Plant-Microbe Interactions in Adaptation of Agricultural Crops to Abiotic Stress Conditions

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Abstract

Abiotic stresses are an increasing challenge to crop production all over the world. These stresses include high and low temperatures, salinity, flooding, drought, nutrient limitation, and toxic metals and organic pollutants. The costs associated with abiotic stresses are potentially enormous, indicating a need for sound, affordable, environmentally friendly approaches to decrease the adverse effects of these stresses on plants. Unlike animals, plants cannot use avoidance and escape as mechanisms of stress tolerance; consequently, their evolution is marked by the development of highly beneficial interactions with their more mobile companions, microbes. Some of these interactions involve highly sophisticated symbioses that confer stress tolerance, such as with mycorrhizae and rhizobia that help ameliorate nutritional and water deficiencies, while others are more transitory. The agricultural application of beneficial microorganisms is increasingly of widespread interest, with many research programs evaluating microbial strains for their ability to provide protection against a single stress, such as phosphate limitation and cross-protection against multiple stresses. Knowledge of the underlying physiological mechanisms by which diverse microbes mediate stress tolerance, including cross-protection, is critical to the effective use of these microbes to assure sustained agricultural production in changing environmental conditions. Here we provide an overview of current knowledge on the physiological impacts and modes of action of microbial mitigation of abiotic stress symptoms in plants. We indicate further research avenues to enable better use of the protection capabilities of root-colonizing beneficial microbes in agricultural

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production systems affected by a changing climate. As a complement to previous reviews summarizing the mechanisms of resistance to biotic stresses, this review will focus on the mechanisms underlying microbially mediated abiotic stress tolerance, especially tolerance conferred by plant growth-promoting rhizobacteria (PGPRs).

7.1 Introduction

Food security is a fundamental need for society and one that is being threatened by an exponentially increasing global population, unsustainable agricultural practices, and a changing global climate. Developing countries in Africa and Asia account for approximately 80% of the projected population growth, and, with an estimated 800 million people in these countries already undernourished, the Food and Agriculture Organization (FAO) of the United Nations predicts that a 60% increase in world food production over the next two decades is required to sustain these populations (Jewell et al. 2010). This will require a significant increase in grain yields of major crop plants, including rice, wheat, and maize (Godfray et al. 2010). Climate change has exacerbated the frequency and severity of droughts, floods, and high temperatures, causing yield reductions in our major cereal crops (Carmen and Roberto 2011; David and Christopher 2007), and decreased predictability of rainfall in many parts of the world (Jewell et al. 2010).

The pressure to increase agricultural output has increased cultivation on marginal lands and accelerated the rate of land degradation. For example, irrigation has led to salinity across large tracts of agricultural land (Shahbaz and Ashraf 2013), as illustrated by the threat of dry land salinity in almost 32 million hectares in Iran. Similarly, the widespread and intense application of fertilizers has incurred environmental costs in the form of nitrate contamination of groundwater, greenhouse gas (GHG) production associated with industrial nitrogen fixation, GHG production due to microbial-mediated denitrification, and depletion of global phosphorus reserves. The need for fertilizers to achieve higher yields has also contributed to rising costs for farmers worldwide. Our challenge for achieving global food security in the upcoming decades is to increase yields in a sustainable manner; that is, growers need access to a portfolio of production practices that collectively enable sufficiently high yields and profits to meet global food demand, but with sufficiently low environmental costs as to ensure sustainability (Glick 2012, 2014).

Abiotic stress conditions are among the most important constraints to global agricultural production (Jewell et al. 2010; Shrivastava and Kumar 2015), with losses due to abiotic stress estimated at 70% worldwide (Acquaah 2007). Plant-associated microorganisms are increasingly recognized for their potential contributions to enhancing crop growth, crop nutrition, and crop tolerance to abiotic stress (Fig. 7.1).

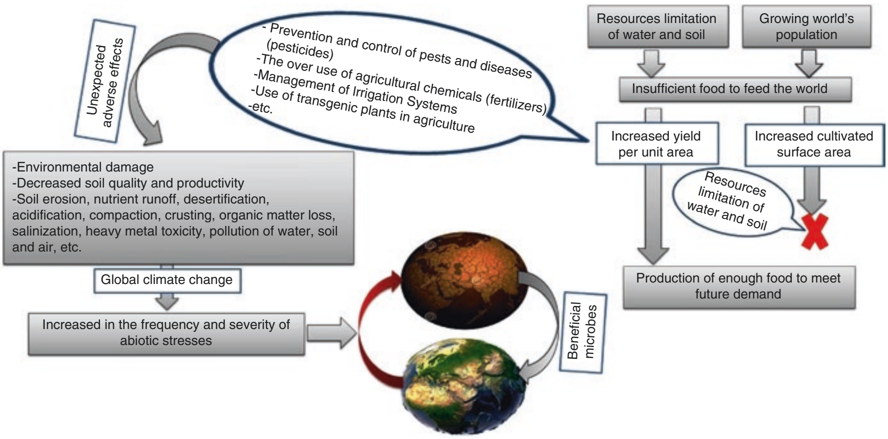


Fig. 7.1 Role of beneficial microbes in sustainable agriculture and environmental health (converting drought earth to green one)

A growing body of research is expanding our understanding of how plant growth-promoting microorganisms (PGPMs) enable agricultural plants to maintain productivity under stressed conditions (Dimkpa et al. 2009; Grover et al. 2010; Porcel et al. 2011; Shrivastava and Kumar 2015). Knowledge of these mechanisms has increased dramatically in the past 15–20 years (Glick 2012) and may serve as the basis for new strategies for selecting or engineering crop plants for an increased ability to cope with climate change-induced stresses (Grover et al. 2010). This chapter will focus on the role of PGPMs in the adaptation of agricultural crops to abiotic stress conditions and will outline the major yield-limiting abiotic stresses faced by crop plants: drought, salinity, nutrient deficiency, temperature, and metal toxicity. For each stress, we will highlight mechanisms by which PGPMs enhance plant tolerance to the stress, if known, and will focus especially on stresses associated with climate change.

7.2 Abiotic Stresses

Stress may be defined as any condition negatively affecting a living organism. Abiotic stresses originate from the surrounding environment, such as in the form of a physical or chemical condition that hinders plant growth, whereas biotic stresses are caused by living organisms, such as those that cause disease or damage. Abiotic stresses encountered by agricultural plants can broadly include low water availability in the form of salinity or drought, flooding, high and low temperatures, high light or ozone, anoxic conditions, high or low pH, nutrient deficiency, and exposure to detrimental chemicals including some agricultural inputs, toxic metals, and organic pollutants.

7.2.1 Effect of Abiotic Stresses on Plants

Abiotic stresses can cause deleterious effects in almost all phenological plant stages. They can cause changes in biochemistry, morphology, and physiology that adversely affect plant growth and productivity (Paul 2012; Wang et al. 2001). These are illustrated by the ability of various stresses to disrupt metabolism, promote membrane disorganization, generate reactive oxygen species, inhibit photosynthesis, reduce the potential for nutrient uptake, and alter hormone levels (Hasegawa et al. 2000). The following section focuses on some of the most serious abiotic stresses limiting the productivity of agricultural crops.

7.2.1.1 Salinity Stress

Soil salinity is one of the most devastating environmental factors limiting the productivity and quality of crop plants in the semiarid areas of the world (Allakhverdiev et al. 2000; Dodd and Perez-Alfocea 2012; Jamil et al. 2011; Ondrasek et al. 2009; Paul 2012; Paul and Lade 2014; Ramadoss et al. 2013a; Shahbaz and Ashraf 2013; Shanker and Venkateswarlu 2011; Yamaguchi and Blumwald 2005). It is responsible for major reductions in cultivated land area, particularly in areas where rising sea levels are promoting encroachment into agricultural lands, and is affecting extensive areas of land in both developed and developing countries. Soils are considered to have high salinity if their electrical conductivity (EC) at saturation is above 4 dS m^{-1} (America 2001), that is, above about 40 mM NaCl (Munns and Tester 2008). This salinity can result from the combined processes of irrigation, fertilization, and desertification (Munns and Tester 2008). The FAO reported that more than 1 billion hectares of land throughout the world have been affected by salinity (Ahmad 2013; FAO 2008). Because of global climate change, this area is increasing (Shrivastava and Kumar 2015) and is estimated to exceed 50% of the arable land by the year 2050 (Jamil et al. 2011).

Salinity has a broad range of negative effects on plant growth. It can reduce germination, plant vigor, and crop yield for many crops, from cereals to horticultural species (Munns and Tester 2008). It has a particularly negative effect on biological nitrogen fixation, as it can reduce nodulation, nitrogen fixation, and the total nitrogen content in legumes (van Hoorn et al. 2001; Mensah and Ihenyen 2009; Rabie and Almadini 2005; Egamberdieva et al. 2013; Paul and Lade 2014). This is consistent with the finding that symbiotic nitrogen fixation is among the most sensitive plant processes to water deficits, with sensitivity occurring during both the formation of symbiotic nodules and the subsequent period of nitrogen fixation and plant nitrogen uptake (Sinclair et al. 2010). Salinity also reduces the photosynthetic capacity of plants, due at least in part to the partial closure of stomata (Meloni et al. 2003) and can reduce protein synthesis and lipid metabolism (Parida and Das 2005).

Almost all micro- and macronutrients decrease in plant roots and shoots with increasing salinity of the growth medium (Paul and Lade 2014). The high Na^+ and Cl^- content on the roots affects the activity of the uptake systems and alters competitive interactions among ions for binding and transport into root cells (Tester and Davenport 2003); this can affect the uptake of nutrients as well as water (Paul and

Lade 2014). The accumulation of Na^+ and Cl^- ions may cause metabolic disturbances, with buildup in the intercellular spaces leading to cell dehydration and death. The dehydration that accompanies high salinity is associated with oxidative stress (Hichem et al. 2010; Johnson et al. 2003) and thus can involve damage to membranes and other macromolecules by ROS (Carmen and Roberto 2011; Pitzschke et al. 2006; Porcel et al. 2011). ROS-induced cellular damage is associated with drought and heat stress as well as salinity (Zhu 2001a), with all potentially promoting protein denaturation (Smirnoff 1998) and activating similar cell signaling pathways (Knight 2000; Shinozaki and Yamaguchi-Shinozaki 2000; Zhu 2001b; Zhu 2002) and responses, including the accumulation of stress proteins, antioxidants, and compatible solutes (Cushman and Bohnert 2000; Pitzschke et al. 2006; Wang et al. 2003).

In general, saline conditions inhibit plant growth through two phases. During the first phase, inhibition is mainly achieved by the decreased water availability due to higher solute concentration of the soil solution. Salt stress increases external osmotic pressure, which decreases leaf water potential and turgor, and ultimately causes stomatal closure. If the salt stress is prolonged, the second, salt-specific phase sets in, and ion toxicity is the main factor that constrains plant metabolism and survival (Chen et al. 2007; Munns 2002; Munns 2005; Munns and Tester 2008; Pandolfi et al. 2012; Sanchez et al. 2008; Tester and Davenport 2003).

7.2.1.2 Drought Stress

By some estimates, drought is the most significant environmental stress impacting global agricultural production (Cattivelli et al. 2008; Kijne 2006; Tuberosa and Salvi 2006). Approximately, 60% of all crops produced in developing countries are grown without irrigation (FAO 2009b), indicating that the majority of crops are vulnerable to drought. Agriculture accounts for approximately 70% of global water use, and irrigation account for up to 90% of total water withdrawals in arid nations (Council 2008; FAO 2009a). The water withdrawal requirement for irrigation is expected to increase by another 14% in developing countries by 2030, with an increase of 10% for every 1 °C increase in temperature in arid and semiarid regions (Grover et al. 2010); these statistics illustrate how strategies to decrease water demands for agriculture will be critical.

Similar to salinity stress, soil water deficits can reduce the photosynthetic capacity, increase photorespiration, and cause increased ROS production (Miller et al. 2010). On a whole-plant level, water-stressed plants wilt and are unable to sequester assimilates into the appropriate plant organs. Severe drought conditions result in reduced yield and plant death (Jewell et al. 2010).

7.2.1.3 Salinity-Induced Nutrient Deficiencies

Crop performance may be adversely affected by salinity-induced nutrient deficiencies. Nitrogen (N) accounts for about 80% of the total mineral nutrients absorbed by plants, and inadequate N is often a growth-limiting nutritional stress (Marschner 1995). Salinity reduces N uptake and accumulation (Feigin 1985). Salinity also reduces phosphorus (P) uptake and accumulation (Paul and Lade 2014); this effect is due to a reduction in P availability due to the formation of calcium phosphate precipitates (Navarro et al. 2001; Parida and Das 2005; Rogers et al. 2003). The maintenance of adequate levels of potassium (K) is also jeopardized by salinity, with sodium-induced K deficiency implicated in various crops (Botella et al. 1997).

7.2.1.4 Temperature Stress

Global climate change is predicted to result in increases in the air temperature on Earth's surface by 3–5 °C in the coming 50–100 years (Polle and Luo 2014), with a consequent increase in frequency and intensity of drought and heat waves (Hansen et al. 2012). High soil temperatures in tropical and subtropical areas are already a major problem for crop production. Higher temperatures influence photosynthetic rate, plant water relations, flowering, and fruit set. In some regions, low temperatures limit the productivity and areas of cultivation of agricultural crops (Grover et al. 2010).

7.2.1.5 Pollutant Stress

Heavy metals are natural constituents of the environment, but due to indiscriminate use, heavy metal contamination has become a serious problem worldwide, including in some agricultural regions (Luo et al. 2011). All heavy metals are toxic to plants when present in high soil concentrations (Riesen and Feller 2005). High concentrations of heavy metals can decrease nutrient uptake, inhibit various enzymatic activities, induce oxidative stress, inhibit root and shoot growth, and lower yields (Athar and Ahmad 2002; Sandalio et al. 2001). Heavy metals can also be accumulated by agriculturally important crops; their entry into the food chain can negatively impact animal and human health (Sanità di Toppi and Gabbrielli 1999). In addition to heavy metals, many organic contaminants can be present in soil (Chen et al. 2015) and impact plant health.

7.3 Response of Plants to Stresses

Plants can generally tolerate moderate and transient exposure to environmental stresses, with severe stress sometimes causing extreme responses, including inhibiting flowering and seed formation and inducing senescence or plant death. Among the general responses of plants to stress (Fig. 7.2), a primary response is typically modification of gene expression to promote adaptation to a specific stress (Bhatnagar-Mathur et al. 2008).

An example of this is the induction of genes that promote the synthesis and accumulation of compatible solutes in response to soil water deficits. Other examples are the activation of ROS scavenging systems, transporter systems, and proteins involved in plant hormone regulation (Des Marais and Juenger 2010; Hiz et al. 2014; Parida and Das 2005; Santner et al. 2009). Plant hormone signaling pathways may be involved in biotic and abiotic stress responses (Egamberdieva et al. 2015; Khan and Khan 2013; Li et al. 2012; Shabani et al. 2009). Among the most extensively studied hormonal pathways, including the methyl jasmonate, salicylic acid,

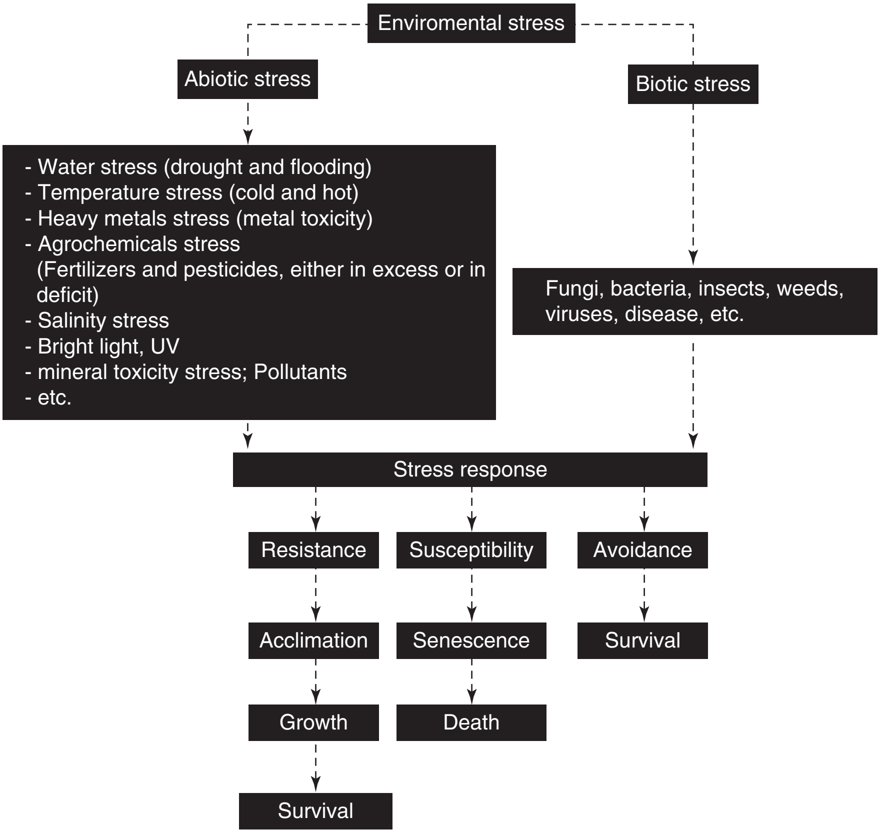


Fig. 7.2 The effect of environmental stresses on plant survival (Hopkins and Huner 2009)

and ethylene pathways (Egamberdieva et al. 2015; Khan and Khan 2013; Li et al. 2012; Shabani et al. 2009), only ethylene will be discussed here due to its key role in plant responses to a variety of abiotic stresses.

7.3.1 Ethylene Production

The phytohormone ethylene (C_2H_4) is found only in gaseous form and is produced endogenously by almost all plants (Babalola 2010); it mediates a wide range of developmental processes as well as responses to stress. Ethylene is an efficient plant growth regulator (Arshad and Frankenberger 2002), but can inhibit growth when its concentrations are high. Stress conditions such as flooding, wounding, drought, chilling, pathogen infection, and salinity may induce the accumulation of ethylene to high concentrations (Babalola 2010; Gnanamanickam 2006). The ethylene biosynthetic pathway is of interest because of the presence of microbial enzymes that interfere with this pathway, described below. Ethylene is synthesized from the precursor 1-aminocyclopropane-1-carboxylate (ACC) by the enzyme ACC oxidase, and this ACC is derived from S-adenosyl methionine (SAM) by the enzyme ACC synthase (ACS). This synthesis occurs in two phases in response to stress. First, low levels of ethylene induce the expression of stress-related genes; and second, high levels of ethylene cause plant growth inhibition and detrimental effects such as chlorosis and abscission (Glick et al. 2007b), as well as inhibition of developmental processes including root elongation, lateral root growth, root hair formation, and nodulation (Alikhani et al. 2010; Belimov et al. 2009; Botella et al. 2000; Guinel and Sloetjes 2000; Ligero et al. 1999; Mayak et al. 2004; Pierik et al. 2006; Saleem et al. 2007; Yuhashi et al. 2000).

7.4 Improving Plants to Increase Abiotic Stress Tolerance

Plant breeding and plant engineering are both tools that have been used to improve the tolerance of crops to abiotic stress (Jewell et al. 2010; Araus et al. 2008; Ashraf and Akram 2009; Dwivedi et al. 2010; Mittler and Blumwald 2010; Sreenivasulu et al. 2007; Valliyodan and Nguyen 2006; Witcombe et al. 2008). The major constraint to improving the abiotic stress tolerance of crops are the gaps in our understanding of the complex physiological, biochemical, developmental, and genetic mechanisms involved in stress tolerance and the difficulty in combining favorable alleles to create improved high-yielding genotypes. Transgenic plants are primarily tested under controlled greenhouse conditions, with only a few reports of evaluating performance under field conditions. Challenges to enhancing the stress tolerance of crops include the polygenic nature of stress resistance, the time requirements for introducing multiple genes into a plant, and insufficient knowledge of the dynamics of the expression of the introduced genes following a stress stimulus (Bhatnagar-Mathur et al. 2008; Dodd and Perez-Alfocea 2012; Manchanda and Garg 2008; Schubert et al. 2009). Unfortunately, transgenic approaches and molecular breeding programs for improving crop tolerance to stress have generally not brought promising results in farmers' fields (Bhatnagar-Mathur et al. 2008; Dodd and Perez-Alfocea 2012; James et al. 2008; Munns and Tester 2008; Ramadoss et al. 2013a; Schubert et al. 2009; Wang et al. 2003) with some notable exceptions (Munns et al. 2006). In general, the development of stress-tolerant crop varieties through genetic engineering and plant breeding is an essential but a long and expensive process.

7.5 Using Microbes to Enhance the Abiotic Stress Tolerance of Plants

Microorganisms have been found to enhance the growth of diverse crops grown under a range of stresses. This finding suggests that microbial inoculants can be an effective practice to alleviate crop stress and one that complements the development of stress-tolerant plant germplasm (Paul and Lade 2014). Microbial inoculants that alleviate plant stress offer a possible cost-effective, environmentally friendly, agricultural input, which can generally be developed in a shorter time frame than new plant germplasm (Dodd and Perez-Alfocea 2012; Shrivastava and Kumar 2015). Additional advantages of developing microbial products over plant products for improving plant abiotic stress tolerance include the more rapid screening and modification of microbes than plants, the relative ease with which multiple plant growth-promoting (PGP) traits can be identified or engineering in a single microbe, and the potential application of a single inoculant to multiple crops. Evidence supporting the contribution of microbes to abiotic stress tolerance will be elaborated below, but includes the finding that genetic differentiation in plant-associated microbes can drive local adaptation of plants to their environment (Rodriguez and Redman 2008) and the evolutionary history of mutualistic interactions between plants and microbes that helped drive plant adaptation to stressful conditions (Glick 2012).

7.6 The Rhizosphere as a Selective Force for Microbes

The rhizosphere, which is the region of soil influenced by plant roots, offers an environment rich in nutrients for microorganisms (Bais et al. 2006). Plants release as much as 20% of their fixed carbon into the rhizosphere. These rhizodeposits contain an array of organic compounds, including sugars (such as glucose, xylose, fructose, maltose, sucrose, and ribose), organic acids (such as citric, malic, lactic, succinic, oxalic, and pyruvic acids), amino acids, fatty acids, nucleotides, putrescine, and vitamins. Microbes use these compounds for nutrition and as signal molecules to indicate the presence of the plant (Lugtenberg 2015). Microbes also influence the chemical milieu of the rhizosphere by secreting an array of compounds, including enzymes, waste products, secondary metabolites, and even phytohormones, which may influence plant growth and defense (Ortíz-Castro et al. 2009).

Although the microbial communities on roots are diverse, the composition of these communities may be influenced by the plant (Sessitsch et al. 2002), suggesting the possibility that plants select or enrich for microbes that provide a benefit to the plant. Distinct plant species, and even distinct cultivars, have been found to have a detectable influence on the diversity of their rhizosphere communities (Berg and Smalla 2009; Buée et al. 2009; Hartmann et al. 2008; Acosta-Martínez et al. 2008; Marschner et al. 2001; Germida and Siciliano 2001; Manter et al. 2010; Siciliano and Germida 1999; Van Overbeek and Van Elsas 2008). Whereas some microbes are found primarily outside of the roots, those that colonize the intercellular sites within roots, designated endophytes, may have the greatest impact on the plant due to their close proximity to the plant tissues and thus greater opportunities for chemical exchange.

A breadth of rhizosphere microorganisms have been found to promote plant growth in the absence of plant exposure to environmental stress. These are generally referred to as plant growth-promoting rhizobacteria (PGPRs) (Hayat et al. 2010), but can more generically be called plant growth-promoting microorganisms

(PGPMs). About 2–5% of rhizobacteria exert a beneficial effect on plant growth following inoculation onto plants in a soil containing competitive microflora (Paul and Lade 2014). PGPRs include bacteria of diverse genera such as *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas*, *Rhizobium*, and *Serratia* (Gray and Smith 2005), as well as *Streptomyces* spp. (Dimkpa et al. 2009; Tokala et al. 2002). Although the arbuscular mycorrhizal fungi (AMF) (Jeffries et al. 2003) and symbiotic nitrogen-fixing bacteria also provide clear benefits to plant growth, they are generally not regarded as PGPMs (Franche et al. 2008). PGPMs may benefit plants via a diversity of mechanisms (Hayat et al. 2010; Lugtenberg and Kamilova 2009; Paul 2012), and these include, but are not limited to, the production of a compounds such as plant growth regulators, siderophores, and enzymes that influence plant hormone accumulation, biological nitrogen fixation, and activities that enhance nutrient solubilization, protection from phytopathogens, and protection from abiotic stresses. The main focus of this review is on the mechanisms by which rhizosphere bacteria, including endophytes, benefit plant health by modulating the effects of abiotic stress.

7.7 Mechanisms by Which Microbes Enhance Abiotic Stress Tolerance in Plants

The importance of environmental stress in reducing crop yields has fostered a large body of research exploring the role of rhizosphere organisms in plant health in stressed environments (Grover et al. 2010; Paul 2013; Paul and Lade 2014; Venkateswarlu et al. 2008; Yang et al. 2009). Bacteria and fungi have been identified that can improve plant yields in these stressed environments (Banik et al. 2006; Barassi et al. 2006; Belimov et al. 2015; Chakraborty et al. 2015; Choudhary 2012, 2015; Dahmardeh et al. 2009; Damodaran et al. 2014; Davies et al. 2011; del Amor Francisco and Cuadra-Crespo 2012; Dimkpa et al. 2009; Egamberdieva et al. 2008; Egamberdieva 2009; Egamberdieva 2011; Etesami and Alikhani 2016a, b; Fu et al. 2010; Gray and Smith 2005; Hamilton et al. 2016; Kaymak et al. 2009; Khan et al. 2012; Mayak et al. 2004; Milošević et al. 2012; Nadeem et al. 2007; Paul 2012; Paul and Nair 2008; Ramadoss et al. 2013a; Rojas-Tapias et al. 2012; Shrivastava and Kumar 2015; Soleimani et al. 2011; Tiwari et al. 2011; Upadhyay et al. 2009; Yang et al. 2009, 2010; Yildirim and Taylor 2005; Vurukonda et al. 2016). The bacterial genera that have been implicated in these benefits include *Rhizobium*, *Bacillus*, *Pseudomonas*, *Pantoea*, *Paenibacillus*, *Burkholderia*, *Achromobacter*, *Azospirillum*, *Microbacterium*, *Methylobacterium*, *Variovorax*, and *Enterobacter* (Barassi et al. 2006; Dodd and Perez-Alfocea 2012; Grover et al. 2010; Nia et al. 2012; Ramadoss et al. 2013a; Selvakumar et al. 2009; Upadhyay et al. 2009; Yang et al. 2009, 2010; Yildirim and Taylor 2005). Some of these organisms are capable of activating systemic changes in plants that confer tolerance to abiotic stress; this phenomenon has been designated *induced systemic tolerance* (Yang et al. 2009). This section explores our understanding, to date, of the mechanisms by which PGPMs alleviate abiotic stress tolerance in plants.

7.7.1 Indole Acetic Acid Production

Plants regulate their resource allocation to roots versus shoots to optimally balance the size of their root systems, which are critical for nutrient and water uptake, and their aboveground tissues, which are required for photosynthesis and reproduction. Some microbes promote greater root growth by interfering with this regulation. Although this interference could conceivably come at the cost of fitness to the plant, many studies have shown that under conditions of environmental stress, microbial inoculants that promote plant root growth provide measurable benefits to plant growth and/or plant health. In particular, inoculation of plants with various PGPRs have been shown to enhance the formation of lateral roots and root hairs (Paul and Lade 2014) and roots with a larger root surface area (Diby et al. 2005; Paul and Sarma 2006); collectively, these morphological changes increase the opportunities for water and nutrient uptake.

A major mechanism by which bacteria can influence plant root system development is via the production of the auxin indole-3-acetic acid (IAA). This phytohormone is a major hormone used by plants to regulate growth. It is involved in a breadth of physiological processes including plant cell division and differentiation, germination, vascular development, and root growth. Of particular interest for the study of PGPR is the influence of IAA on root length and the initiation of lateral roots. Low IAA production levels generally increase root length and lateral root initiation, whereas high levels promote the opposite. The ability of bacteria to produce IAA was recognized, in part, due to the negative impacts of high IAA production on plant development (Costacurta and Vanderleyden 1995; Ludwig-Müller 2004). IAA production has been detected in diverse bacteria, including methylobacteria, streptomycetes, cyanobacteria, and archaea, with the percentage of soil bacteria capable of IAA production estimated to be as high as 80% (Khalid et al. 2004). At present, the majority of known PGPRs are capable of IAA production (Hayat et al. 2010).

The contribution of IAA production by *Azospirillum brasilense* to root growth under nonstressed conditions has been well documented (Spaepen and Vanderleyden 2011; Spaepen et al. 2007). *A. brasilense* strains induce morphological changes in plant roots (Spaepen et al. 2008). For example, cell-free supernatants of *A. brasilense* cultures induced root elongation and increased root surface area, dry weight, and lateral root development in rice (El-Khawas and Adachi 1999) and soybean (Molla et al. 2001) under hydroponic conditions. Moreover, similar responses by bean plants were observed upon the exogenous application of IAA and PGPR strains (Remans et al. 2008). Lastly, the association of a loss of IAA production via mutagenesis with a loss of root enhancement activity provided direct evidence that IAA production was at least one mechanism responsible for plant growth promotion by *A. brasilense* (Kundu et al. 1997).

The contribution of IAA production to root growth under environmentally stressful conditions has been identified with other microbes. Sadeghi et al. (2012) demonstrated that a *Streptomyces* isolate produced IAA and promoted growth of wheat under high salinity conditions. Similarly, Yao et al. (2010) found that an IAA-producing *Pseudomonas putida* strain promoted the growth of cotton seedlings under high salinity conditions. The finding that this *P. putida* strain also inhibited production of the stress-inducible phytohormone abscisic acid illustrates the complexity of elucidating mechanisms underlying plant growth promotion. The benefits of IAA production by PGPR may be augmented by the production of an enzyme, ACC deaminase (Etesami et al. 2014a, 2015a, b); this enzyme is described below. Bacteria can produce other phytohormones as well, including cytokinins (Arkhipova et al. 2007) and gibberellins (Botinni et al. 2004), which may contribute to plant growth under stressful conditions (Arkhipova et al. 2007), but the research on these phytohormones in PGPR is far less extensive than for IAA.

7.7.2 ACC Deaminase Production

PGPRs that produce the enzyme ACC deaminase can modulate plant growth by modulating the level of ethylene in the roots (Glick 2014; Singh et al. 2011). The enzyme ACC deaminase catalyzes the cleavage of ACC, which is an immediate precursor of ethylene in the ethylene biosynthetic pathway (Glick et al. 2007a). This cleavage reaction releases ammonia and α-ketobutyrate, both of which can be metabolized by bacteria (Glick et al. 2007b), and concurrently limits further production of ethylene by the plant (Fig. 7.3).

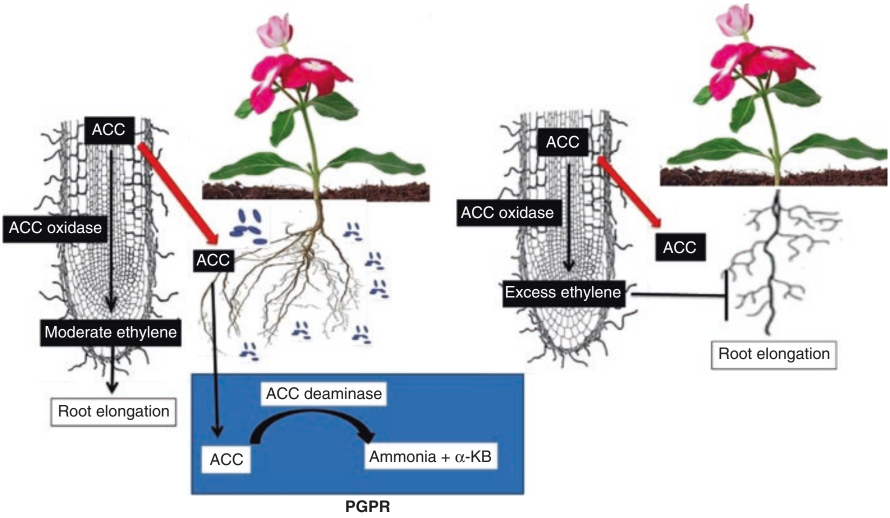


Fig. 7.3 A model to explain how ACC deaminase-producing bacteria lower ethylene in roots. A significant portion of the ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) is exuded from plant roots or seeds and is subject to hydrolysis by ACC deaminase-producing bacteria, releasing ammonia and α-ketobutyrate (α-KB). This hydrolysis reduces the ACC levels outside of the plant, which, due to the equilibrium between internal and external ACC levels, results in decreased ACC levels inside the plant. The metabolic benefit of the ACC degradation to the growth of ACC-producing microorganisms increases their growth, and this provides a positive feedback to further decrease the ACC levels, ultimately resulting in a reduction in the endogenous biosynthesis of ethylene (Glick 2012)

As described above, plants respond to a variety of stresses by accumulating ethylene, and this accumulation can inhibit root development. By decreasing ACC levels in plants, ACC deaminase-producing microorganisms decrease plant ethylene levels and alleviate this inhibition (Glick et al. 2007b). Interestingly, the cost of overriding this endogenously induced growth inhibition does not seem to outweigh the benefit for plants grown under stressful conditions, as plants inoculated with ACC deaminase-producing bacteria, or expressing a bacterial ACC deaminase transgene, develop a more extensive root system and exhibit enhanced tolerance to environmental stresses (Arshad et al. 2007; Safronova et al. 2006; Stearns et al. 2005).

ACC deaminase-producing PGPRs have been used successfully to protect a variety of plant species against growth inhibition resulting from stress exposure (Ali et al. 2012, 2014; Barnawal et al. 2012; Etesami et al. 2014b; Glick 2014; Li et al. 2012, 2013; Ramadoss et al. 2013b; Shakir et al. 2012; Siddikee et al. 2011). Although a diversity of bacteria and fungi express ACC deaminase, this activity has been studied most extensively in PGPRs (Glick 2005), including the genera *Achromobacter*, *Acidovorax*, *Alcaligenes*, *Enterobacter*, *Klebsiella*, *Methylobacterium*, *Pseudomonas*, *Rhizobium*, and *Variovorax* (Esquivel-Cote et al. 2010). Bacteria in the symbiotic nitrogen-fixing genus *Bradyrhizobium* can also reduce ethylene accumulation in plants, and this activity enhances nodulation by helping prevent plant suppression of new nodule primordia. Unlike PGPR, however, these symbiotic bacteria do not secrete ACC deaminase, but rather secrete a modified amino acid, rhizobitoxine, that inhibits the ethylene biosynthetic enzymes ACC synthase and β-cystathionase (Sugawara et al. 2006). To date, rhizobitoxine production has been found in some plant pathogens, but not in PGPRs.

7.7.3 Increased Nutrient Mobilization

Many of the soil nutrients required by plants are present in soil but not in an available form because they are in the form of insoluble precipitates or are bound to inorganic and organic soil constituents. Plant nutrient deficiency is stressful but can also exacerbate the adverse effects of other abiotic stresses (Baligar et al. 2001; Grieve and Grattan 1999; Khoshgoftarmanesh et al. 2010). Several studies show that plants exposed to environmental stresses require additional supplies of mineral nutrients to minimize the adverse effects of stress (Endris and Mohammad 2007; Heidari and Jamshid 2010; Kaya et al. 2002). The best-characterized mutualistic interactions in the rhizosphere, namely, the AMF- and symbiotic nitrogen-fixing bacteria-plant interactions, help plants overcome nutrient deficiencies that are incurred in soils with low fertility (Glick 2012). PGPRs can enhance the availability of these nutrients by increasing their solubility or uptake. A diversity of mechanisms by which microorganisms may increase nutrient availability is shown in Fig. 7.4. In this section, we will discuss the ways in which PGPR can be applied to improve crop health and productivity in nutrient-poor environments. The discussion will focus on the most limiting nutrient, N, with some discussion of P and iron, for which the solubility is especially affected by the soil pH (Jewell et al. 2010).

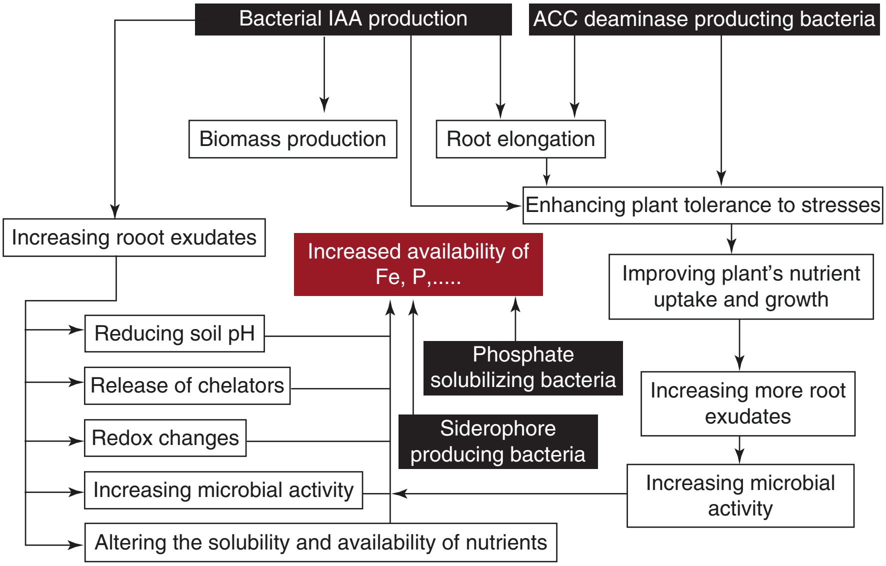


Fig. 7.4 Schematic representation of mechanisms by which PGPR may affect nutrient availability in the rhizosphere (Etesami et al. 2015a)

7.7.3.1 Nitrogen

Environmental stress can reduce the fixed nitrogen that legumes obtain from symbiotic nitrogen fixation. The process of infection and formation of root nodules is strongly repressed by ethylene (Peters and Crist-Estes 1989; Sugawara et al. 2006); therefore, the ethylene that accumulates in response to environmental stresses such as drought and salinity may be responsible, at least in part, for stress-mediated reductions in available nitrogen. This mechanism suggests that PGPR interference in ethylene signaling (Sect. 7.7.2) could help ensure continued fixation under stressful conditions. Other environmental stresses, including iron and phosphorus (P) deficiencies, also depress symbiotic nitrogen fixation, such as by reducing nodule mass, leghemoglobin content, and nitrogenase activity (Garcia et al. 2015; Tang et al. 1990; Pereira and Bliss 1989).

PGPRs may alleviate the effects of these stresses on symbiotic nitrogen fixation by a variety of mechanisms, as shown in Fig. 7.5. These include producing IAA that increases the size of the root system (Parmar and Dadarwal 1999) or number of root hairs (Yahalom et al. 1991), thus increasing the opportunities for nodulation (Glick 2012; Theunis 2005).

They also include enhancing the uptake of iron and P and thus preventing nutrient deficiencies that inhibit nodulation and nodule function. Co-inoculation of PGPR with rhizobia has been explored as a mechanism of ensuring adequate fixed nitrogen under stressful conditions. For example, Egamberdieva et al. (2015) showed that co-inoculation of *Mesorhizobium* spp. symbionts with *Pseudomonas extremorientalis* strain TSAU20 restored growth and nodulation to a legume, *Glycyrrhiza uralensis*, exposed to high salinity. This strain produces IAA

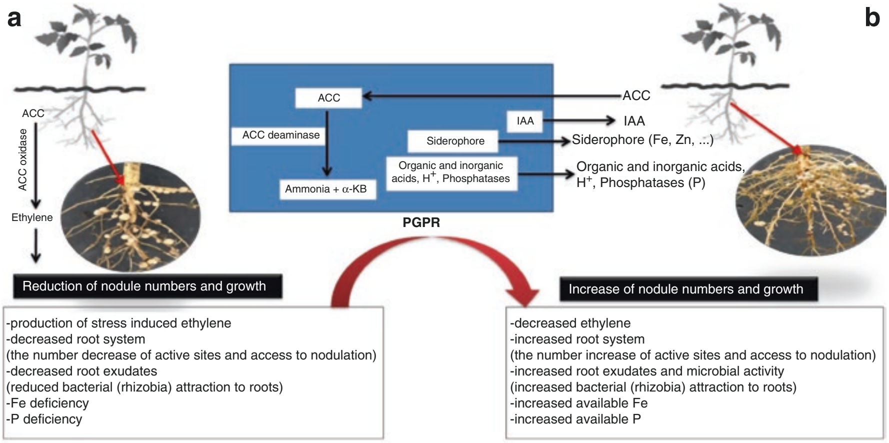


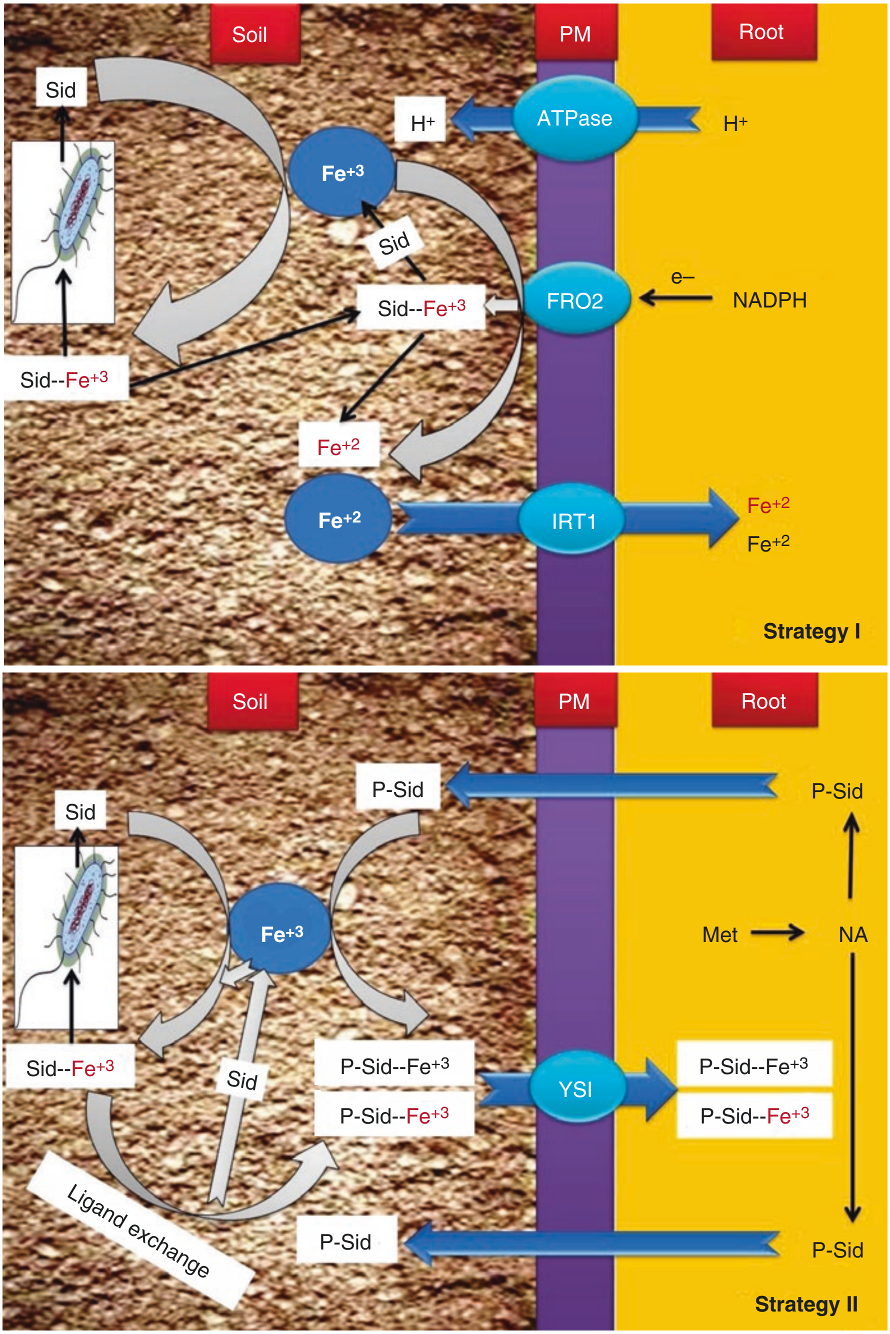
Fig. 7.5 Mechanisms by which PGPRs may alleviate the effects of stress on nodule number and nitrogen fixation in a legume plant. A, Stress-affected legume plant in the absence of inoculation by PGPR; B, stress-affected legume plant inoculated with PGPRs

(Egamberdieva and Kucharova 2009) and was previously shown to alleviate salt stress in the legume *Galega officinalis* when applied alone or with the rhizobial symbiont (Egamberdieva et al. 2013).

Environmental stresses such as salinity and drought may also influence plant N content by reducing root growth and thus reducing the surface area for uptake of nutrients, such as inorganic fertilizers. PGPRs that enhance root growth may therefore restore N nutrition. Although many bacteria enhance plant growth under high salinity conditions (Egamberdieva and Kucharova 2009; Selvakumar et al. 2009; Upadhyay et al. 2009), *Azospirillum* spp. were shown to increase plant N content (Nia et al. 2012) and the uptake of N, as well as P and K, under high salinity and other stressful environmental conditions (Carmen and Roberto 2011). Similarly, a *Streptomyces* sp. isolate increased wheat growth in saline soils as well as increased the concentration of N, P, Fe, and Mn in wheat shoots grown in normal and saline soil (Sadeghi et al. 2012).

7.7.3.2 Iron

Despite the abundance of iron in soils, its availability for plants and microbes is low (Schmidt 2003; Wintergerst et al. 2007). Under aerobic conditions, iron exists predominantly as ferric iron (Fe^{3+}), which reacts to form highly insoluble hydroxides and oxyhydroxides (Desai and Archana 2011; Zuo and Zhang 2010). These insoluble precipitates have a very low bioavailability to plants and microbes and are even less bioavailable in alkaline soils, such as calcareous soils, than in acidic soils. Concentrations of soluble Fe^{3+} are optimal for most plants at 10^{-4} to 10^{-8} M, but are insufficient for growth at 10^{-9} M or lower. Due to the generally low bioavailability of iron, plants and microbes have evolved effective mechanisms for iron sequestration. Plants have two strategies for mobilizing iron (Fig. 7.6).


Soil
PM
Root
Sid
H+
ATPase
H+
Fe+3
Sid
e–
Sid--Fe+3
FRO2
NADPH
Sid--Fe+3
Fe+2
Fe+2
IRT1
Fe+2
Fe+2
Strategy I
Soil
PM
Root
P-Sid
P-Sid
Sid
Fe+3
Met
NA
Sid--Fe+3
Sid
P-Sid--Fe+3
P-Sid--Fe+3
YSI
P-Sid--Fe+3
P-Sid--Fe+3
Ligand exchange
P-Sid
P-Sid
Strategy II

In the first, designated *Strategy I*, the soil is acidified in the rhizosphere through the activity of a root plasma membrane-bound H^+-ATPase, Fe^{3+} is reduced into ferrous iron (Fe^{2+}) by an iron chelate reductase enzyme, and Fe^{2+} is taken up by a membrane-bound Fe^{2+} transporter (Hartmann et al. 2008). All plant species except grasses use this iron acquisition mechanism. In contrast, grasses synthesize, secrete, and take up low-molecular-weight phytosiderophores; we designate this as *Strategy II*. Phytosiderophores are a form of mugineic acids that strongly chelate ferric iron and solubilize it for plant uptake by specialized ferric iron transport proteins, such as the yellow stripe protein in corn (Charlson and Shoemaker 2006; Curie et al. 2001; Guerinot 2010). Strategies I and II are often not sufficient to meet the iron nutritional needs of plants, particularly in calcareous and alkaline soils. One approach to enhance iron mobilization to plants is amending soils with synthetic iron-chelating compounds such as ethylenediaminetetraacetic acid (EDTA) and ethylenediamine-N,N′-bis (2-hydroxyphenylacetic acid) EDDHA could provide a solution, but these are poorly biodegradable and can pose a threat to the environment, the main risk being the accumulation in groundwater (Kaparullina et al. 2011). An alternative approach is to exploit the iron mobilization abilities of microorganisms (Zuo and Zhang 2010).

Iron-chelating compounds called siderophores are produced by diverse plant-associated bacteria. These low-molecular-weight organic compounds are induced under low-iron conditions. Following secretion, they bind ferric iron with a high affinity, increasing its solubilization from iron oxide precipitates in the soil; the subsequent binding of the Fe^{3+}-siderophore complexes to highly specific bacterial siderophore receptors facilitates concurrent uptake and reduction of Fe^{3+} to Fe^{2+}

Fig. 7.6 Schematic representations of iron uptake systems of plant roots and role of siderophore (Sid)-producing bacteria in enhancing iron availability for plant. Plants acquire iron from the soil through the plasma membrane (PM) of their root epidermal cells by two different strategies (Strategies I and II). In non-grass species (Strategy I), acidification of the rhizosphere occurs in part through the activity of a plasma membrane (PM) H^+-ATPase. This H^+ excretion contributes to the solubilization of Fe^{+3}, which is reduced to Fe^{+2} by the FRO2 ferric chelate reductase, transferring electrons (e^-) from NADPH to Fe^{+3}. Fe^{+2} is then transported through the plasma membrane of root epidermal cells by the iron-regulated transporter 1 (IRT1) (Lemanceau et al. 2009). In grasses, Strategy II involves the synthesis of phytosiderophores (P-Sid) from nicotianamine (NA), which is derived from methionine (Met). P-Sid is secreted from the roots by an uncharacterized mechanism into the rhizosphere where it chelates Fe^{+3}. The Fe^{+3}-P-Sid complex is then transported into the epidermal cells of the roots by proteins such as the yellow stripe 1 (YS1) transporter. Bacteria do not take up Fe^{+3}-Sid complexes, but rather obtain iron through a reduction-based mechanism involving Fe-Sid membrane receptors, acquiring Fe^{2+} while releasing Sid for subsequent reuse. Sid increases the Fe^{+3} pools in the rhizosphere, increasing Fe^{+3} available to the root P-Sid. Given the differences in the binding affinity among siderophores, P-Sids that have a higher affinity for Fe^{3+} than Sid may acquire it via ligand exchange

(Boukhalfa and Crumbliss 2002). PGPR inoculants that increased iron uptake into plants with concurrent stimulation of plant growth have been reported (Barzanti et al. 2007; Burd et al. 2000; Carrillo-Castañeda et al. 2002; Lemanceau et al. 2009). Moreover, a contribution of microbial siderophores to the iron nutrition of plants using Strategies I and II has been reported (Jin et al. 2006; Johnson et al. 2002; Rasouli-Sadaghiani et al. 2014; Robin et al. 2008; Vansuyt et al. 2007).

The opportunities for ligand exchange between microbial siderophores and phytosiderophores suggest a role for microbial siderophores in enhancing the iron nutrition of gramineous plants. In particular, when plants use Strategy II for iron acquisition, their phytosiderophores may be able to compete with the bacterial siderophores for iron binding, as supported by studies showing differences among bacterial siderophores in their affinity for iron (Dulla et al. 2010), and the fact that a siderophore or phytosiderophore with a high affinity for Fe^{3+} will be able to steal the Fe^{3+} from one with a lower affinity for Fe^{3+}. This mechanism of uptake, designated *ligand exchange*, was first demonstrated with a fungal siderophore that enhanced iron uptake by barley (Yehuda et al. 1996). However, the extent to which bacterial siderophores are produced in sufficiently high amounts in the rhizosphere to impact the iron nutrition of plants remains an unanswered question (Crowley et al. 1988).

Microbial siderophores may also enhance iron uptake by plants that use Strategy I for iron acquisition. One proposed mechanism is via the transfer of ferric ions from a microbial siderophore to a plant ferric chelate reductase, thus promoting iron reduction and transport into the plant. The extent to which this mechanism facilitates enhanced iron uptake into the plant is not yet known (Crowley et al. 1988). Alternatively, bacteria may alter the signaling pathways that are involved in the physiological responses of the plant to iron deficiency. For example, IAA has a major role in activating plant responses that lead to rhizosphere acidification and iron acquisition by roots (Bacaicoa et al. 2011), with roles for ethylene implicated as well (Lucena et al. 2006). The ability of bacteria to produce IAA (Sect. 7.7.3) and alter plant ethylene signaling (Sect. 7.7.2) suggests mechanisms by which PGPR may influence the iron nutrition of plants. The finding that PGPRs enhance iron acquisition in non-gramineous (Sharma et al. 2003; Johnson et al. 2002; Vansuyt et al. 2007) indicates that one or more of these mechanisms may promote physiologically relevant levels of iron uptake into plants.

7.7.3.3 Phosphorus

Phosphorus (P) is generally the second most limiting nutrient for plant growth after nitrogen. P is soluble in a monobasic ($H_2PO_4^-$) or dibasic ($HPO_4{}^{2-}$) form, but even in soils with abundant P, usually only about 1% of the soil P is actually in a soluble form. Over 90% of soil P is generally insoluble in an inorganic form, such as apatite, or in an organic form, such as inositol phosphate (soil phytate), phosphomonoesters, and phosphotriesterase (Khan et al. 2007); these require mineralization before they become plant available. Due to limited P bioavailability in most soils, P limitation is often a limiting factor for plant growth (Khan et al. 2007). Plant strategies to acquire P include the root exudation of organic acids or enzymes to chelate inorganic P or enzymatically release phosphate from organic compounds (Hong et al. 2008; Park et al. 2007; Xiao et al. 2007). In addition, plants adjust their root architecture to low-P conditions through inhibition of primary root growth, promotion of lateral root growth, enhancement of root hair development, and cluster root formation, which all promote P acquisition by plants (Jain et al. 2007; Ma et al. 2003; Niu et al. 2013; Osmont et al. 2007). Lateral roots, in particular, play an important role in P acquisition by increasing soil exploration (Zhu et al. 2005), the absorptive surface of the root system (Pérez-Torres et al. 2008), and P solubilization (Lynch 2007).

Microorganisms have been widely shown to enhance plant growth by enhancing the bioavailability of P for plants. This is a well-known function of mycorrhizal fungi, which form an extensive network that can extract P from a large volume of soil, but is also a function of many bacterial genera. In fact, enhancing plant P bioavailability is the most common mode of action identified in the PGPRs that have been characterized. The major mechanisms by which PGPR do this are by converting insoluble phosphates such as $Ca_3(PO_4)_2$ (Rodriguez et al. 2004) into soluble forms through the release of organic acids that promote acidification and releasing phosphates from organic phosphates via the secretion of extracellular phosphatases (Glick 2012; Gyaneshwar et al. 2002; Van Der Heijden et al. 2008). The ease of with which P-solubilizing bacteria can be identified using a classic plate assay (Pilovskaya 1948) enabled an extensive number of studies that have screened bacteria for P solubilization activities. These studies have identified diverse bacteria and have often screened and identified strains with resistance to target environmental stresses, such as high salinity (Barassi et al. 2006; Son et al. 2006), high concentrations of heavy metals (Zaidi et al. 2006), and low pH (Son et al. 2006), as well as with an ability to colonize roots and promote plant growth (Taurian et al. 2010). Consequently, P solubilization is a common trait in characterized PGPRs.

7.7.4 Induction of Increased Plant Osmolyte Accumulation

The accumulation of osmolyte compounds can enhance plant tolerance to salinity, drought, and heat (Chen et al. 2007; Dodd and Perez-Alfocea 2012). Osmolytes are low-molecular-weight organic compounds that are used by cells to maintain turgor pressure and cell volume, especially under water-limited conditions. To withstand water limitation, cells of all organisms synthesize metabolites to maintain turgor pressure and full hydration of cytoplasmic constituents, which is critical to the structural integrity of membranes, enzymes, and other cellular components (Majumder et al. 2010). Major types of osmolytes are sugar alcohols (glycerol and methylated inositols), complex sugars (trehalose, raffinose and fructans), quaternary amino acid derivatives (proline, glycine betaine, b-alanine betaine, proline betaine), tertiary amines (ectoine) and sulfonium compounds (dimethyl sulfonium propionate) (Majumder et al. 2010). The accumulation of proline, a widely distributed osmolyte in plants, correlates with tolerance to drought and salinity stress (Szabados and Savouré 2010; Wang et al. 2015). Proline accumulation is a sensitive physiological index of the response of plants to salt and other stresses (Peng et al. 2008) and helps maintain higher leaf water potentials during stress and protect against oxidative stress, potentially by function as an antioxidant (Hayat et al. 2012).

PGPRs can favor osmolyte accumulation in plants exposed to salinity stress. To date, this has been shown for the osmolyte proline. Plants inoculated with PGPR strains showed increased proline accumulation when grown under high salinity conditions (Bano and Fatima 2009; Jha et al. 2011; Kohler et al. 2009; Upadhyay et al. 2012; Zarea et al. 2012), and this occurred in a variety of plant species, including lettuce, wheat, and corn. These results suggest that PGPR can promote an enhanced adaptive response of plants to high external salt concentrations, namely, osmolyte accumulation, indicating that this is one of the many mechanisms by which microbes promote plant tolerance to salinity stress (Bianco and Defez 2009; Munns and Tester 2008; Dodd and Perez-Alfocea 2012).

7.7.5 Exopolymer production

Many soil microbes secrete extracellular polymeric substances (EPSs) into the environment, and these EPS can confer a wide range of benefits to plants. For example, these high-molecular-weight secreted compounds promote soil aggregate stability, which is one of the most important properties controlling plant growth in semiarid environments (Paul and Lade 2014). These EPS, which are comprised primarily of extracellular polysaccharides, proteins, and DNA, are also central to the function and structural integrity of biofilms (Donlan 2002). They serve as a matrix that promotes biofilm adherence to surfaces and as a matrix that binds water, thus contributing greatly to the water-holding capacity of the soil and the biofilms on root surface (Grover et al. 2010). EPS-producing PGPRs have been associated with aggregation of root-adhering soils (Alami et al. 2000; Upadhyay et al. 2011) and improved soil structure (Sandhya et al. 2009), both of which are associated with increased plant resistance to water stress. EPS-producing PGPRs have also been proposed to bind cations including Na^+, thus potentially decreasing the content of Na^+ available for plant uptake and thus helping to ameliorate the negative impact of salinity on plant growth (Ashraf et al. 2004; Geddie and Sutherland 1993; Grover et al. 2010; Upadhyay et al. 2009).

7.7.6 Promotion of Ion Homeostasis in Plants

PGPR may alter ion homeostasis in plants such that the plants are better able to tolerate salinity stress. Salinity stress generally results in the accumulation of Na^+ in leaves due to transport in the transpiration stream and an accompanying deficit in K^+. This physiological response is so consistent that the K^+/Na^+ ratio is used as an indicator of plant salt tolerance (Hamdia et al. 2004). A breadth of reports have documented that PGPR-inoculated plants grown in saline soils have a higher K^+ ion concentration and, in turn, a higher K^+/Na^+ ratio, than uninoculated plants (Jiang et al. 2012; Kasotia et al. 2015; Kohler et al. 2009; Nadeem et al. 2012; Rojas-Tapias et al. 2012; Safronova et al. 2012; Shrivastava and Kumar 2015; Yao et al. 2010; Nadeem et al. 2007; Chang et al. 2014; Egamberdieva et al. 2015; Nadeem et al. 2009; Wang et al. 2016; Mayak et al. 2004). Potassium plays a key role in plant water stress tolerance and is responsible for stomatal movements in response to changes in leaf water status (Caravaca et al. 2004); thus, PGPR-associated increases in K^+ concentration may help prevent salinity-induced stomatal closure. Although the mechanism by which PGPR alter ion uptake into roots is largely unknown, Zhang et al. (2008) demonstrated that a *Bacillus subtilis* strain can mediate the level of salt tolerance in *Arabidopsis thaliana* by regulating the K^+ transporter HKT1. Interestingly, these changes in HKT1 expression, namely, downregulation in roots and upregulation in shoots, were induced by the mixture of volatile compounds emitted by this *B. subtilis* strain, demonstrating that volatile bacterial signals can affect ion homeostasis and salinity stress tolerance in plants via an effect on a high-affinity K^+ transporter. Some reports also suggest that bacteria influence Ca^{2+} levels, which have an early signaling role in the response to high salinity (Fu et al. 2010).

7.7.7 Induction of Plant Production of Antioxidant Enzymes

Microbes may help prevent or reduce oxidative damage to plants by secreting antioxidant enzymes. The production of oxygen-based radicals is the bane of all aerobic species. These radicals, collectively called reactive oxygen species (ROS), include peroxides, superoxide, hydroxyl radical, and singlet oxygen. Due to their reactive nature, ROS can damage cellular macromolecules and organelles. Various abiotic stresses lead to the production of ROS in plants; these include salinity and drought stress (Hichem et al. 2010; Johnson et al. 2003). To protect against oxidative stress, plant cells produce both antioxidant enzymes and nonenzymatic antioxidants (Hasegawa et al. 2000; Mayak et al. 2004; Miller et al. 2010). Plant tolerance to high salinity has been correlated with high antioxidant enzyme activities, including catalase, ascorbate peroxidase, glutathione reductase, and superoxide dismutase (Apel and Hirt 2004; Miller et al. 2010; Mittova et al. 2002, 2003).

Several studies have reported that rhizobacteria induce plant synthesis of antioxidant enzymes in response to salinity stress (Heidari and Golpayegani 2012; Paul and Lade 2014; Singh et al. 2013; Chakraborty et al. 2013; Nautiyal et al. 2008; Bianco and Defez 2009; Kohler et al. 2009; Jha and Subramanian 2013). These PGPR-induced antioxidant enzymes are believed to contribute to salinity stress tolerance by eliminating hydrogen peroxide from salt-stressed roots (Kim et al. 2005). PGPRs may also alleviate drought stress, as shown following inoculation of maize with five drought-tolerant plant growth-promoting *Pseudomonas* sp. strains (Sandhya et al. 2009).

7.7.8 Reduction of Toxicity of Heavy Metals and Organic Pollutants to Plants

Heavy metals at elevated levels are generally toxic to plants, impairing their metabolism and reducing plant growth. Previous studies have demonstrated that most heavy metal and other xenobiotic contaminants inhibit the root growth of plants

(Arshad et al. 2007). Microbes have a variety of mechanisms for detoxifying heavy metals (Chen et al. 2015; Gadd 2000; Glick 2010; Lim et al. 2003; Lin and Lin 2005; Malik 2004; Soleimani et al. 2011). For example, microbial cell walls have functional groups that can bind heavy metal ions, and this binding and immobilization may have contributed to the reduced uptake of cadmium (Cd) into barley plants following inoculation with PGPR (Luo et al. 2011; Scott and Karanjkar 1992). PGPRs may also promote plant health by reducing the phytotoxic effects of heavy metals, as shown for nickel (Ni) and Cd toxicity following inoculation of *Methylobacterium oryzae* and *Burkholderia* sp. strains on tomato (Madhaiyan et al. 2007).

Organic pollutants may also be harmful to plants. Some endophytes enhance plant tolerance to pollutants and do so by degrading them (Garipova 2014). Organic pollutants may accumulate in plant tissues in the absence of degradative enzymes (Burken 2004), but may be completely degraded in the presence of an endophyte capable of degradation (Lodewyckx et al. 2002a, b; Moore et al. 2006). Although pollutant degradation abilities are found in both endophytes (Barzanti et al. 2007) and free-living bacteria (Mrozik and Piotrowska-Seget 2010), genes encoding the degradative enzymes for specific pollutants occurred more frequently in endophytic bacteria in the presence of those pollutants than in bacteria isolated from soil (Siciliano et al. 2001). The ability of endophytes to degrade pollutants following their extraction from the soil by plants illustrates the contribution of endophytes to both bioremediation of soils and safe cultivation of agricultural products in contaminated soils (Garipova 2014). For example, it was shown experimentally that pea plants treated with the endophyte *Pseudomonas* utilized the 2,4-D herbicide from soil without accumulating it in tissues (Germaine et al. 2006).

Plants synthesize and accumulate ethylene in response to contaminant-induced stresses (Arshad et al. 2007); thus, microbes may influence plant responses to heavy metal contaminants by interfering with ethylene synthesis. Bacteria that produce ACC deaminase (Sect. 7.7.2) have been examined for their ability to mitigate the ill effects of soil contamination caused by xenobiotic chemicals and heavy metals on plants. These bacteria have been shown to promote plant growth in the presence of heavy metals by reducing the stress ethylene synthesized in plants (Arshad et al. 2007, 2008; Belimov et al. 2005; Glick et al. 2007b; Ma et al. 2010; Madhaiyan et al. 2007; Rajkumar et al. 2006; Safronova et al. 2006). In addition to ACC deaminase activity, bacterial siderophores may help plants reduce heavy metal toxicity by increasing the supply of iron to the plant (Burd et al. 2000).

7.7.9 Induction of Resistance to Temperature Stress

Microbes can also increase plant resistance to temperature stress (Su et al. 2015; Selvakumar et al. 2008a, b). For example, a thermotolerant *Pseudomonas* sp. strain induced thermotolerance in sorghum seedlings (Ali et al. 2009), and a *Burkholderia phytofirmans* strain capable of epiphytic and endophytic colonization of grapevines

(Compant et al. 2005) protected plants against heat as well as chilling stress (Ait Barka et al. 2006; Bensalim et al. 1998). The mechanisms by which these benefits are conferred, however, are poorly understood.

7.8 Selection of the Most Stress-Tolerant Microorganisms

The ability to use microbial inoculants to enhance plant tolerance to abiotic stress requires that the introduced microbes tolerate the stressful conditions (Devliegher et al. 1995), as well as compete effectively with the native microflora after inoculation (Rekha et al. 2007). Thus, the selection of most effective root-colonizing bacterial strains is required to fully realize the benefits of inoculation. A general approach to identifying potential PGPR strains to promote plant growth under environmentally stressful conditions has therefore been to isolate organism from a stressful environment, as illustrated by the isolation of halotolerant bacteria from wheat roots grown in saline soil and their subsequent success in stimulating plant growth (Egamberdieva et al. 2008). An alternative approach is to screen bacterial isolates for those that are tolerant to the relevant stress (Lifshitz et al. 1986; Shrivastava and Kumar 2015). In general, microorganisms tolerating extreme environmental conditions have been found suitable for use in various agricultural practices (Egamberdieva and Kucharova 2009). Thus, an effective strategy for the rapid identification of efficacious PGPR strains to use as bioinoculants for stressed crops may be the isolation of indigenous microorganisms from stress-affected soils and from plants grown in such soils, with subsequent screening on the basis of traits contributing to stress tolerance and plant growth promotion and ultimately screening for improved growth or health of plants growth under environmentally stressful conditions (Grover et al. 2010).

7.9 Concluding Remarks and Future Perspectives

Plants developed mutualistic associations with mycorrhizal fungi very early following their transition from aquatic to terrestrial habitats. They embraced these fungi as a means of establishing a network for acquiring enough water and nutrients to meet their needs in their new, water-limited home. This mutualism illustrates the early dependence of plants on microbes in their adaptation to environmental stress. Microbes still play a critical role in conferring the phenotypic plasticity necessary to tolerate a wide range of environmental insults. Although we have identified some of the mechanisms by which bacteria can promote plant tolerance to abiotic stress, ranging from the secretion of bioactive compounds to interference in plant hormonal signaling, many mechanisms have yet to be discovered. Knowledge of these mechanisms, and the full complement of mechanisms expressed by any given microbial inoculant, is important in moving forward in evaluating the growth-promoting potential and plant-protective effects of inoculants in the field. Given the increasing exposure of our agricultural crops to abiotic stresses, and particularly to drought, salinity, and nutrient limitation, the optimization of inoculants for agricultural use is critical as a complement to the on-going efforts to develop stress-tolerant crop varieties.

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References

Acosta-Martínez V, Dowd S, Sun Y, Allen V (2008) Tag-encoded pyrosequencing analysis of bacterial diversity in a single soil type as affected by management and land use. Soil Biol Biochem 40:2762–2770

Acquaah G (2007) Principles of plant genetics and breeding. Blackwell, Oxford, UK

Ahmad P (2013) Oxidative damage to plants, antioxidant networks and signaling. Academic/Elsevier, San Diego

Ait Barka 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 72:7246–7252

Alami Y, Achouak W, Marol C, Heulin T (2000) Rhizosphere soil aggregation and plant growth promotion of sunflowers by an exopolysaccharide-producing *Rhizobium* sp. strain isolated from sunflower roots. Appl Environ Microbiol 66:3393–3398

Ali S, Charles TC, Glick BR (2012) Delay of flower senescence by bacterial endophytes expressing 1-aminocyclopropane-1-carboxylate deaminase. J Appl Microbiol 113:1139–1144

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

Ali S, 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 Fertil Soils 46:45–55

Alikhani HA, Etesami H, Mohammadi L (2010) Effect of superior indole-3-acetic acid producing Rhizobia and the combination with Ag and L-Tryptophan on wheat growth indices under in vitro conditions. Food Agri Environ 3:949–954

Allakhverdiev SI, Sakamoto A, Nishiyama Y, Inaba M, Murata N (2000) Ionic and Osmotic Effects of NaCl-Induced Inactivation of Photosystems I and II in *Synechococcus* sp. Plant Physiol 123:1047–1056

America SSSO (2001) Glossary of soil science terms. Soil Science Society of America, Madison

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399

Araus JL, Slafer GA, Royo C, Serret MD (2008) Breeding for yield potential and stress adaptation in cereals. Critl Rev Plant Sci 27:377–412

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

Arshad M, Frankenberger WTJ (2002) Ethylene: agricultural sources and applications. Kluwer Academic, New York, NY, p 342

Arshad M, Saleem M, Hussain S (2007) Perspectives of bacterial ACC deaminase in phytoremediation. Trends Biotechnol 25:356–362

Arshad M, Shaharoona B, Mahmood T (2008) Inoculation with *Pseudomonas* spp. Containing ACC-deaminase partially eliminates the effects of drought stress on growth, yield, and ripening of pea (*Pisum sativum* L.) Project supported by the Higher Education Commission, Islamabad, Pakistan (No. PIN 041 211534 A-031). Pedosphere 18:611–620

Ashraf M, Akram NA (2009) Improving salinity tolerance of plants through conventional breeding and genetic engineering: an analytical comparison. Biotechnol Adv 27:744–752

Ashraf M, Hasnain S, Berge O, Mahmood T (2004) Inoculating wheat seedlings with exopolysaccharide-producing bacteria restricts sodium uptake and stimulates plant growth under salt stress. Biol Fertil Soils 40:157–162

Athar R, Ahmad M (2002) Heavy Metal Toxicity: Effect on plant growth and metal uptake by wheat, and on free living *Azotobacter*. Water Air Soil Pollut 138:165–180

Babalola OO (2010) Beneficial bacteria of agricultural importance. Biotechnol Lett 32:1559–1570

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57:233–266

Baligar VC, Fageria NK, He ZL (2001) Nutrient use efficiency in plants. Commun Soil Sci Plant Anal 32:921–950

Banik P, Midya A, Sarkar BK, Ghose SS (2006) Wheat and chickpea intercropping systems in an additive series experiment: advantages and weed smothering. Eur J Agro 24:325–332

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

Barassi CA, Ayrault G, Creus CM, Sueldo RJ, Sobrero MT (2006) Seed inoculation with Azospirillum mitigates NaCl effects on lettuce. Sci Hortic 109:8–14

Barnawal D, Bharti N, Maji D, Chanotiya CS, Kalra A (2012) 1-Aminocyclopropane-1-carboxylic acid (ACC) deaminase-containing rhizobacteria protect *Ocimum sanctum* plants during waterlogging stress via reduced ethylene generation. Plant Physiol Biochem 58:227–235

Barzanti R, Ozino F, Bazzicalupo M, Gabbrielli R, Galardi F, Gonnelli C, Mengoni A (2007) Isolation and characterization of endophytic bacteria from the nickel hyperaccumulator plant Alyssum bertolonii. Microb Ecol 53:306–316

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

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

Belimov AA, Hontzeas N, Safronova VI, Demchinskaya SV, Piluzza G, Bullitta S, Glick BR (2005) Cadmium-tolerant plant growth-promoting bacteria associated with the roots of Indian mustard (*Brassica juncea* L. Czern.) Soil Biol Biochem 37:241–250

Bensalim S, Nowak J, Asiedu S (1998) A plant growth promoting rhizobacterium and temperature effects on performance of 18 clones of potato. Am J Pot Res 75:145–152

Berg G, Smalla K (2009) Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiol Ecol 68:1–13

Bhatnagar-Mathur P, Vadez V, Sharma KK (2008) Transgenic approaches for abiotic stress tolerance in plants: Retrospect and prospects. Plant Cell Rep 27:411–424

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

Botella MÁ, Del Amor F, Amorós A, Serrano M, Martínez V, Cerdá A (2000) Polyamine, ethylene and other physico-chemical parameters in tomato (*Lycopersicon esculentum*) fruits as affected by salinity. Physiol Plantarum 109:428–434

Botella MA, Martinez V, Pardines J, Cerdá A (1997) Salinity induced potassium deficiency in maize plants. J Plant Physiol 150:200–205

Boukhalfa H, Crumbliss AL (2002) Chemical aspects of siderophore mediated iron transport. Biometals 15:325–339

Buée M, Boer W, Martin F, Overbeek L, Jurkevitch E (2009) The rhizosphere zoo: An overview of plant-associated communities of microorganisms, including phages, bacteria, archaea, and fungi, and of some of their structuring factors. Plant Soil 321:189–212

Burd GI, Dixon DG, Glick BR (2000) Plant growth-promoting bacteria that decrease heavy metal toxicity in plants. Can J Microbiol 46:237–245

Burken JG (2004) Uptake and metabolism of organic compounds: Green-Liver model. In: Phytoremediation. Wiley, pp 59–84

Caravaca F, Figueroa D, Barea JM, Azcón-Aguilar C, Roldán A (2004) Effect of mycorrhizal inoculation on nutrient acquisition, gas exchange, and nitrate reductase activity of two mediterranean-autochthonous shrub species under drought stress. J Plant Nutr 27:57–74

Carmen B, Roberto D (2011) Soil bacteria support and protect plants against abiotic stresses abiotic stress in plants mechanisms and adaptations. In: Shan A (ed) InTech. pp 143–170

Carrillo-Castañeda G, Juárez Muñoz J, Ramón Peralta-Videa J, Gomez E, Gardea-Torresdey JL (2002) Plant growth-promoting bacteria promote copper and iron translocation from root to shoot in alfalfa seedlings. J Plant Nutr 26:1801–1814

Cattivelli L, Rizza F, Badeck FW, Mazzucotelli E, Mastrangelo AM, Francia E, Marè C, Tondelli A, Stanca AM (2008) Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. Field Crop Res 105:1–14

Chakraborty N, Ghosh R, Ghosh S, Narula K, Tayal R, Datta A, Chakraborty S (2013) Reduction of oxalate levels in tomato fruit and consequent metabolic remodeling following overexpression of a fungal oxalate decarboxylase. Plant Physiol 162:364–378

Chakraborty U, Chakraborty B, Dey P, Chakraborty AP (2015) 15 Role of microorganisms in alleviation of abiotic stresses for sustainable agriculture abiotic stresses in crop plants. 232pp

Chang P, Gerhardt KE, Huang XD, XM Y, Glick BR, Gerwing PD, Greenberg BM (2014) Plant growth-promoting bacteria facilitate the growth of barley and oats in salt-impacted soil: implications for phytoremediation of saline soils. Int J Phytoremediation 16:1133–1147

Charlson DV, Shoemaker RC (2006) Evolution of iron acquisition in higher plants. J Plant Nutr 29:1109–1125

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 Mole Biol 40:396–403

Chen M, Xu P, Zeng G, Yang C, Huang D, Zhang J (2015) Bioremediation of soils contaminated with polycyclic aromatic hydrocarbons, petroleum, pesticides, chlorophenols and heavy metals by composting: Applications, microbes and future research needs. Biotechnol Adv 33:745–755

Choudhary D (2012) Microbial rescue to plant under habitat-imposed abiotic and biotic stresses. Appl Microbiol Biotechnol 96:1137–1155

Choudhary DK, Kasotia A, Jain S, Vaishnav A, Kumari S, Sharma KP, Varma A (2015) Bacterial-mediated tolerance and resistance to plants under abiotic and biotic stresses. J Plant Growth Regul:1–25

C. Lucena, B. M. Waters, F. J. Romera, M. J. Garcia, M. Morales, E. Alcantara, R. Perez-Vicente, (2006) Ethylene could influence ferric reductase, iron transporter, and H+-ATPase gene expression by affecting FER (or FER-like) gene activity. Journal of Experimental Botany 57(15):4145–4154

Compant S, Reiter B, Sessitsch A, Nowak J, Clement C, Ait Barka E (2005) Endophytic colonization of *Vitis vinifera* L. by plant growth-promoting bacterium *Burkholderia* sp. strain PsJN. Appl Environ Microbiol 71:1685–1693

Costacurta A, Vanderleyden J (1995) Synthesis of phytohormones by plant-associated bacteria. Critl Rev Microbiol 21:1–18

Council WW (2008) Water crisis. In: World Water Council (ed) Water at a Glance. World Water Council, Marseilles

Crowley DE, Reid CPP, Szaniszlo PJ (1988) Utilization of microbial siderophores in iron acquisition by oat. Plant Physiol 87:680–685

Curie C, Panaviene Z, Loulergue C, Dellaporta SL, Briat JF, Walker EL (2001) Maize yellow stripe1 encodes a membrane protein directly involved in Fe(III) uptake. Nature 409:346–349

Cushman JC, Bohnert HJ (2000) Genomic approaches to plant stress tolerance. Curr Opin Plant Biol 3:117–124

Dahmardeh M, Ghanbari A, Syasar B, Ramroudi M (2009) Effect of intercropping maize (*Zea mays* L.) with cow pea (*Vigna unguiculata* L.) on green forage yield and quality evaluation. Asian J Plant Sci 8:235

Damodaran T, Rai B, Jha SK, Kannan R, Pandey BK, Vijayalaxmi S, Mishra VK, Sharma DK (2014) Rhizosphere and endophytic bacteria for induction of salt tolerance in gladiolus grown in sodic soils. J Plant Interact 9:577–584

David BL, Christopher BF (2007) Global scale climate–crop yield relationships and the impacts of recent warming. Environ Res Lett 2:014002

Davies WJ, Zhang J, Yang J, Dodd IC (2011) Novel crop science to improve yield and resource use efficiency in water-limited agriculture. J Agri Sci 149:123–131

Des Marais DL, Juenger TE (2010) Pleiotropy, plasticity, and the evolution of plant abiotic stress tolerance. Ann N Y Acad Sci 1206:56–79

Desai A, Archana G (2011) Role of siderophores in crop improvement. In: Maheshwari KD (ed) Bacteria in agrobiology: plant nutrient management. Springer, Berlin, pp 109–139

Devliegher W, Arif M, Verstraete W (1995) Survival and plant growth promotion of detergent-adapted *Pseudomonas fluorescens* ANP15 and *Pseudomonas aeruginosa* 7NSK2. Appl Environ Microbiol 61:3865–3871

Diby P, Sarma YR, Srinivasan V, Anandaraj M (2005) *Pseudomonas fluorescens* mediated vigour in black pepper (*Piper nigrum* L.) under green house cultivation. Ann Microbiol 55:171–174

Dimkpa C, Weinand T, Asch F (2009) Plant-rhizobacteria interactions alleviate abiotic stress conditions. Plant Cell Environ 32:1682–1694

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

Donlan RM (2002) Biofilms: microbial life on surfaces. Emerg Infect Dis 8:881–890

Dwivedi S, Upadhyaya H, Subudhi P, Gehring C, Bajic V, Ortiz R (2010) Enhancing abiotic stress tolerance in cereals through breeding and transgenic interventions. Plant Breeding Rev 33:31–114

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

Egamberdieva D (2011) Survival of *Pseudomonas extremorientalis* TSAU20 and *P. chlororaphis* TSAU13 in the rhizosphere of common bean (*Phaseolus vulgaris*) under saline conditions. Plant Soil Env 57:122–127

Egamberdieva D, Berg G, Lindström K, Räsänen L (2013) Alleviation of salt stress of symbiotic *Galega officinalis* L. (goat's rue) by co-inoculation of *Rhizobium* with root-colonizing Pseudomonas. Plant Soil 369:453–465

Egamberdieva D, Kamilova F, Validov S, Gafurova L, Kucharova Z, Lugtenberg B (2008) High incidence of plant growth-stimulating bacteria associated with the rhizosphere of wheat grown on salinated soil in Uzbekistan. Environ Microbiol 10:1–9

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

Egamberdieva D, Li L, Lindström K, Räsänen L (2015) A synergistic interaction between salt-tolerant *Pseudomonas* and *Mesorhizobium* strains improves growth and symbiotic performance of liquorice (*Glycyrrhiza uralensis* Fish.) under salt stress. Appl Microbiol Biotechnol:1–13

El-Khawas H, Adachi K (1999) Identification and quantification of auxins in culture media of *Azospirillum* and *Klebsiella* and their effect on rice roots. Biol Fertil Soils 28:377–381

Endris S, Mohammad MJ (2007) Nutrient acquisition and yield response of Barley exposed to salt stress under different levels of potassium nutrition. Int J Environ Sci Technol 4:323–330

Esquivel-Cote R, Ramírez-Gama RM, Tsuzuki-Reyes G, Orozco-Segovia A, Huante P (2010) *Azospirillum lipoferum* strain AZm5 containing 1-aminocyclopropane-1-carboxylic acid deaminase improves early growth of tomato seedlings under nitrogen deficiency. Plant Soil 337:65–75

Etesami H, Alikhani H, Mirseyed Hosseini H (2015a) Indole-3-Acetic Acid and 1-Aminocyclopropane-1-Carboxylate Deaminase: Bacterial traits required in rhizosphere, rhizoplane and/or endophytic competence by beneficial bacteria. In: Maheshwari DK (ed) Bacterial metabolites in sustainable agroecosystem, Sustainable development and biodiversity, vol 12. Springer International Publishing, New York, pp 183–258

Etesami H, Alikhani HA (2016a) Co-inoculation with endophytic and rhizosphere bacteria allows reduced application rates of N-fertilizer for rice plant. Rhizosphere 2:15. doi:10.1016/j.rhisph.2016.09.003

Etesami H, Alikhani HA (2016b) Rhizosphere and endorhiza of oilseed rape (*Brassica napus* L.) plant harbor bacteria with multifaceted beneficial effects. Biol Con 94:11–24

Etesami H, Alikhani HA, Hosseini HM (2015b) Indole-3-acetic acid (IAA) production trait, a useful screening to select endophytic and rhizosphere competent bacteria for rice growth promoting agents. MethodsX 2:72–78

Etesami H, Hosseini H, Alikhani H, Mohammadi L (2014a) Bacterial biosynthesis of 1-aminocyclopropane-1-carboxylate (ACC) deaminase and indole-3-acetic acid (IAA) as endophytic preferential selection traits by rice plant seedlings. J Plant Growth Regul 33:654–670

Etesami H, Mirseyed Hosseini H, Alikhani HA (2014b) Bacterial biosynthesis of 1-aminocyclopropane-1-caboxylate (ACC) deaminase, a useful trait to elongation and endophytic colonization of the roots of rice under constant flooded conditions. Physiol Mole Biol Plant 20:425–434

Eva Bacaicoa, Verónica Mora, Ángel María Zamarreño, Marta Fuentes, Esther Casanova, José María García-Mina, (2011) Auxin: A major player in the shoot-to-root regulation of root Fe-stress physiological responses to Fe deficiency in cucumber plants. Plant Physiology and Biochemistry 49(5):545–556

FAO (2008) Land and plant nutrition management service. http://www.fao.org/ag/agl/agll/spush

FAO (2009a) Aquastat www.faoorg/nr/water/aquastat/data/query/indexhtml

FAO (2009b) Food and Agriculture Organisation of the United Nations. www.faoorg/askfao/topicsListdo?mainAreaId=20263

Feigin A (1985) Fertilization management of crops irrigated with saline water. Plant Soil 89:285–299

Franche C, Lindström K, Elmerich C (2008) Nitrogen-fixing bacteria associated with leguminous and non-leguminous plants. Plant Soil 321:35–59. doi:10.1007/s11104-008-9833-8

Francisco M. del Amor, Paula Cuadra-Crespo, (2012) Plant growth-promoting bacteria as a tool to improve salinity tolerance in sweet pepper. Functional Plant Biology 39(1):82

Fu Q, Liu C, Ding N, Lin Y, Guo B (2010) Ameliorative effects of inoculation with the plant growth-promoting rhizobacterium *Pseudomonas* sp. DW1 on growth of eggplant (*Solanum melongena* L.) seedlings under salt stress. Agri Water Manage 97:1994–2000

Gadd GM (2000) Bioremedial potential of microbial mechanisms of metal mobilization and immobilization. Curr Opin Biotechnol 11:271–279

Garcia NS, Fu F, Sedwick PN, Hutchins DA (2015) Iron deficiency increases growth and nitrogen-fixation rates of phosphorus-deficient marine cyanobacteria. ISME J 9:238–245

Garipova SR (2014) Perspectives on using endophytic bacteria for the bioremediation of arable soils polluted by residual amounts of pesticides and xenobiotics. Biol Bulletin Rev 4:300–310

Geddie JL, Sutherland IW (1993) Uptake of metals by bacterial polysaccharides. J Appl Bacteriol 74:467–472

Germaine KJ, Liu X, Cabellos GG, Hogan JP, Ryan D, Dowling DN (2006) Bacterial endophyte-enhanced phytoremediation of the organochlorine herbicide 2,4-dichlorophenoxyacetic acid. FEMS Microbiol Ecol 57:302–310

Germida J, Siciliano S (2001) Taxonomic diversity of bacteria associated with the roots of modern, recent and ancient wheat cultivars. Biol Fertil Soils 33:410–415

Glick BR (2005) Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. FEMS Microbiol Llett 251:1–7

Glick BR (2010) Using soil bacteria to facilitate phytoremediation. Biotechnol Adv 28:367–374

Glick BR (2012) Plant growth-promoting bacteria: mechanisms and applications. Scientifica:1–15

Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 169:30–39

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

Glick BR, Todorovic B, Czarny J, Cheng Z, Duan J, McConkey B (2007b) Promotion of plant growth by bacterial ACC Deaminase. Crit Rev Plant Sci 26:227–242

Glenn F. J. Dulla, Ksenia V. Krasileva, Steven E. Lindow, Interference of quorum sensing in Pseudomonas syringae by bacterial epiphytes that limit iron availability. Environmental Microbiology 12(6):1762–1774

Gnanamanickam SS (2006) Plant-associated bacteria, vol 1. Springer, New York

Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C (2010) Food security: The challenge of feeding 9 billion people. Sci 327:812–818

Gray EJ, Smith DL (2005) Intracellular and extracellular PGPR: commonalities and distinctions in the plant-bacterium signaling processes. Soil Biol Biochem 37:395–412

Grieve CM, Grattan SR (1999) Mineral nutrient acquisition and response by plants grown in saline environments. In: Pessarakli M (ed) Handbook of plant and crop stress, Books in soils, plants, and the environment, vol 2. CRC Press, New York, pp 203–229

Grover M, Ali SZ, Sandhya V, Rasul A, Venkateswarlu B (2010) Role of microorganisms in adaptation of agriculture crops to abiotic stresses. World J Microbiol Biotechnol 27:1231–1240

Guerinot ML (2010) Iron. In: Hell R, Mendel R-R (eds) Cell biology of metals and nutrients. Springer, Berlin, pp 75–94

Guinel FC, Sloetjes LL (2000) Ethylene is involved in the nodulation phenotype of *Pisum sativum* R50 (sym 16), a pleiotropic mutant that nodulates poorly and has pale green leaves. J Exp Bbot 51:885–894

Gyaneshwar P, Kumar GN, Parekh L, Poole P (2002) Role of soil microorganisms in improving P nutrition of plants. In: Food security in nutrient-stressed environments: exploiting plants' genetic capabilities. Springer, pp 133–143

Hamdia MAE-S, Shaddad MAK, Doaa MM (2004) Mechanisms of salt tolerance and interactive effects of *Azospirillum brasilense* inoculation on maize cultivars grown under salt stress conditions. Plant Growth Reg 44:165–174

Hamilton CE, Bever JD, Labbé J, Yang X, Yin H (2016) Mitigating climate change through managing constructed-microbial communities in agriculture. Agri Ecosys Environ 216:304–308

Hansen J, Sato M, Ruedy R (2012) Perception of climate change. Proc Natl Acad Sci U S A 109:E2415–E2423

Hartmann A, Schmid M, Dv T, Berg G (2008) Plant-driven selection of microbes. Plant Soil 321:235–257

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) plant cellular and molecular responses to high salinity. Ann Rev Plant Physiol Plant Mole Biol 51:463–499. doi:10.1146/annurev.arplant.51.1.463

Hayat R, Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60:579–598

Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, Ahmad A (2012) Role of proline under changing environments: A review. Plant Signaling Behavior 7:1456–1466

Heidari M, Golpayegani A (2012) Effects of water stress and inoculation with plant growth promoting rhizobacteria (PGPR) on antioxidant status and photosynthetic pigments in basil (*Ocimum basilicum* L.) J Saudi Soc Agril Scie 11:57–61

Heidari M, Jamshid P (2010) Interaction between salinity and potassium on grain yield, carbohydrate content and nutrient uptake in pearl millet ARPN. J Agri Biol Sci 5:39–46

Hichem H, Naceur A, Mounir D (2010) Effects of salt stress on photosynthesis, PSII photochemistry and thermal energy dissipation in leaves of two corn (*Zea mays* L.) varieties. Photosynthetica 47:517–526

Hiz MC, Canher B, Niron H, Turet M (2014) Transcriptome Analysis of salt tolerant common bean (*Phaseolus vulgaris* L.) under saline conditions. PLoS One 9:e92598

Hong YF, Liu CY, Cheng KJ, Hour AL, Chan MT, Tseng TH, Chen KY, Shaw JF, SM Y (2008) The sweet potato sporamin promoter confers high-level phytase expression and improves organic phosphorus acquisition and tuber yield of transgenic potato. Plant Mole Bbiol 67:347–361

Hopkins WG, Huner NPA (2009) Introduction to plant physiology. Wiley, Hoboken

Jain A, Poling MD, Karthikeyan AS, Blakeslee JJ, Peer WA, Titapiwatanakun B, Murphy AS, Raghothama KG (2007) Differential effects of sucrose and auxin on localized phosphate deficiency-induced modulation of different traits of root system architecture in *Arabidopsis*. Plant Physiol 144:232–247

James RA, von Caemmerer S, Condon AG, Zwart AB, Munns R (2008) Genetic variation in tolerance to the osmotic stress componentof salinity stress in durum wheat. Functional Plant Biol 35:111–123

Jamil A, Riaz S, Ashraf M, Foolad MR (2011) Gene expression profiling of plants under salt stress. Crit Rev Plant Sci 30:435–458

Jeffries P, Gianinazzi S, Perotto S, Turnau K, Barea J-M (2003) The contribution of arbuscular mycorrhizal fungi in sustainable maintenance of plant health and soil fertility. Biol Fertil Soils 37:1–16

Jewell MC, Campbell BC, Godwin ID (2010) Transgenic plants for abiotic stress resistance. In: Kole C, Michler CH, Abbott AG, Hall TC (eds) Transgenic crop plants. Springer, Berlin, pp 67–132

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

Jha Y, Subramanian RB, Patel S (2011) Combination of endophytic and rhizospheric plant growth promoting rhizobacteria in *Oryza sativa* shows higher accumulation of osmoprotectant against saline stress. Acta Physiol Plant 33:797–802

Jiang F, Chen L, Belimov AA, Shaposhnikov AI, Gong F, Meng X, Hartung W, Jeschke DW, Davies WJ, Dodd IC (2012) Multiple impacts of the plant growth-promoting rhizobacterium *Variovorax paradoxus* 5C-2 on nutrient and ABA relations of *Pisum sativum*. J Exp Bot 63:6421–6430

Jin CW, He YF, Tang CX, Wu P, Zheng SJ (2006) Mechanisms of microbially enhanced Fe acquisition in red clover (*Trifolium pratense* L.) Plant Cell Environ 29:888–897

Johnson GV, Lopez A, La Valle Foster N (2002) Reduction and transport of Fe from siderophores. Plant Soil 241:27–33

Johnson HE, Broadhurst D, Goodacre R, Smith AR (2003) Metabolic fingerprinting of salt-stressed tomatoes. Phytochemistry 62:919–928

Kaparullina EN, Doronina NV, Trotsenko YA (2011) Aerobic degradation of ethylenediaminetetraacetate (review). Appl Biochem Microbiol 47:460–473

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

Kaya C, Kirnak H, Higgs D, Saltali K (2002) Supplementary calcium enhances plant growth and fruit yield in strawberry cultivars grown at high (NaCl) salinity. Sci Hortic 93:65–74

Kaymak HC, Guvenc I, Yarali F, Donmez MF (2009) The effects of bio-priming with PGPR on germination of radish (*Raphanus sativus* L.) seeds under saline conditions. Turk J Agric For 33:173–179

Khalid A, Arshad M, Zahir ZA (2004) Screening plant growth-promoting rhizobacteria for improving growth and yield of wheat. J Appl Mmicrobiol 96:473–480

Khan AL, Hamayun M, Kang S-M, Kim Y-H, Jung H-Y, Lee J-H, Lee I-J (2012) Endophytic fungal association via gibberellins and indole acetic acid can improve plant growth under abiotic stress: an example of *Paecilomyces formosus* LHL10. BMC Microbiol 12:1

Khan M, Khan NA (2013) Salicylic acid and jasmonates: approaches in abiotic stress tolerance. J Plant Biochem Physiol 1

Khan MS, Zaidi A, Wani PA (2007) Role of phosphate-solubilizing microorganisms in sustainable agriculture—a review. Agron Sustain Dev 27:29–43

Khoshgoftarmanesh AH, Schulin R, Chaney RL, Daneshbakhsh B, Afyuni M (2010) Micronutrient-efficient genotypes for crop yield and nutritional quality in sustainable agriculture. A review. Agron Sustain Dev 30:83–107

Kijne JW (2006) Abiotic stress and water scarcity: Identifying and resolving conflicts from plant level to global level. Field Crop Res 97:3–18

Kim SY, Lim JH, Park MR, Kim YJ, Park TI, Seo YW, Choi KG, Yun SJ (2005) Enhanced antioxidant enzymes are associated with reduced hydrogen peroxide in barley roots under saline stress. J Biochem Mole Biol 38:218–224

Knight H (2000) Calcium signaling during abiotic stress in plants. Int Rev Cytol 195:269–324

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

Kundu BS, Sangwan P, Sharma PK, Nandwal AS (1997) Response of pearl millet to phytohormones produced by *Azospirillum brasilense*. Indian J Plant Physiol 2:101–104

Lemanceau P, Expert D, Gaymard F, Bakker PAHM, Briat JF (2009) Chapter 12 Role of iron in plant–microbe interactions. In: Advances in botanical research, vol 51, Academic Press, New York. pp 491–549

Li J, McConkey BJ, Cheng Z, Guo S, Glick BR (2013) Identification of plant growth-promoting bacteria-responsive proteins in cucumber roots under hypoxic stress using a proteomic approach. J Proteome 84:119–131

Li J, Sun J, Yang Y, Guo S, Glick BR (2012) Identification of hypoxic-responsive proteins in cucumber roots using a proteomic approach. Plant Physiol Biochem 51:74–80

Lifshitz R, Kloepper JW, Scher FM, Tipping EM, Laliberté M (1986) Nitrogen-fixing Pseudomonads isolated from roots of plants grown in the Canadian High Arctic. Appl Environ Microbiol 51:251–255

Ligero F, Poveda JL, Gresshoff PM, Caba JM (1999) Nitrate- and inoculation-enhanced ethylene biosynthesis in soybean roots as a possible mediator of nodulation control. J Plant Physiol 154:482–488

Lim PE, Mak KY, Mohamed N, Noor AM (2003) Removal and speciation of heavy metals along the treatment path of wastewater in subsurface-flow constructed wetlands. Water Sci Technol J Int Assoc Water Pollut Res 48:307–313

Lin CC, Lin HL (2005) Remediation of soil contaminated with the heavy metal (Cd^{2+}). J Hazard Mater 122:7–15

Lodewyckx C, Mergeay M, Vangronsveld J, Clijsters H, Van der Lelie D (2002a) Isolation, characterization, and identification of bacteria associated with the zinc hyperaccumulator *Thlaspi caerulescens* subsp. Calaminaria. Int J Phytoremediation 4:101–115

Lodewyckx C, Vangronsveld J, Porteous F, Moore ERB, Taghavi S, Mezgeay M, Lelie Dv d (2002b) Endophytic bacteria and their potential applications. Critl Rev Plant Sci 21:583–606

Ludwig-Müller J (2004) From auxin homeostasis to understanding plant pathogen and plant symbiont interaction: editor's research interests. J Plant Growth Regul 23:1–8

Lugtenberg B (2015) Life of microbes in the rhizosphere. In: Lugtenberg B (ed) Principles of plant-microbe interactions: microbes for sustainable agriculture. Springer, Cham, pp 7–15

Lugtenberg B, Kamilova F (2009) Plant-growth-promoting rhizobacteria. Ann Review Microbiol 63:541–556

Luo S, Wan Y, Xiao X, Guo H, Chen L, Xi Q, Zeng G, Liu C, Chen J (2011) Isolation and characterization of endophytic bacterium LRE07 from cadmium hyperaccumulator *Solanum nigrum* L. and its potential for remediation. Appl Microbiol Biotechnol 89:1637–1644

Lynch JP (2007) Turner review no. 14. Roots of the second green revolution. Aust J Bot 55:493–512

Ma Y, Rajkumar M, Vicente J, Freitas H (2010) Inoculation of Ni-resistant plant growth promoting bacterium *Psychrobacter* sp. strain SRS8 for the improvement of nickel phytoextraction by energy crops. Int J Phytoremediation 13:126–139

Ma Z, Baskin TI, Brown KM, Lynch JP (2003) Regulation of root elongation under phosphorus stress involves changes in ethylene responsiveness. Plant Physiol 131:1381–1390

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

Majumder AL, Sengupta S, Goswami L (2010) Osmolyte regulation in abiotic stress. In: Pareek A, Sopory SK, Bohnert JH (eds) Abiotic stress adaptation in plants: physiological, molecular and genomic foundation. Springer, Dordrecht, pp 349–370

Malik A (2004) Metal bioremediation through growing cells. Environ Intl 30:261–278

Manchanda G, Garg N (2008) Salinity and its effects on the functional biology of legumes. Acta Physiol Plantarum 30:595–618

Manter DK, Delgado JA, Holm DG, Stong RA (2010) Pyrosequencing reveals a highly diverse and cultivar-specific bacterial endophyte community in potato roots. Microb Ecol 60:157–166

Marschner H (1995) Mineral nutrition of higher plant, 2nd edn. Academic Press, New York

Marschner P, Yang CH, Lieberei R, Crowley DE (2001) Soil and plant specific effects on bacterial community composition in the rhizosphere. Soil Biol Biochem 33:1437–1445

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

Meloni DA, Oliva MA, Martinez CA, Cambraia J (2003) Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress. Environ Exp Bot 49:69–76

Mensah JK, Ihenyen J (2009) Effects of salinity on germination, seedling establishment and yield of three genotypes of mung bean (*Vigna mungo* L. Hepper) in Edo State, Nigeria. Nigerian Ann Nat Sci 8:17–24

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

Milošević NA, Marinković JB, Tintor BB (2012) Mitigating abiotic stress in crop plants by microorganisms. Zbornik Matice srpske za prirodne nauke:17–26

Mittler R, Blumwald E (2010) Genetic engineering for modern agriculture: challenges and perspectives. Ann Rrev Plant Biol 61:443–462

Mittova V, Tal M, Volokita M, Guy M (2002) Salt stress induces up-regulation of an efficient chloroplast antioxidant system in the salt-tolerant wild tomato species *Lycopersicon pennellii* but not in the cultivated species. Physiol Plantarum 115:393–400

Mittova V, Tal M, Volokita M, Guy M (2003) Up-regulation of the leaf mitochondrial and peroxisomal antioxidative systems in response to salt-induced oxidative stress in the wild salt-tolerant tomato species *Lycopersicon pennellii*. Plant Cell Environt 26:845–856

Molla AH, Shamsuddin ZH, Halimi MS, Morziah M, Puteh AB (2001) Potential for enhancement of root growth and nodulation of soybean co-inoculated with *Azospirillum* and *Bradyrhizobium* in laboratory systems. Soil Biol Biochem 33:457–463

Moore FP, Barac T, Borremans B, Oeyen L, Vangronsveld J, van der Lelie D, Campbell CD, Moore ER (2006) Endophytic bacterial diversity in poplar trees growing on a BTEX-contaminated site: the characterisation of isolates with potential to enhance phytoremediation. Sys Appl Microbiol 29:539–556

Mrozik A, Piotrowska-Seget Z (2010) Bioaugmentation as a strategy for cleaning up of soils contaminated with aromatic compounds. Microbiol Res 165:363–375

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25:239–250

Munns R (2005) Genes and salt tolerance: bringing them together. New Phytol 167:645–663

Munns R, James RA, Lauchli A (2006) Approaches to increasing the salt tolerance of wheat and other cereals. J Exp Bot 57:1025–1043

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

Nicholas Smirnoff, (1998) Plant resistance to environmental stress. Current Opinion in Biotechnology 9(2):214–219

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

Nadeem SM, Zahir ZA, Naveed M, Arshad M (2009) Rhizobacteria containing ACC-deaminase confer salt tolerance in maize grown on salt-affected fields. Can J Microbiol 55:1302–1309

Nadeem SM, Zahir ZA, Naveed M, Nawaz S (2012) Mitigation of salinity-induced negative impact on the growth and yield of wheat by plant growth-promoting rhizobacteria in naturally saline conditions. Ann Microbiol 63:225–232

Nautiyal CS, Govindarajan R, Lavania M, Pushpangadan P (2008) Novel mechanism of modulating natural antioxidants in functional foods: Involvement of Plant Growth Promoting Rhizobacteria NRRL B-30488. J Agri Food Chem 56:4474–4481

Navarro JM, Botella MA, Cerdá A, Martinez V (2001) Phosphorus uptake and translocation in salt-stressed melon plants. J Plant Physiol 158:375–381

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

Niu YF, Chai RS, Jin GL, Wang H, Tang CX, Zhang YS (2013) Responses of root architecture development to low phosphorus availability: a review. Ann Bot 112:391–408

Ondrasek G, Rengel Z, Romic D, Poljak M, Romic M (2009) Accumulation of non/essential elements in radish plants grown in salt-affected and cadmium contaminated environment. Cereal Res Comm 37:9–12

Ortíz-Castro R, Contreras-Cornejo HA, Macías-Rodríguez L, López-Bucio J (2009) The role of microbial signals in plant growth and development. Plant Signaling Behavior 4:701–712

Osmont KS, Sibout R, Hardtke CS (2007) Hidden branches: developments in root system architecture. Annu Rev Plant Biol 58:93–113

Pandolfi C, Mancuso S, Shabala S (2012) Physiology of acclimation to salinity stress in pea (*Pisum sativum*). Environ Exp Bot 84:44–51

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

Park MR, Baek S-H, Reyes BG, Yun SJ (2007) Overexpression of a high-affinity phosphate transporter gene from tobacco (NtPT1) enhances phosphate uptake and accumulation in transgenic rice plants. Plant Soil 292:259–269

Parmar N, Dadarwal KR (1999) Stimulation of nitrogen fixation and induction of flavonoid-like compounds by rhizobacteria. J Appl Mmicrobiol 86:36–44

Paul D (2012) Osmotic stress adaptations in rhizobacteria. J Basic Microbiol 52:1–10

Paul D (2013) Osmotic stress adaptations in rhizobacteria. J Basic Microbiol 53:101–110

Paul D, Lade H (2014) Plant-growth-promoting rhizobacteria to improve crop growth in saline soils: a review. Agron Sustain Dev 34:737–752

Paul D, Nair S (2008) Stress adaptations in a plant growth promoting rhizobacterium (PGPR) with increasing salinity in the coastal agricultural soils. J Basic Microbiol 48:378–384

Paul D, Sarma YR (2006) Plant growth promoting rhizhobacteria (PGPR)-mediated root proliferation in black pepper (*Piper nigrum* L.) as evidenced through GS root software. Arch Phytopathol Plant Protect 39:311–314

Peng YL, Gao ZW, Gao Y, Liu GF, Sheng LX, Wang DL (2008) Eco-physiological characteristics of alfalfa seedlings in response to various mixed salt-alkaline stresses. J Integrative Plant biol 50:29–39

Pereira PAA, Bliss FA (1989) Selection of common bean (*Phaseolus vulgaris* L.) for N_2 fixation at different levels of available phosphorus under field and environmentally-controlled conditions. Plant Soil 115:75–82

Pérez-Torres C-A, López-Bucio J, Cruz-Ramírez A, Ibarra-Laclette E, Dharmasiri S, Estelle M, Herrera-Estrella L (2008) Phosphate availability alters lateral root development in *Arabidopsis* by modulating auxin sensitivity via a mechanism involving the TIR1 auxin receptor. Plant Cell 20:3258–3272

Peters NK, Crist-Estes DK (1989) Nodule formation is stimulated by the ethylene inhibitor aminoethoxyvinylglycine. Plant Physiol 91:690–693

Pierik R, Tholen D, Poorter H, Visser EJ, Voesenek LA (2006) The Janus face of ethylene: growth inhibition and stimulation. Trends Plant Sci 11:176–183

Pikovskaya RI (1948) Mobilization of phosphorus in soil in connection with vital activity of some microbial species Mikrobiologiya 17:362–370

Pitzschke A, Forzani C, Hirt H (2006) Reactive oxygen species signaling in plants. Antioxidants Redox Signaling 8:1757–1764

Polle A, Luo Z-B (2014) Biotic and abiotic interactions in plants: Novel ideas for agriculture and forestry in a changing environment. Environ Exp Bot 108:1–3

Porcel R, Aroca R, Ruiz-Lozano JM (2011) Salinity stress alleviation using arbuscular mycorrhizal fungi. A review. Agron Sustain Dev 32:181–200

Rabie G, Almadini AM (2005) Role of bioinoculants in development of salt-tolerance of *Vicia faba* plants under salinity stress. Afr J Biotech 4:210–222

Rubén Bottini, Fabricio Cassán, Patricia Piccoli, (2004) Gibberellin production by bacteria and its involvement in plant growth promotion and yield increase. Applied Microbiology and Biotechnology 65 (5)

Rajkumar M, Nagendran R, Lee KJ, Lee WH, Kim SZ (2006) Influence of plant growth promoting bacteria and Cr^{6+} on the growth of Indian mustard. Chemosphere 62:741–748

Ramadoss D, Lakkineni VK, Bose P, Ali S, Annapurna K (2013a) Mitigation of salt stress in wheat seedlings by halotolerant bacteria isolated from saline habitats. Springer Plus 2(1):6

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

Rasouli-Sadaghiani M, Malakouti MJ, Khavazi K, Miransari M (2014) Siderophore efficacy of Fluorescent Pseudomonades affecting labeled iron (59Fe) uptake by wheat (Triticum aestivum L.) genotypes differing in Fe efficiency. In: Miransari M (ed) Use of microbes for the alleviation of soil stresses, Alleviation of soil stress by PGPR and Mycorrhizal Fungi, vol 2. Springer, New York, pp 121–132

Rekha PD, Lai W-A, Arun AB, Young CC (2007) Effect of free and encapsulated *Pseudomonas putida* CC-FR2-4 and Bacillus subtilis CC-pg104 on plant growth under gnotobiotic conditions. Bioresour Technol 98:447–451

Remans R, Beebe S, Blair M, Manrique G, Tovar E, Rao I, Croonenborghs A, Torres-Gutierrez R, El-Howeity M, Michiels J, Vanderleyden (2008) Physiological and genetic analysis of root responsiveness to auxin-producing plant growth-promoting bacteria in common bean (*Phaseolus vulgaris* L.). Plant Soil 302:149–161

Riesen O, Feller U (2005) Redistribution of nickel, cobalt, manganese, zinc, and cadmium via the phloem in young and maturing wheat. J Plant Nutr 28:421–430

Robin A, Vansuyt G, Hinsinger P, Meyer JM, Briat J-F, Lemanceau P (2008) Iron dynamics in the rhizosphere: consequences for plant health and nutrition. Adv Agron 99:183–225

Rodriguez H, Gonzalez T, Goire I, Bashan Y (2004) Gluconic acid production and phosphate solubilization by the plant growth-promoting bacterium *Azospirillum* spp. Naturwissenschaften 91:552–555

Rodriguez R, Redman R (2008) More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. J Exp Bot 59:1109–1114

Rogers ME, Grieve CM, Shannon MC (2003) Plant growth and ion relations in lucerne (*Medicago sativa* L.) in response to the combined effects of NaCl and P. Plant Soil 253:187–194

Rojas-Tapias D, Moreno-Galván A, Pardo-Díaz S, Obando M, Rivera D, Bonilla R (2012) Effect of inoculation with plant growth-promoting bacteria (PGPB) on amelioration of saline stress in maize (*Zea mays*). Appl Soil Ecol 61:264–272

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

Safronova VI, Piluzza G, Zinovkina NY, Kimeklis AK, Belimov AA, Bullitta S (2012) Relationships between pasture legumes, rhizobacteria and nodule bacteria in heavy metal polluted mine waste of SW Sardinia. Symbiosis 58:149–159

Safronova VI, Stepanok VV, Engqvist GL, Alekseyev YV, Belimov AA (2006) Root-associated bacteria containing 1-aminocyclopropane-1-carboxylate deaminase improve growth and nutrient uptake by pea genotypes cultivated in cadmium supplemented soil. Biol Fertil Soils 42:267–272

Saleem M, Arshad M, Hussain S, Bhatti A (2007) Perspective of plant growth promoting rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. J Ind Microbiol Biotechnol 34:635–648

Sanchez DH, Lippold F, Redestig H, Hannah MA, Erban A, Krämer U, Kopka J, Udvardi MK (2008) Integrative functional genomics of salt acclimatization in the model legume Lotus japonicus. The Plant J 53:973–987

Sandalio LM, Dalurzo HC, Gomez M, Romero-Puertas MC, del Rio LA (2001) Cadmium-induced changes in the growth and oxidative metabolism of pea plants. J Exp Bot 52:2115–2126

Sandhya V, Sk ZA, Grover M, Reddy G, Venkateswarlu B (2009) Alleviation of drought stress effects in sunflower seedlings by the exopolysaccharides producing *Pseudomonas putida* strain GAP-P45. Biol Fertil Soils 46:17–26

Sanità di Toppi L, Gabbrielli R (1999) Response to cadmium in higher plants. Environ Exp Bot 41:105–130

Santner A, Calderon-Villalobos LIA, Estelle M (2009) Plant hormones are versatile chemical regulators of plant growth. Nature Chem Biol 5:301–307

Schmidt W (2003) Iron solutions: acquisition strategies and signaling pathways in plants. Trends Plant Sci 8:188–193

Schubert S, Neubert A, Schierholt A, Sümer A, Zörb C (2009) Development of salt-resistant maize hybrids: The combination of physiological strategies using conventional breeding methods. Plant Sci 177:196–202

Scott JA, Karanjkar AM (1992) Repeated cadmium biosorption by regenerated *Enterobacter aerogenes* biofilm attached to activated carbon. Biotechnol Lett 14:737–740

Selvakumar G, Joshi P, Mishra P, Bisht J, Gupta H (2009) Mountain aspect influences the genetic clustering of psychrotolerant phosphate solubilizing *Pseudomonads* in the Uttarakhand Himalayas. Curr Microbiol 59:432–438

Selvakumar G, Kundu S, Joshi P, Nazim S, Gupta AD, Mishra PK, Gupta HS (2008a) 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 (2008b) Cold tolerance and plant growth promotion potential of *Serratia marcescens* strain SRM (MTCC 8708) isolated from flowers of summer squash (*Cucurbita pepo*). Lett Appl Microbiol 46:171–175

Sessitsch A, Reiter B, Pfeifer U, Wilhelm E (2002) Cultivation-independent population analysis of bacterial endophytes in three potato varieties based on eubacterial and Actinomycetes-specific PCR of 16S rRNA genes. FEMS Microbiol Ecol 39:23–32

Shabani L, Ehsanpour AA, Asghari G, Emami J (2009) Glycyrrhizin production by in vitro cultured *Glycyrrhiza glabra* elicited by methyl Jasmonate and salicylic acid. Russ J Plant Physiol 56:621–626

Shahbaz M, Ashraf M (2013) Improving salinity tolerance in cereals. Crit Rev Plant Sci 32:237–249

Shakir MA, Bano A, Arshad M (2012) Rhizosphere bacteria containing ACC-deaminase conferred drought tolerance in wheat grown under semi-arid climate. Soil Environ 31:108–112

Shanker AK, Venkateswarlu B (2011) Abiotic stress in plants—mechanisms and adaptations. InTech, Rijeka

Sharma A, Johri BN, Sharma AK, Glick BR (2003) Plant growth-promoting bacterium Pseudomonas sp. strain GRP 3 influences iron acquisition in mung bean (*Vigna radiata* L. Wilzeck). Soil Biol Biochem 35:887–894

Shinozaki K, Yamaguchi-Shinozaki K (2000) Molecular responses to dehydration and low temperature: differences and cross-talk between two stress signaling pathways. Curr Opin Plant Biol 3:217–223

Shrivastava P, Kumar R (2015) Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. Saudi J Biol Sci 22:123–131

Siciliano SD, Fortin N, Mihoc A, Wisse G, Labelle S, Beaumier D, Ouellette D, Roy R, Whyte LG, Banks MK, Schwab P, Lee K, Greer CW (2001) Selection of specific endophytic bacterial genotypes by plants in response to soil contamination. Appl Environ Microbiol 67:2469–2475

Siciliano SD, Germida JJ (1999) Taxonomic diversity of bacteria associated with the roots of field-grown transgenic *Brassica napus* cv. Quest, compared to the non-transgenic *B. napus* cv. Excel and *B. rapa* cv. Parkland. FEMS Microbiol Ecol 29:263–272

Siddikee MA, Glick BR, Chauhan PS, Wj Y, Sa T (2011) Enhancement of growth and salt tolerance of red pepper seedlings (*Capsicum annuum* L.) by regulating stress ethylene synthesis with halotolerant bacteria containing 1-aminocyclopropane-1-carboxylic acid deaminase activity. Plant Physiol Biochem 49:427–434

Singh A, Sarma BK, Upadhyay RS, Singh HB (2013) Compatible rhizosphere microbes mediated alleviation of biotic stress in chickpea through enhanced antioxidant and phenylpropanoid activities. Microbiol Res 168:33–40

Singh JS, Pandey VC, Singh D (2011) Efficient soil microorganisms: a new dimension for sustainable agriculture and environmental development. Agri Ecosys Environ 140:339–353

Soleimani M, Akbar S, Hajabbasi MA (2011) Enhancing phytoremediation efficiency in response to environmental pollution stress. Plants Environ 23:10–14

Son HJ, Park GT, Cha MS, Heo MS (2006) Solubilization of insoluble inorganic phosphates by a novel salt- and pH-tolerant *Pantoea agglomerans* R-42 isolated from soybean rhizosphere. Bioresour Technol 97:204–210

Spaepen S, Dobbelaere S, Croonenborghs A, Vanderleyden J (2008) Effects of *Azospirillum* brasilense indole-3-acetic acid production on inoculated wheat plants. Plant Soil 312:15–23

Spaepen S, Vanderleyden J (2011) Auxin and plant-microbe interactions. Cold Spring Harb Perspect Biol 3:a001438

Spaepen S, Vanderleyden J, Remans R (2007) Indole-3-acetic acid in microbial and microorganism-plant signaling. FEMS Microbiol Rev 31:425–448

Sreenivasulu N, Sopory SK, Kishor PBK (2007) Deciphering the regulatory mechanisms of abiotic stress tolerance in plants by genomic approaches. Gene 388:1–13

Stearns JC, Shah S, Greenberg BM, Dixon DG, Glick BR (2005) Tolerance of transgenic canola expressing 1-aminocyclopropane-1-carboxylic acid deaminase to growth inhibition by nickel. Plant Physiol Biochem 43:701–708

Steve J. Sinclair, Matthew D. White, Graeme R. Newell, (2010) How Useful Are Species Distribution Models for Managing Biodiversity under Future Climates?. Ecology and Society 15 (1)

Su F, Jacquard C, Villaume S, Michel J, Rabenoelina F, Clément C, Barka EA, Dhondt-Cordelier S, Vaillant-Gaveau N (2015) Burkholderia phytofirmans PsJN reduces impact of freezing temperatures on photosynthesis in *Arabidopsis thaliana*. Frontiers Plant Sci 6

Sugawara M, Okazaki S, Nukui N, Ezura H, Mitsui H, Minamisawa K (2006) Rhizobitoxine modulates plant-microbe interactions by ethylene inhibition. Biotechnol Adv 24:382–388

Szabados L, Savouré A (2010) Proline: a multifunctional amino acid. Trends Plant Sci 15:89–97

Tang C, Robson AD, Dilworth MJ (1990) A split-root experiment shows that iron is required for nodule initiation in *Lupinus angustifolius* L. New Phytol 115:61–67

Taurian T, Soledad Anzuay M, Angelini JG, Tonelli ML, Ludueña L, Pena D, Ibáñez F, Fabra A (2010) Phosphate-solubilizing peanut associated bacteria: screening for plant growth-promoting activities. Plant Soil 329:421–431

Tester M, Davenport R (2003) Na^+ tolerance and Na^+ transport in higher plants. Ann Bot 91:503–527

Theunis M (2005) IAA biosynthesis in rhizobia and its potential role in symbiosis PhD thesis, Universiteit Antwerpen

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

Tokala RK, Strap JL, Jung CM, Crawford DL, Salove MH, Deobald LA, Bailey JF, Morra MJ (2002) Novel plant-microbe rhizosphere interaction involving *Streptomyces* lydicus WYEC108 and the pea plant (*Pisum sativum*). Appl Environ Microbiol 68:2161–2171

Tuberosa R, Salvi S (2006) Genomics-based approaches to improve drought tolerance of crops. Trends Plant Sci 11:405–412

Upadhyay S, Singh D, Saikia R (2009) Genetic diversity of plant growth promoting rhizobacteria isolated from rhizospheric soil of wheat under saline condition. Curr Microbiol 59:489–496

Upadhyay SK, Singh JS, Saxena AK, Singh DP (2012) Impact of PGPR inoculation on growth and antioxidant status of wheat under saline conditions. Plant Biol (Stuttgart, Germany):14, 605–611

Upadhyay SK, Singh JS, Singh DP (2011) Exopolysaccharide-producing plant growth-promoting rhizobacteria under salinity condition. Pedosphere 21:214–222

Valliyodan B, Nguyen HT (2006) Understanding regulatory networks and engineering for enhanced drought tolerance in plants. Curr Opin Plant Biol 9:189–195

Van Der Heijden MG, Bardgett RD, Van Straalen NM (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett 11:296–310

van Hoorn JW, Katerji N, Hamdy A, Mastrorilli M (2001) Effect of salinity on yield and nitrogen uptake of four grain legumes and on biological nitrogen contribution from the soil. Agri Water Manage 51:87–98

Van Overbeek L, Van Elsas JD (2008) Effects of plant genotype and growth stage on the structure of bacterial communities associated with potato (*Solanum tuberosum* L.) FEMS Microbiol Ecol 64:283–296

Vansuyt G, Robin A, Briat J-F, Curie C, Lemanceau P (2007) Iron acquisition from Fe-pyoverdine by *Arabidopsis thaliana*. Mole Plant-Microbe Interact 20:441–447

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

Vurukonda SSKP, Vardharajula S, Shrivastava M, SkZ A (2016) Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. Microbiol Res 184:13–24

Wang H, Tang X, Wang H, Shao H-B (2015) Proline accumulation and metabolism-related genes expression profiles in *Kosteletzkya virginica* seedlings under salt stress. Frontiers Plant Sci 6:792

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

Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218:1–14

Wang WX, Vinocur B, Shoseyov O, Altman A (2001) Biotechnology of plant osmotic stress tolerance: physiological and molecular considerations. International Society for Horticultural Science (ISHS), Leuven, Belgium, pp 285–292

Wintergerst ES, Maggini S, Hornig DH (2007) Contribution of selected vitamins and trace elements to immune function. Ann Nutr Metabol 51:301–323

Witcombe JR, Hollington PA, Howarth CJ, Reader S, Steele KA (2008) Breeding for abiotic stresses for sustainable agriculture. Philos Trans R Soc Lond B Biol Sci 363:703–716

Xiao B, Huang Y, Tang N, Xiong L (2007) Over-expression of a LEA gene in rice improves drought resistance under the field conditions. Theor Appl Genet 115:35–46

Yahalom E, Dovrat A, Okon Y, Czosnek H (1991) Effect of inoculation with *Azospirillum brasilense strain* Cd and *Rhizobium* on the root morphology of burr medic (*Medicago polymorpha* L.) Israel J Bot 40:155–164

Yamaguchi T, Blumwald E (2005) Developing salt-tolerant crop plants: Challenges and opportunities. Trends Plant Sci 10:615–620

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

Yao L, Wu Z, Zheng Y, Kaleem I, Li C (2010) Growth promotion and protection against salt stress by *Pseudomonas putida* Rs-198 on cotton. Eur J Soil Biol 46:49–54

Yehuda Z, Shenker M, Romheld V, Marschner H, Hadar Y, Chen Y (1996) The role of ligand exchange in the uptake of iron from microbial siderophores by gramineous plants. Plant Physiol 112:1273–1280

Yildirim E, Taylor AG (2005) Effect of biological treatments on growth of bean plans under salt stress. Ann Rep Bean Improve Cooperative 48:176–177

Yuhashi K, Ichikawa N, Ezura H, Akao S, Minakawa Y, Nukui N, Yasuta T, Minamisawa K (2000) Rhizobitoxine production by Bradyrhizobium elkanii enhances nodulation and competitiveness on *Macroptilium atropurpureum*. Appl Environm Microbiol 66:2658–2663

Zaidi S, Usmani S, Singh BR, Musarrat J (2006) Significance of *Bacillus subtilis* strain SJ-101 as a bioinoculant for concurrent plant growth promotion and nickel accumulation in *Brassica juncea*. Chemosphere 64:991–997

Zarea MJ, Hajinia S, Karimi N, Mohammadi Goltapeh E, Rejali F, Varma A (2012) Effect of *Piriformospora indica* and *Azospirillum* strains from saline or non-saline soil on mitigation of the effects of NaCl. Soil Biol Biochem 45:139–146

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

Zhu D, Kwon S, Pignatello JJ (2005) Adsorption of single-ring organic compounds to wood charcoals prepared under different thermochemical conditions. Environ Sci Technol 39:3990–3998

Zhu J-K (2001a) Plant salt tolerance. Trends Plant Sci 6:66–71

Zhu JK (2001b) Cell signaling under salt, water and cold stresses. Curr Opin Plant Biol 4:401–406

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

Zuo Y, Zhang F (2010) Soil and crop management strategies to prevent iron deficiency in crops. Plant Soil 339:83–95