2007), a process in which phytohormones are known to play a key role (Spaepen et al., 2007; Spaepen & Vanderleyden, 2010). The majority of root associated bacteria that display beneficial effects on plant growth produce indole-3-acetic acid (IAA) (Hayat et al., 2010). Inoculation of various plant species with such bacteria lead to increased root growth and/or enhanced formation of lateral roots and root hairs that can result in enhanced tolerance to abiotic stress. Bacterial IAA production also stimulates the activity of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase involved in the degradation of the ethylene precursor ACC (Glick, 2005). ACC deaminase activity could be helpful in sustain plant growth and development under stress conditions by reducing stress-induced ethylene production. Modulation of other major plant hormones could improve crop salt tolerance by reducing the toxic effects of salinity (Bianco & Defez, 2009). A number of nitrogen-containing compounds accumulate in plants exposed to saline stress (Mansour, 2000; Parida & Das, 2005). The accumulation of the amino acid proline is one of the most frequently reported modifications induced by water and salt stress as well as other stresses in plants (Hare & Gress, 1997; Kavi Kishor, 2005; Verbruggen & Hermans, 2008). It has been found that Medicago plants infected by IAA-overproducing PGPR strains are able to overcome different stressful environmental conditions and accumulate high levels of proline. The increased expression levels of two genes involved in the first two steps of proline biosynthesis from glutamic acid confirmed these results (Bianco & Defez, 2009).

When plants are subjected to environmental stress conditions such as those listed above, the balance between the production of ROSs and the quenching activity of the antioxidants is upset, often resulting in oxidative damage (Jubany-Marì et al., 2010; Miller et al., 2010). Plants with high levels of antioxidants, either constitutive or induced, have been reported to have greater resistance to this oxidative damage (Ahmad et al., 2008; Kohler et al., 2008). The activities of the antioxidative enzymes such as catalase (CAT), ascorbate peroxidase (APX), guaicol peroxidase (POX), glutathione reductase (GR), and superoxide dismutase (SOD) increase under salt stress in plants, and a correlation between these enzyme levels and salt tolerance has been described (Apel & Hirt, 2004). It has been found that Medicago plants infected with IAA-overproducing PGPR strains showed high antioxidant enzymes activity which contributed to enhance plant protection against salt stress (Bianco & Defez, 2009).

Considering the positive effects of PGPR strains on different plant cultivars and lines grown under salt stress conditions, we propose that such bacteria might be tested in field trial offering an economical and simple treatment to salt sensitive plants.

A fruitful strategy to alleviate negative effects of salt stress in plants might be the co-inoculation of seeds with different PGPR species, such as *Rhizobium* and *Azospirillum*. Indeed, dual inoculation with *Rhizobium* and *Azospirillum* and other plant growth promoting rhizobacteria was shown to increase the total nodule number of several legumes, acetylene reduction activities, and the total N content of mineral macro- and micronutrients as compared to inoculation with *Rhizobium* alone (Burdman, 1996; Molla et al., 2001a; Remans et al., 2008b). The presence of *Azospirillum* in the rhizosphere was reported to elicit or activate the hydrolysis of conjugated phytohormones and flavonoids in the root tissue, thus bringing about the release of compounds in their active forms (Dardanelli et al., 2008; Saikia et al., 2010; Spaepen et al., 2007).

In addition, even under stress conditions, the use of PGPR inoculants in intercropping systems such as legume-cereal might contribute to the improvement of cereal crop yield that take advantage from the legume release of multiple nutrients and growth promoters (Banik et al., 2006; Dahmardeh et al., 2009; Davies et al., 2010; Dhima et al., 2007; Hauggaard-Nielsen et al., 2001; Javanmard et al., 2009; Tsubo et al., 2005; Li et al., 2006).

The objective of this synthesis paper is to review the pivotal role of plant growth-promoting bacteria in developing sustainable systems for crop production under abiotic stress conditions. In this review, much research information about salt-stress has been gathered because soil salinity, which limits crop yield and restricts use of land, is a major constrain to food production. We start by reviewing the root zone bacteria that have been found to possess plant growth-promoting properties. We then review how plant growth-promoting bacteria act as enhancers of the main biochemical and molecular mechanisms developed by plants to cope with salt stress. We then discuss the potential role that agronomic manipulations can play in ameliorating the impact of salinity stress on plants. The body of studies suggests that, under abiotic stress conditions, the use of improved PGPR inoculants might be advantageous for the development of sustainable agriculture in which yield losses are reduced and plant growth is improved.

2. Beneficial rhizobacteria

Populations of microorganisms live in close contact with the plants root zone called rhizosphere. Here the number of microorganisms is usually higher than in other soil area. Thus, the plant root is thought to be a major source of nutrients for microorganisms living in

the rhizosphere. Indeed, plants supply organic carbon to their surroundings in the form of root exudates and rhizobacteria respond to this exudation by means of chemotaxis towards the exudate source modulating their metabolism to optimize nutrient acquisition (Hardoim et al., 2008).

Soil bacteria beneficial to plant growth are usually referred to as plant growth promoting rhizobacteria (PGPR), capable of promoting plant growth by colonizing the plant root (Hayat et al., 2010). Bacteria of diverse genera such as *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas* and *Serratia* (Gray & Smith, 2005), as well as *Streptomyces* spp. (Dimkpa *et al.* 2008, 2009b; Tokala *et al.* 2002) were identified as PGPR.

According to their residing sites, PGPR can be divided in iPGPR, which live inside the plant cells and are localized in specialized structures, the so-called nodules, and ePGPR which live outside the plant cells and do not produce organs like nodules, but still prompt plant growth (Gray & Smith, 2005).

Although the exact mechanisms of plant growth stimulation remain largely speculative, possible explanation includes: (1) production of hormones like abscisic acid, gibberellic acid, cytokinins, and auxin, i.e IAA,; (2) production of essential enzymes, 1-aminocyclopropane-1-carboxylate (ACC) deaminase to reduce the level of ethylene in the root of developing plants; (3) nitrogen fixation; (4) production of siderophores; (5) solubilization and mineralization of nutrients, particularly mineral phosphate; (6) improvement of abiotic stresses resistance (Hayat et al., 2010).

3. Abiotic stresses in plant: Improving mechanisms of stress response by rhizobacteria

Dehydratation, salinity, low as well as high-temperature stresses and other abiotic stresses lead to metabolic toxicity, membrane disorganization, generation of ROS, inhibition of photosinthesis, reduced nutrient acquisition and altered hormones levels. Accumulation of osmoprotectants, production of superoxide radical scavenging mechanisms, exclusion or compartmentation of ions by efficient transporter and symporter systems, production of specific enzymes involved in the regulation of plant hormones are some of the mechanisms that plants have evolved for adaptation to abiotic stresses (Des Marais & Juenger, 2010; Mahajan & Tuteja, 2005; Parida & Das, 2005; Santner et al., 2009; Shao et al., 2009). Many studies have been published on beneficial effects of bacterial inoculation on plant physiology and growth under abiotic stress conditions and some examples are summarized in Table 2.

3.1 Phytohormones synthesis and modulation

Plants are sessile organisms with a high level of physiological plasticity, enabling survival under a wide variety of environmental insults. This is due to the continuously active shoot and root meristems and their capability to generate new organs after embryogenesis (Wolter & Jurgens, 2009). They have developed an extensive array of defensive responses that includes changes in the root morphology. The root architecture of the plants, which is determined by the pattern of root branching (lateral root formation) and by the rate and direction of growth of individual roots (Malamy, 2005), constitutes an important model to study how developmental plasticity is translated into growth responses under several environmental stresses. Morphogenesis is tightly linked to hormonal homeostasis, with several hormones controlling cell elongation, cell division and re-orientation of growth. The

Stress type	Bacterial inoculate	Plant Species	Reference
Salt	*Pseudomonas pseudoalcaligenes, Bacillus pumilus*	Rice (*Oryza sativa*)	Jha et al. (2010)
Salt	*Bacillus megaterium*	Maize (*Zea maize* L.)	Marulanda et al. (2010)
Salt	*Azospirillum brasilense*	Barley (*Hordeum vulgare*)	Omar et al. (2009)
Salt	*Pseudomonas mendocina*	Lettuce (*L. sativa* L. cv. Tafalla)	Kohler et al. (2009)
Salt	*Azospirillum* sp.	Pea (*Phaseolus vulgaris*)	Dardanelli *et al.* (2008)
Salt	*Bacillus subtilis*	*Arabidopsis thaliana*	Zhang et al. (2008)
Salt	*Pseudomonas syringae, Pseudomonas fluorescens, Enterobacter aerogenes*	Maize (*Zea maize*)	Nadeem *et al.* (2007)
Salt	*P. fluorescens*	Groundnut (*Arachis hypogaea*)	Saravanakumar & Samiyappan (2007)
Salt	*Azospirillum*	Lettuce (*Lactuca sativa*)	Barassi *et al.* (2006)
Salt	*Achromobacter piechaudii*	Tomato (*Lycopersicon esculentum*)	Mayak et al. (2004)
Salt	*Aeromonas hydrophila/caviae Bacillus insolitus, Bacillus* sp.	Wheat (*Triticum aestivum*)	Ashraf *et al.* (2004)
Salt	*Azospirillum*	Maize (*Z. maize*)	Hamdia et al. (2004)
Salt	*A. brasilense*	Chickpeas (*Cicer arietinum*), faba beans (*Vicia faba* L.)	Hamaoui *et al.* (2001)
Drought	*Pseudomonas spp.*	Maize (*Zea mays* L. cv. Kaveri)	Sandhya et al. (2010)
Drought	*Pseudomonas spp.*	Asparagus (*Asparagus officinalis* L.)	Liddycoat et al. (2009)
Drought	*Pseudomonas mendocina*	Lettuce (*Lactuca sativa* L.)	Kohler et al. (2008)
Drought	*Rhizobium tropici, Paenibacillus polymyxa*	Common bean (*Phaseolus vulgaris* L.)	Figueiredo et al. (2008)
Drought	*Bacillus*	Lettuce (*Lactuca sativa* L.)	Arkhipova et al. (2007)
Drought	*Ensifer meliloti* bv. *mediterranense*	Bean (*Phaseolus vulgaris* cv. Flamingo)	Mnasri et al. (2007)
Drought	*Bradyrhizobium elkanii*	Flat crown (*Albizia adianthifolia*)	Swaine et al. (2007)
Drought	*Achromobacter piechaudii*	Tomato (*L. esculentum*), pepper (*Capsicum annuum*)	Mayak et al. (2004)
Drought	*Azospirillum*	Wheat (*T. aestivum*)	Creus et al. (2004)
Drought	*A. brasilense*	Maize (*Z. mays*)	Casanovas et al. (2002)
Drought	*A. brasilense*	Common bean (*P. vulgaris*)	German *et al.* (2000)
Osmotic stress	*Bacillus subtilis*	*Arabidopsis*	Zhang et al. (2010)
Osmotic stress	*A. brasilense*	Rice (*Oryza sativa* L.)	Cassan et al. (2009)
Osmotic stress (45% PEG)	*Arthrobacter* sp., *Bacillus* sp.	Pepper (*C. annuum*)	Sziderics *et al.* (2007)
Osmotic stress (20% PEG)	*Azospirillum*	Wheat (*T. aestivum*)	Pereyra et al. (2006)
Flooding	*Enterobacter cloacae, Pseudomonas putida*	Tomato (*L. esculentum*)	Grichko and Glick (2001)
Temperature	*Burkholderia phytofirmans*	Grapevine (*Vitis vinifera*)	Barka et al. (2006)
Temerature	*Pseudomonas fluorescens, Pantoea agglomerans, Mycobacterium* sp.	Wheat (*Triticum aestivum*)	Egamberdiyeva & Hoflich (2003)
Temperature	*B. phytofirmans*	Potato (*Solanum tuberosum*)	Bensalim et al. (1998)

Stress type	Bacterial inoculate	Plant Species	Reference
Temperature	*Aeromonas hydrophila, Serratia liquefaciens, Serratia proteamaculans*	Soy bean (*Glycine max*)	Zhang *et al.* (1997)
Temperature	*Burkholderia phytofirmans*	Grapevine (*Vitis vinifera*)	Barka et al. (2006)
Temperature	*B. phytofirmans*	Potato (*Solanum tuberosum*)	Bensalim et al. (1998)
Temperature	*Aeromonas hydrophila, Serratia liquefaciens, Serratia proteamaculans*	Soy bean (*Glycine max*)	Zhang *et al.* (1997)
Nutrient deficiency	*Azospirillum* sp., *Azotobacter chroococcum, Mesorhizobium ciceri, Pseudomonas fluorescens*	Chickpea (*Cicer arietinum* L.)	Rokhzadi & Toashih (2011)
Nutrient deficiency	*Azotobacter coroocoocum, Azospirillum brasilens, Pseudomonas putida, Bacillus lentus*	*Zea maize* L. (*Zea maize* L.)	Yazdani et al. (2009)
Nutrient deficiency	*Bacillus* sp., *Burkholderia* sp., *Streptomyces platensis*	*Zea maize* L.	Oliveira et al. (2009)
Nutrient deficiency	*Bacillus* sp.,	*Zea maize* L.	Adesemoye et al. (2008)
Nutrient deficiency	*Bacillus polymyxa, Mycobacterium phlei, Pseudomonas alcaligenes*	*Zea maize* L. (*Zea maize* cv. Felix)	Egamberdiyeva (2007)
Heavy metals toxicity	*Sanguibacter* sp., *Pseudomonas* sp.	*Nicotina tabacum*	Mastretta et al. (2009)
Heavy metals toxicity	*Bacillus subtilis, Pantoea agglomerans*	Oat (*Avena sativa*)	Pishchik et al. (2009)
Heavy metals toxicity	*Pseudomonas fluorescens, Microbacterium* sp.	Rape (*Brassica napus*)	Sheng et al. (2008)
Heavy metals toxicity	*Methylobacterium oryzae, Burkholderia* sp.	Tomato (*Lycopersicon esculentum* L.)	Madhaiyan et al. (2007)
Heavy metals toxicity	*Bacillus subtilis, Bacillus megaterium, Bacillus* sp.	Rice (*O. sativa*)	Asch & Padham (2005), Terré et al. (2007)

Table 2. Bacterially mediated plant tolerance to abiotic stress. Some of the data reported in this Table were adapted from Dimkpa et al. (2009a), whereas recent publications have been included *de novo*.

physiologically most active auxin in plants is indole-3-acetic acid (IAA), and the fact that no fully auxin-deficient mutant plants have been identified so far reflects the importance of auxin in plant development. There is a high capacity for auxin biosynthesis not only in young aerial tissues, but also in roots, particularly in the meristematic primary root tip (Teale et al., 2006). Auxin, and its fine concentration gradients have powerful effects on plant development and in particular on lateral root formation and branching, two key components of the response phenotype induced in plants under stress conditions (Potters et al., 2007, 2009). Alteration in the pattern of lateral root formation and emergence in response to P availability is mediated by changes in auxin sensitivity in *Arabidopsis thaliana* roots. These changes alter the expression of auxin-responsive genes and stimulate pericycle cells to proliferate (Pérez-Torres et al., 2008).

Exogenous auxin application results in formation of branched root and, similarly, mutants that accumulate high levels of auxin, or mutants with an altered auxin distribution, produce excess of lateral roots. A broad range of abiotic stresses induce lateral root formation, therefore auxin may be an intermediate between the action of a stressor and the realization of response phenotype. Several mechanisms have been proposed to explain stress-induced changes in auxin metabolism and/or receptiveness; however, evidences for stress-induced changes in auxin transport and catabolism are predominantly found in literature. For example, water and osmotic stresses impact on auxin transport by altering the expression of PIN genes and/or by inhibition of polar auxin transport (Potters et al., 2009). Moreover, auxin conjugates and the respective hydrolases were shown to be involved in the reaction of plant to stress (Muller, 2011). Interestingly, overexpression of an auxin-amidohydrolase in *Arabidopsis* is associated with a reduced inhibition of root elongation and increased resistance to salt stress. This effect was probably due to the increase in the content of free auxin sufficiently to provide a protective effect against salt stress (Junghans et al., 2006).

As more plant tissues are analyzed for the presence of bacteria, an increased number of IAA-producing PGPR strains are detected inside the plant tissue (Spaepen et al., 2007). Various plant species inoculated with such bacteria showed increased root growth and/or enhanced formation of lateral roots and roots hairs (Dimkpa et al., 2009a). For example, the stimulatory effect of *Azospirillum* strains on the development of roots is well documented. Morphological plant root changes have been observed repeatedly upon *Azospirillum* inoculation and have been attributed to the production of plant-growth promoting substances: auxins, cytokinins and gibberellins, with auxin production being quantitatively the most important (Spaepen et al., 2008). Specific evidences for the involvement of auxins produced by *Azospirillum* in roots proliferation were obtained in many cases. Addition of filter-sterilized culture supernatants of *A. brasiliense* to rice roots grown in hydroponic tanks increased root elongation, root surface area, root dry matter, and development of lateral roots and root hairs, compared with untreated roots (El-Khawas & Adachi, 1999). Similarly, a cell-free supernatant of *A. brasiliense* Cd applied to soybean plants induced many roots and increased root length (Molla et al., 2001a). Exogenous application of IAA to bean roots resembled responses of these plants to inoculation with *Azospirillum* (Remans et al., 2008a). More direct evidence for the importance of IAA was provided when several IAA-attenuate mutants were compared with their parental wild types for their effect on plant growth. A mutant of *A. brasiliense* with low production of phytohormones, but high N_2-fixing activity, did not enhance root growth over uninoculated controls (Kundu et al., 1997).

Considering the relationship between IAA and ethylene precursor ACC (Dimkpa et al., 2009a), the positive effects of IAA on root growth can be either direct or indirect through the reduction of ethylene levels (Lugtenberg & Kamilova, 2009).

Indeed, under stress conditions, including drought and salinity, the plant hormone ethylene endogenously regulates plant homeostasis and results in reduced root and shoot growth.

It has been shown that plants produce ethylene at two different phases in response to stressful stimuli. In the first phase, the small amount of ethylene produced promotes the activity of stress-related genes. In the second phase (1–3 days after stimulus application) the larger amount of ethylene produced lead to inhibition of growth and harmful effects on plants including senescence, chlorosis, and abscission (Glick et al., 2007).

Degradation of the ethylene precursor ACC into 2-oxobutanoate and ammonia by bacterial ACC-deaminase lowers the ethylene concentration in plant roots, relieves the ethylene repression of auxin response factors synthesis, and indirectly increases plant growth (Glick

et al., 2007; Kang et al., 2010). It has been proposed that ACC might be exuded from plant roots and that soil bacteria containing ACC-deaminase could convert this for their growth. As result, the hydrolyzed ACC products would enhance bacterial growth. Taken together, the ACC-deaminase function seems to be mutually beneficial between plants and PGPR, because ethylene in plants can be reduced by continuous ACC secretion and degradation by bacteria, and bacteria can use metabolized ACC (Glick et al., 1998).

ACC deaminase-containing PGPR strains have found practical application in protecting different plant species against growth inhibition caused by various environmental stresses. Mayak et al. (2004) reported that *Achromobacter piechaudii* having ACC deaminase activity significantly increased the fresh and dry weights of tomato seedlings grown in the presence of NaCl salt (up to 172 mM). *Pseudomonas fluorescens* strain TDK1 containing ACC deaminase activity enhanced the saline resistance in groundnut plants and increased yield as compared to plants inoculated with *Pseudomonas* strains lacking ACC deaminase activity (Saravanakumar & Samiyappan). *Pseudomonas putida* UW4, which produces IAA and ACC deaminase, protected canola seedling from growth inhibition by high levels of salt. 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 (Kausar & Shahzad, 2006). Inoculation with *Pseudomonas* spp. containing ACC-deaminase partially eliminates the effects of drought stress on growth, yield, and ripening of pea (*Pisum sativum* L.) (Arshad et al., 2008). Nadeem et al. (2010) reported that rhizobacteria capable of producing ACC deaminase mitigate salt stress in wheat.

We also analysed the growth of *Medicago truncatula* plants nodulated by *Sinorhizobium meliloti* strains under severe salt stress conditions. Medicago plants nodulated by the IAA-overproducing RD64 strain (*Mt*-RD64) showed a phytohormones re-modulation, with a higher IAA content in nodules and roots and a reduced accumulation of IAA in the shoot strain as compared to plants nodulated by the wild-type strain 1021 (*Mt*-1021). Transcriptional analysis of the main ethylene signalling genes showed that, when compared to *Mt*-1021 plants, *Mt*-RD64 plants did not showed and induction of this pathway when 150 mM NaCl was applied, which means less plants stress damages (Bianco & Defez, 2009).

3.2 Accumulation of protective compounds

Several studies correlated accumulation of nitrogen-containing compounds (NCC) with drought and salt tolerance in plants (Parida & Das, 2005). The most frequently accumulating NCC includes amino acids, amides, imino acids, proteins, quaternary ammonium compounds and polyamines.

Very high accumulation of cellular proline (up to 80% of the amino acids pool under stress and 5% under normal conditions) due to increased synthesis and decreased degradation under a variety of stress conditions such as salt and drought has been documented in many plant species (Szabados & Savourè, 2009). Several comprehensive studies using transgenic plants or mutants demonstrate that proline metabolism has a complex effect on development and stress responses. Proline has been proposed to act as a compatible osmolyte and to be a way to store carbon and nitrogen. Saline and drought are known to induce oxidative stress. Several studies showed that proline may have an antioxidant activity acting as a ROS scavenger. Proline may also function as molecular chaperones able to stabilize the structures of proteins and enhance the activity of different enzymes, and its

accumulation play a role in maintenance of cytosolic pH and regulation of intracellular redox potential (Hare & Cress, 1997; Kavi Kishor et al., 2005; Verbruggen & Hermans, 2008). Under abiotic stress conditions, increased proline biosynthesis was observed for various plant species inoculated with different PGPR (Barka et al., 2006; Jha et al., 2010; Kohler et al., 2009; Sandhya et al., 2010; Vardharajula et al., 2011). The synthesis of proline as well as other compatible solutes require an energy cost (41 moles of ATP) and occur at the expense of plant growth, but may allow the plant to survive and recover from the presence of high external salt concentration (Munns & Tester, 2008).

We found a significant correlation between reduced symptoms of senescence, such as chlorosis, necrosis and drying, and 2-fold increased proline content in the shoot of *Mt*-RD64 as compared to *Mt*-1021 plants, after exposure to 150 mM NaCl (Bianco & Defez, 2009).

3.3 Biosynthesis of antioxidative enzymes

In plants ROS such as superoxide ($\cdot O_2$-), hydrogen peroxide (H_2O_2), hydroxyl radical ($\cdot OH$), and singlet oxygen ($^1O_2$) are continuously produced as byproducts of various metabolic pathways localized in different cellular compartments (Apel & Hirt, 2004). A common feature of these species is their capacity to cause oxidative damage to proteins, DNA, and lipids. Since internal O_2 concentrations are high during photosynthesis, chloroplasts are especially prone to generate activated oxygen species (Gill & Tuteja, 2010). Under physiological steady-state conditions, these molecules are scavenged by different anti-oxidative defence components that are often confined to particular compartments (Apel & Hirt, 2004). Under normal growth conditions, the production of ROS in cells is low, whereas, during stress their rate of production is enhanced. ROS accumulation during stress results from the imbalance between production and scavenging of ROS. Major ROS-scavenging mechanisms of plants include SOD, APX and CAT enzymes. Antioxidants such as ascorbic acid and glutathione, which are found in high concentration in chloroplasts and other cellular compartments, are also crucial for plant defence against oxidative stress (Miller et al., 2010). For the detoxification of excess ROS in plant, the overall balance between different antioxidants is crucial for determining the steady-state level of superoxide radicals and hydrogen peroxide, and has to be tightly controlled (Mittler, 2002).

Induction of antioxidant enzymes (catalase and total peroxidase) is involved in the alleviation of salinity stress in lettuce plants inoculated with PGPR strains (Kohler et al., 2010). Under non-saline conditions, inoculation with *Pseudomonas mendocina* and fertilization led to similar increases in plant growth (about 30% greater than the control plants). Salinity decreased the dry weight of the shoots and roots for all lettuce plants. However, the plants inoculated with *P. mendocina* had significantly greater shoot biomass than the control plants at both medium and high salinity levels. We reported that salt-stressed *Mt*-RD64 plants showed much less oxidative damage (reduced chlorosis, necrosis, and drying) compared with salt-stressed *Mt*-1021 plants. These effects were connected to the enhanced activity of the antioxidant enzymes SOD, APX, GR and POX (Bianco & Defez, 2009).

Recent study reports the potential of PGPR strains in alleviating drought stress effects in maize. Maize plants inoculated with five drought tolerant plant growth promoting *Pseudomonas* spp. strains namely *P. entomophila*, *P. stutzeri*, *P. putida*, *P. syringae*, and *P. montelli* were subjected to drought stress and the effects of inoculation on growth, osmoregulation and antioxidant status was investigated. Inoculated plants showed significantly lower activity of antioxidant enzymes plants as compared to uninoculated

plants (Sandhya et al. 2010). Reduction in the activity of antioxidant enzymes was also observed in barley plants. Omar et al. (2009) reported that, without inoculation, salinity led to a significant increase of catalase and peroxidase activities in salt-stressed leaves of two barley cultivars differing in salinity tolerance. Inoculation of the two cultivars with *Azospirillum brasilense* lowered the magnitude of increase and significantly ameliorated the deleterious effects of salinity improving crop productivity.

These results, which apparently seem to be in contradiction with the assumption that stress resistance in plants is related to more effective antioxidant systems, are an implication of the same positive effect and indicate that inoculated plants felt less stress as compared to uninoculated plants.

3.4 Enhancement of nutrients up-take

Survival and productivity of crop plants exposed to environmental stresses are dependent on their ability to develop adaptive mechanisms to avoid or tolerate stress (Munns & Tester, 2008). Accumulating evidence suggests that mineral nutritional status of plants greatly affects their ability to adapt to adverse environmental conditions and in particular to abiotic stress factors. Impairment of the mineral nutrition status of plants exacerbates the adverse effects of abiotic stresses and the exogenous addition of high levels of macronutrients can alleviate the adverse effects of stress on plant growth (Baligar et al., 2001; Endris & Mohammed, 2007; Grattan & Grieve, 1999; Heidari & Jamshid, 2010; Kaya et al., 2001; Kaya et al., 2002; Khoshgoftarmanesh et al., 2010).

After nitrogen, phosphorous is the second major nutrient for plant growth as it is an integral part of different biochemicals like nucleic acids, nucleotides, phospholipids and phosphoproteins. In most cases salinity decreased P accumulation in plant, which developed P-deficiency symptoms (Martinez & Lauchli, 1994; Navarro et al., 2001; Parida & Das, 2004; Rogers et al., 2003). The reduction in P availability in saline soils was suggested to be a result of ionic strength effects that reduce the activity of phosphate and the tight control of P concentrations by sorption processes and by low solubility of Ca-P minerals. The concentration of soluble P in soil is usually very low (1 ppm or less) (Hinsinger, 2001). The cell might take up several P forms but the major part is adsorbed in the forms of HPO_4^{-2} or $H_2PO_4^{-1}$. Phosphorus exists in two forms in soil, as organic and inorganic phosphate, and like other nutrient elements such as potassium, iron, zinc and copper, possesses limited mobility in the soil (Hayat et al., 2010; Rodrìguez & Fraga, 1999). The conversion of insoluble phosphate compounds (both organic and inorganic) in a form accessible to the plant is an important trait of PGPR strains. PGPR strains belonging to various genera have the ability to solubilize insoluble inorganic phosphate compounds such as tricalcium phosphate, dicalcium phosphate, hydroxyapatite, and rock phosphate (Richardson et al., 2009; Khan et al., 2009; Rodrìguez & Fraga, 1999).

It is generally accepted that the major mechanism of mineral phosphate solubilization is the action of organic acids synthesized by soil microorganisms (Rodrìguez & Fraga, 1999). Production of organic acids results in acidification of the microbial cell and its surroundings. Consequently, P may be released from a mineral phosphate by proton substitution for Ca^{2+}. The production of organic acids has been well documented for different PGPR genera such as *Pseudomonas*, *Erwinia*, *Rhizobium* and *Bacillus* (Rogrìguez & Fraga, 1999).

As discussed previously, soil contains a wide range of organic substrates, which can be a source of P for plant growth. To make this form of P available for plant nutrition, it must be hydrolyzed to inorganic P. Mineralization of most organic phosphorous compounds is

carried out by means of phosphatase enzymes (phosphohydrolases). Considering that the pH of most soils ranger from acid to neutral values, acid phosphatases should play the major role in this process (Rogrìguez & Fraga, 1999).

Under P-limiting conditions, the IAA-overproducing RD64 strain showed high P-mobilizing activity that is connected to the synthesis of high levels of acid phosphatase enzymes and the secretion into the growth medium of malic, succinic, and fumaric acids in large quantities. As compared to *Mt*-1021 plants, *Mt*-RD64 plants released large amount of another P-solubilizing organic acid, 2-hydroxyglutaric acid and showed significant increase in both shoot and root fresh weights, when grown under P-deficient conditions (Bianco & Defez, 2010a).

4. Agronomic approaches for crop improvement under abiotic stress conditions

The increase in the frequency and severity of abiotic stresses is one of the main consequences of climate change. In particular, extreme weather events will result in more frequent drought and salinity.

To mitigate the effects of these stresses, appropriate crop management techniques will be needed to ensure sufficient production of food from crop plants by increasing the productivity per unit of land area. Several low-technology management systems, such as biofertilization (single or mixed inoculation treatments), crop rotation, intercropping, skip rows (decreasing planting density by omitting rows), mulching (with natural or synthetic mulches), and protected cropping (enclosing the aerial environment of the crop under glass, plastic or netting) can be used to improve crop productivity (Davies et al., 2010). The impact of two of the techniques described above is considered in the current review.

4.1 Co-inoculation of plant growth-promoting bacteria

Co-inoculation is based on mixed inoculants, combination of microorganisms that interact synergistically, or when microorganisms such as *Azospirillum* are functioning as "helper" bacteria to enhance the performance of other beneficial microorganisms. In the rhizosphere the synergism between various bacterial genera such as *Bacillus*, *Pseudomonas* and *Rhizobium* has been demonstrated to promote plant growth and development. Compared to single inoculation, co-inoculation improved the absorption of nitrogen, phosphorus and mineral nutrients by plants (Figueiredo et al., 2010; Yadegari et al., 2010). A significant increase in root and shoot biomass was observed in chickpea plants when co-inoculated with *Mesorhizobium* and *Pseudomonas* (Sindhu et al., 2002a, b). Increased nodule weight, root and shoot biomass and total nitrogen of chickpea plants was also reported due to co-inoculation of *Rhizobium*, *Pseudomonas* and *Bacillus* (Parmar & Dadarweal, 1999). Co-inoculation with *Bradyrhizobium japonicum* and *Pseudomonas fluorescens* increased colonization *B japonicum* on soybean roots, nodule number and acetylene reduction assay (Tchebotar et al., 1998). Combined inoculation of *Rhizobium* with *Pseudomonas striata* or *Bacillus megaterium* led to increased dry matter, grain yield and phosphorus uptake significantly over the uninoculated control in legumes (Elkoca et al., 2008). Verma et al. (2010) have reported the application of *Rhizobium* spp. and plant growth promoting rhizobacteria on nodulation, plant biomass and yields of chickpea plants. In field studies, the grain and straw yield were significantly increased in co-inoculation of *Rhizobium* with *P. fluorescens* followed by *B. megaterium* and *Azotobacter chroococcum* over uninoculated control. Co-inoculation of

Pseudomonas spp. with *Rhizobium* improves growth and symbiotic performance of fodder galega (Egamberdieva et al., 2010). The greenhouse experiment showed that co-inoculation of fodder galega with *R. galegae* and *P. trivialis* or with *R. galegae* and *P. extremorientalis* improved plant growth, nodulation and N content compared to plants inoculated with *R. galegae* alone in potting soil containing low levels of nitrogen. Co-inoculation of plants with *P. trivialis* and *R. galegae* showed the highest stimulatory effect.

The mechanisms behind these effects are only partially understood. One of the mechanisms used by these PGPR strains is the production of phytohormones such as auxins, gibberellins and cytokinins, which steadily contribute to the plant auxin "pool" in a way that the effect of PGPR inoculation can be mimicked by exogenous auxin application.

The endogenous IAA level in plant regulates growth of the shoots and roots, and in the case of legumes, nodules formation (Teale et al., 2006). It has been observed that low concentrations of exogenously given pure IAA stimulated shoot and root growth of wheat in non-saline and saline conditions, and similar effects were induced by IAA-producing PGPR strains (Egamberdieva, 2009).

Bacteria of the genus *Azospirillum* are free-living, surface colonizing and, sometimes, endophytic diazotroph and plant growth promoting rhizobacteria. *Azospirillum* strains had no preference for crop plants or weeds, or for annual or perennial plants, and can be successfully applied to plants that have no previous history of *Azospirillum* in their roots. Although reports about isolating *Azospirillum* from graminaceous plants are common, other reports showed that the bacterium is a natural inhabitant of many non-graminaceous plants. It appears that *Azospirillum* is a general root colonizer and is not a plants-specific bacterium (Bashan & Holguin, 1997). *Azospirillum* strains are capable of increasing yield of important crops growing in various soils and climatic regions. It has been reported that root elongation rate, mineral N, P and K and microelements uptake are consequently improved after *Azospirillum* inoculation (Bashan et al., 2004), even under stressful environmental conditions (Askary et al., 2009). Dual inoculation of legumes with *Rhizobium* and *Azospirillum* significantly increase several plant-growth variables when compared with single inoculations (Hamaoui et al., 2001; Itzigsohn et al., 2000; Remans et al., 2007; Remans et al., 2008b; Tchebotar et al., 1998). *Azospirillum* is considered a *Rhizobium* helper by stimulating nodulation, nodule function, and possibly plant metabolism (Molla et al., 2001; Verma et al., 2010). Phytohormones produced by *Azospirillum* promote epidermal-cell differentiation in root hairs that increased the number of potential sites for rhizobial infection leading to the formation of more nodules. Morphological and physiological changes in root system are also stimulated (Bashan & Levanony, 1990; Pacovsky, 1990; Sarig et al., 1992; Volpin & Kapulnik, 1994). An increase in the number of lateral roots and root hairs cause addition of root surface available for nutrients and water uptake. Higher water and nutrient uptake by inoculated roots cause an improved water status of plant, which in turn could be the main factor enhancing plant growth (Boddey et al., 1986; Dalla Santa et al., 2004; Fallik & Okon, 1996; Mostajeran et al., 2002).

Positive effects of co-inoculation were also observed on symbiotic performance of common bean, which is usually considered a poor nitrogen-fixing legume. Poor nodulation and variable response to inoculation is mainly attributed to intrinsic characteristics of the host plant, particularly the great sensitivity to nodulation-limiting factors, such as high rate of N fertilizer used in intensive agriculture, high temperature and soil dryness (Bais et al., 2006; Egamberdiyeva, 2007). Indeed, Yadegari & Rahmani (2010) showed that co-inoculation of

three *Phaseouls vulgaris* cultivars with two *Rhizobium* strains, *Pseudomonas fluorescens* and *A. lipoferum* resulted in increased seed yield, number of pods per plant, weight of seeds, seeds protein yield and number of seeds per pod.

Inoculation of common bean or afalfa (*Medicago sativa*) with *Azospirillum brasilense* in the absence of *Rhizobium* resulted in a more persistent exudation of flavonoids by legumes roots. *Azospirillum- Rhizobium* co-inoculation positively affected the expression of *nod*-genes and production of nodulation factor patterns in *Rhizobium tropici* and *Rhizobium etli* in the presence or absence of NaCl at 50 mM. A significant increase of total and upper nodule numbers was observed at different concentrations of *Rhizobium* inoculum (Dardanelli et al., 2008).

Several greenhouse and field experiments demonstrated the potential of co-inoculation to increase grain yield of various legumes (Bashan and Holguin, 1997; Galal et al., 2002; Itzigsohn et al., 1993; Sarig et al., 1986; Yahalom et al., 1989).

4.2 Intercropping systems

Due to climate changed, suitable land area for agricultural production remains fixed or is diminishing and farmers are faced with the task of increasing production demands (Zhang & Cai, 2011). Raising productivity is possible through the introduction of improved genotypes with enhanced resilience to abiotic stresses. In addition to this, agronomic manipulation may impact significantly on crop productivity. Because of restricted availability of water and fertilizer in many part of the world, productivity increase must be accompanied by increase in use efficiency. The cultivation of two or more species in the same field at the same time (intercropping) can boost productivity per unit land area (Davies et al., 2010). Crop mixtures may consist of legume/legume or legume/non-legume systems. Some of the intercropping advantages include: higher yield than sole crop yields, greater yield stability, more efficient use of environmental resources, better weed control and improved quality by variety (Malèzieux et al., 2009). Intercropping is a common practice where land is scarce: beans are mostly intercropped in sub-Saharan Africa, with the major exception of southern Africa where nearly half are monocropped (Kimani et al., 2005); groundnut is often grown as an intercrop in West Africa (Ndjeunga et al., 2008); pigeonpea has been traditionally grown as an intercrop in India; more than half of lentil grown in Bangladesh is planted under mixed cropping (Sarker et al., 2004).

However, the increased awareness of environmental degradation arising from the use of non-renewable artificial fertilizers and pesticides is encouraging the use of mixed cropping even in developed countries (Fujita et al., 1992).

The N_2 fixed by *Rhizobia* in legumes can also benefit associated non-legume via direct transfer of biologically fixed N to cereals growing in intercrops when fertilizer N is limited, which has both economic and environmental benefits. Among the various combinations of cereals and legumes used by small-scale farmers maize-cowpea is one of the most widely used because cowpea fixes atmospheric nitrogen and produces proteins, while maize depletes the soil nitrogen and produce carbohydrates. Maize and cowpea mixtures improve the diets as well as the soil fertility and productivity (Dahmardeh et al., 2009, 2010). PGPR strains may contribute to the benefits of legumes in cropping systems in more way than just fixing atmospheric nitrogen. Indeed, as previously discussed, these bacteria have the ability to promote modifications of root architecture, enabling those plants to accumulate more mineral nutrients than control plants, increase disease resistance and improve plant response to environmental stresses. Therefore, the use of PGPR-inoculated legumes and

non-legumes in mixed cropping systems would be a promising agricultural practice for rehabilitation of extreme wasted lands, after a careful selection of appropriate tolerant bacterial strains and legume genotypes to the prevailing stressful conditions.

5. Discussion and conclusions

A large number of PGPR representing diverse genera have been described over the past 50 years. Despite their appeal as a "natural" means of plant protection few strains have been developed commercially. This is partly because uneconomically large doses often must be applied and performance can be inconsistent in the field. There are several advantages of developing genetically-modified PGPR over transgenic plants for improving plant performance under a variety of stresses: (1) it is far easier to modify a bacterium than complex higher organisms; (2) several plant growth-promoting traits can be combined in a single organism, and (3) instead of engineering crop by crop, a single, engineered inoculant can be used for several crops, especially when using a non-specific genus like *Azospirillum*.

PGPR strains development is hampered mainly by the fact that these organisms not always survive harsh environmental conditions including high concentrations of environmental contaminants, salts, extremis of pH and temperature, and compete with other organisms. Genetically engineered strains offer a means to develop PGPR that are effective at low inoculum doses and under a variety of environmental conditions. Many rhizobacteria produce phytohormones that undoubtedly affect root growth leading to the formation of roots systems with increased exploratory capacity. This morphological modification plays an important role in the mechanisms of stress response (Potterset al., 2007, 2009). Efforts to engineer the rhizosphere through hormone manipulation have focused mainly on degradation of so-called "stress" ethylene, which is synthesized by plants upon exposure to stresses such as flooding, drought, salt, and the presence of metals, organic contaminants and pathogens. The production of ACC deaminase enzyme, which catalyzes the cleavage of ACC, the immediate precursor of ethylene, may be used to modulate ethylene levels. Available data are consistent with the proposed model of plant growth facilitation by ACC deaminase-producing PGPR strains (Glick et al. 2007). We have described an engineered PGPR strain, RD64 (Pii et al., 2007), a derivative of *Sinorhizobium meliloti* 1021, able to release into liquid growth medium up to 78-fold more IAA than wild-type 1021 (Camerini et al., 2008). For this strain, as well as for IAA-treated *Escherichia coli* cells (Bianco et al., 2006a, 2006b), a more resistance to salinity and other abiotic stresses and the induction of tricarboxylic acid cycle (TCA) enzymes was observed as compared to 1021 strain (Bianco & Defez, 2009; Imperlini et al., 2009). In addition, RD64 strain showed enhanced long-term cell survival (Defez, 2006), has improved nitrogen fixation ability (Bianco & Defez, 2010b; Imperlini et al., 2009) and is highly effective in mobilizing P from insoluble source such as Phosphate Rock (Bianco & Defez, 2009). *Mt*-RD64 plants showed an higher degree of protection against oxidative damage induced by salt stress (Bianco & Defez, 2009) and significant increases in both the shoot and root fresh weight under P-starved condition when compared to salt-stressed and P-starved *Mt*-1021 plants (Bianco & Defez, 2010a).

For *Mt*-RD64 plants we also observed a re-modulation of phytohormones, with a higher IAA content in nodules and roots and a decreased IAA levels in shoots, as compared with *Mt*-1021 plants. The modulation of IAA levels in these plants lead to alterations of other important hormones that control plant growth. Indeed, the expression levels of Medicago genes encoding members of cytokinin signalling pathway were induced in the root of *Mt*-

RD64 plants (Bianco et al., 2009). In addition, the analysis of the expression levels of the main ethylene signalling genes showed that severe salt stress triggered a high induction of ethylene signalling in *Mt*-1021 plants whereas this pathway was not significantly altered in *Mt*-RD64 plants (Bianco & Defez, 2009).

We speculate that the growth promoting effects observed under stressful environmental conditions for the model legume Medicago might be extended to other plant species. Indeed, for legumes such as pea, alfalfa and bean plants, we previously reported an increase in the shoot or seed production for the plants nodulated by IAA-overproducing strains. In addition, for tropical legumes such as soybean and peanut plants, we also have preliminary data indicating the positive effects triggered by the specific IAA-overproducing rhizobia strains (Bianco et al., 2010c).

A PGPR strain with the characteristics described above is a good candidate to promote plant yield under stressful environmental conditions either in mono-cropping or mixed cropping systems.

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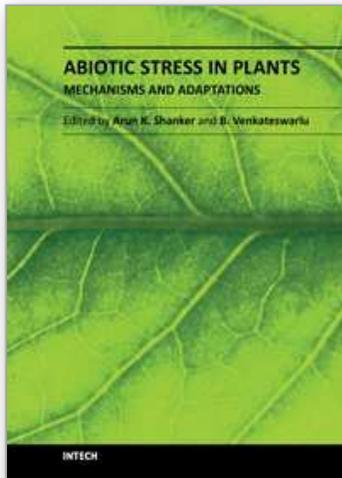
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World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly dived into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

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