J Plant Growth Regul (2016) 35:276–300
DOI 10.1007/s00344-015-9521-x

Bacterial-Mediated Tolerance and Resistance to Plants Under Abiotic and Biotic Stresses

Devendra Kumar Choudhary[1,2] · Amrita Kasotia[2] · Shekhar Jain[1,2] · Anukool Vaishnav[1,2] · Sarita Kumari[1,2] · Kanti Prakash Sharma[2] · Ajit Varma[1]

Received: 14 January 2015 / Accepted: 13 April 2015 / Published online: 1 July 2015

Abstract Plant growth-promoting bacteria (PGPB) are capable of alleviating environmental stress and eliciting tolerance in plants to promote their growth. Several PGPB elicit physical and/or chemical changes related to plant defense in the form of induced systemic resistance (ISR) under biotic stress. Researchers emphasized that PGPB-elicited ISR has suppressed plant diseases caused by a range of pathogens in both the greenhouse and field. PGPB-elicited physical and chemical changes in plants result in enhanced tolerance to drought, salt, and other factors that have been described as a form of induced systemic tolerance under abiotic stress. This review will focus on recent research concerning interactions between PGPB and plants under biotic and abiotic stresses. The use of PGPB requires precise understanding of the interactions between plant-bacteria, among bacteria-microbiota, and how biotic and abiotic factors influence these relationships. Consequently, continued research is needed to develop new approaches to ameliorate the efficiency of PGPB and to understand the ecological, genetic, and biochemical relationships in their habitat.

Keywords Abiotic · Biotic · Plant growth-promoting bacteria · Resistance · Tolerance · Volatile

✉ Devendra Kumar Choudhary
devmicro@rediffmail.com; dkchoudhary1@amity.edu

[1] Amity Institute of Microbial Technology (AIMT), Block 'E-3', 4th Floor, Amity University Campus, Sector-125, Gautam Buddha Nagar, Noida 201313, UP, India

[2] Department of Science, Faculty of Arts, Science & Commerce, Mody University of Science & Technology, Lakshmangarh 332311, Rajasthan, India

Introduction

Exploitation of plant–microbe interactions can result in the promotion of plant health and can play a significant role in low-input sustainable agriculture applications for both food and non-food crops. An understanding of the mechanisms enabling these microbes to interact with plants will be worthwhile to fully achieve the biotechnological potential of efficient partnerships for a range of applications. The most important and promising area of research for future studies is developing microbes to promote the sustainable production of cultivable crops under stresses (abiotic and biotic). In addition, the ability of microbes to confer stress resistance to plants may provide a novel strategy for mitigating the impacts of global climate change on agricultural and native plant communities. Plants possess a range of defense apparatuses that can be actively expressed in response to biotic and abiotic stresses. Microbes could play a significant role in stress management, once their unique properties of tolerance to extremes, their ubiquity, and genetic diversity are understood and methods for their successful deployment in agriculture production have been developed. These microorganisms also provide excellent models for understanding stress tolerance mechanisms that can be subsequently engineered into crop plants (Fig. 1) (Choudhary 2011, 2012).

Soil microorganisms play an important role in soil processes that determine plant and soil productivity. Exhaustive efforts have been made to explore soil microbial diversity of the indigenous community, their distribution and behavior in soil habitats to understand the successful functioning of introduced microbial bio-inoculants, and their influence on soil health. In prototype observation experiments, the content of microbial biomass carbon increased when soil moisture was higher than 19.5 %, whereas the content declined when soil moisture

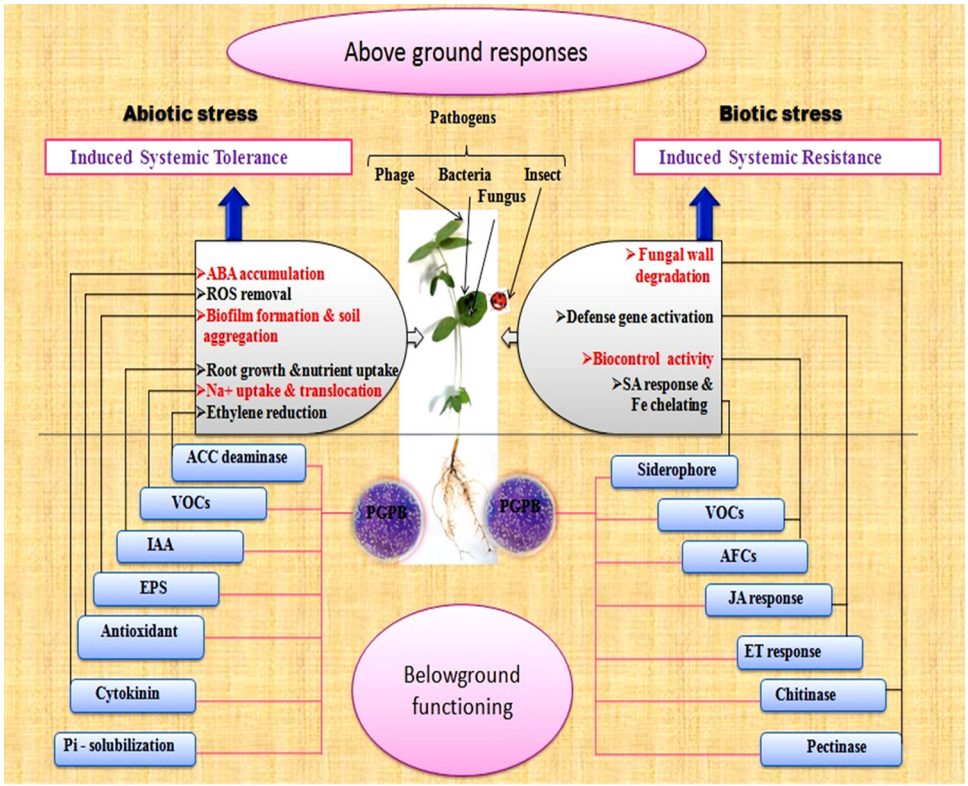

Fig. 1 Interaction between belowground functioning and above-ground responses. *Left* and *right* parts of the figure indicate responses (*below*- and *above*-ground) under abiotic and biotic stresses, respectively. *ABA* abscisic acid, *ROS* reactive oxygen species, *ACC* 1-aminocyclopropane carboxylic acid, *IAA* indole-3-acetic acid, *EPS* exopolysaccharide, *VOCs* volatile organic compounds, *AFCs* antifungal compounds, *JA* jasmonate, *ET* ethylene, *VAM* vesicular–arbuscular mycorrhiza

was lower than 19.5 %. It was concluded that 19.5 % was the optimum water content for microbial biomass carbon in the sampled soil ecosystem and it could be used to demonstrate alterations and degradation of the soil ecosystem as well as the irrigation requirement of crops (Geng and others 2015). Improvement in agricultural sustainability requires optimal use and management of soil fertility and soil physical properties and relies on soil biological processes and soil biodiversity (Tilak and others 2005; Roesti and others 2006). Plants play an important role in selecting and enriching the type of bacteria by the constituents of their root exudates. The bacterial community develops in the rhizosphere which is a result of its diverse nature and concentrations of organic constituents of exudates and the corresponding ability of the bacteria to utilize these as sources of energy. Therefore, the rhizosphere bacterial community has an efficient system for uptake and catabolism of organic compounds present in root exudates (Barraquio and others 2000). It has been described frequently that a plant obtains almost everything directly from the soil to support growth. The soil must have a structure that is physically capable of supporting the above-ground half of the plant through its developing root system as it grows. The soil needs to be maintained at an appropriate pH, provides protection from toxic substances and pathogens, and contains a suitable water level. In addition to this, all the essential mineral elements that a plant requires are obtained from the soil. Most of these elements are taken from the soil solution in their ionic form (White 2003). The interaction between plant roots and organisms within the rhizosphere assists in acquiring essential mineral nutrients and prevents the accumulation of toxic elements. The essential mineral element that most frequently limits plant growth is P (phosphorus); it is taken up in the form of inorganic phosphate (P_i, $H_2PO_4^-$) from the soil solution. The concentration of P_i in the soil solution (2–10 μm) is very low, which limits P_i diffusion to the root system with the resultant P_i depletion in the rhizosphere. Plants have evolved several strategies against the limiting nature of P_i, to release and acquire P_i from the soil wherein the plant increases its carbohydrate allocation to the roots which results in an increased root: shoot ratio and alters the morphology of the root system by accelerating lateral root growth and produces long root hairs to increase the volume of soil explored. In addition, P deficiency increases the abundance of P_i transporter proteins, and promotes the exudation of organic acids, RNases, and phosphatases to mobilize P from organic/insoluble compounds (Raghothama 2005). It is not surprising that a series of generalized and specific plant–microbe associations in the rhizosphere exist that allow efficient solubilization of all the minerals that a plant requires.

The physico-chemical properties of soil are fundamental to soil health including soil texture, which is one of the

most influential factors. Soil particles held together cohesively influence the precise pore structure of the soil. Soil texture stability reflects the prevention of soil erosion when the soil is exposed to climatic stresses. A well-aggregated soil structure ensures soil tilth, soil–plant water relation, water infiltration rates, soil aeration, root penetrability, and organic matter accumulation which all contribute to soil health (Miller and Jastrow 2000; Buscot 2005). It has been demonstrated that microbial cooperation in the rhizosphere reflects the formation and stabilization of soil aggregates wherein soil particles are held together by bacterial products followed by hyphae of saprophytic and arbuscular mycorrhizae (AM) which form stable microaggregates of the size 2–20 μm in diameter. These microaggregates are bound by the microbial products again into quite large microaggregates (20–250 μm in diameter) with bacterial polysacharides acting as the binding agents. Finally, microaggregates are then bound into macroaggregates of the size >250 μm in diameter with bacterial polysaccharides and AM mycelia that increase the size of microaggregates. The branching habit and three-dimensional structure of the external mycelium of AM that colonize the soil surrounding the roots allow persistence up to 22 weeks after the plant has died (Miller and Jastrow 2000).

The formation of water-stable soil aggregates is evident in different ecological situations as a result of the effect of AM fungi in cooperation with other microbes, and the involvement of glomalin, a glycoprotein produced by the external hyphae of AM fungi. Glomalin participates in the initiation and stabilization of soil aggregates because of its glue-like hydrophobic nature (Requena and others 2001). Distribution of natural plant communities is accompanied by loss of physico-chemical and biological properties of soil, for example, soil texture, plant nutrient availability, OM content, and microbial activity which is the ultimate result of degradation/desertification processes. It has been investigated frequently that management of AM fungi together with rhizobacteria can restore soil traits (Jeffries and Barea 2001; Requena and others 2001). The increase in N (nitrogen) content in the rhizosphere of the legumes considerably accounts for improvement in nodulation and N-fixing capacity, resulting from cooperative interaction of the symbionts, for example, *Rhizobium* and AM fungi. There is considerable experimental evidence to show that several bacteria and fungi can colonize the root-soil environment where they carry out a variety of interactive activities known to benefit plant growth and health, as also soil quality. Miransari (2014) reported the differences between AM fungi and rhizobium symbiont mechanism with plants and suggests the importance of such type of interaction in agriculture and ecosystems by including these microorganisms as biological fertilizer under field conditions.

The varied genetic and functional activities of the microbial populations impart critical impacts on soil functions based on the fact that microbes are the driving forces for fundamental metabolic processes which involve specific enzyme activities. Most of the microbial interactions in the rhizosphere are responsible for key environmental processes, that is, the biogeochemical cycling of nutrients and matter and the maintenance of plant and soil health (Nannipieri and others 2003; Barea and others 2004). Several investigators have reported that soil-borne microbes interact with plant roots and soil constituents at the root-soil interface wherein C fluxes are crucial determinants of rhizosphere function (Toal and others 2000). The release of root exudates provides sources of C compounds for the heterotrophic soil biota whereby microbial activity in the rhizosphere affects the rooting pattern and the supply of available nutrients to plants (Gryndler 2000).

Bacterial-Elicited Induced Systemic Tolerance

Environmental stresses such as drought, temperature, salinity, air pollution, heavy metals, pesticides, and soil pH are major limiting factors in crop production because they affect almost all plant functions. Habitat-imposed abiotic and biotic stress is a serious condition and also land-degradation is a problem in arid and semiarid regions, causing major losses in productivity. About 20 % of cultivable and at least half of irrigated lands around the world are severely affected by environmental stresses. However, in these conditions, there are plant populations successfully adapted and evolutionarily different in their strategy of stress tolerance. Vascular plants do not function as autonomous individuals, but house diverse communities of microbes. The role of these microbes can no longer be ignored. Microbial interactions are critical not only for the host, but for fungal survival in stressed environments.

To date, improvements in plant quality, production, abiotic and biotic stress resistance, nutrient, and water use have relied largely on manipulating plant genomes by breeding and genetic modification. Increasing evidence indicates that the function of microbes seems to parallel more than one of these characteristics (Choudhary 2012). Besides developing mechanisms for stress tolerance, microorganisms can also impart some degree of tolerance to plants toward abiotic stresses like drought, chilling injury, salinity, metal toxicity, and high temperature. In the last decade, bacteria belonging to different genera, including *Rhizobium, Bacillus, Pseudomonas, Pantoea, Paenibacillus, Burkholderia, Achromobacter, Azospirillum, Microbacterium, Methylobacterium, variovorax, Enterobacter,* and so on, have been reported to provide tolerance to host plants under different abiotic stress

environments (Table 1). Use of these microorganisms per se can alleviate stresses in agriculture thus opening a new and emerging application of microorganisms. Production of indole acetic acid, gibberellins, and some unknown determinants by microbes results in increased root length, root surface area, and number of root tips, leading to enhanced uptake of nutrients thereby improving plant health under stress conditions (Egamberdieva and Kucharova 2009). Identification of genes controlling stress tolerance traits in microbes would enhance our knowledge about the molecular basis of the stress tolerance mechanisms. In a recent review, authors suggest an important aspect to generate transgenic medicinal plants encoding the genes of particular traits of microbes and these transgenic plants have the ability to withstand the stress environment (Shahzad and others 2015).

Plant growth-promoting bacteria (PGPB) have been found to improve growth of tomato, pepper, canola, bean, and lettuce under saline conditions (Barassi and others 2006a, b; Yildirim and Taylor 2005). Some microbial strains produce cytokinin and antioxidants, which result in abscisic acid (ABA) accumulation and degradation of reactive oxygen species (ROS). Inoculation of *Azospirillum brasilense* Sp245 in wheat (*Triticum aestivum*) under drought stress resulted in a better water status and an additional ''elastic adjustment'' resulting in better grain yield and mineral quality (Mg, K, and Ca) at harvest. Another microbial strain, *Achromobacter piechaudii* ARV8 which produced 1-aminocyclopropane-1-carboxylate (ACC) deaminase, conferred induced systemic tolerance (IST) against drought and salt in pepper and tomato (Mayak and others 2004a, b).

Many aspects of plant life are regulated by ethylene levels and the biosynthesis of ethylene is subjected to tight regulation, involving transcriptional and post-transcriptional factors regulated by environmental cues, including biotic and abiotic stresses (Hardoim and others 2008). In the biosynthetic pathway of ethylene, S-adenosylmethionine (S-AdoMet) is converted by 1-aminocyclopropane-1-carboxylate synthase (ACS) to 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene. Under stress conditions, the plant hormone ethylene endogenously regulates plant homoeostasis and results in reduced root and shoot growth. In the presence of ACC deaminase-producing bacteria, plant ACC is sequestered and degraded by bacterial cells to supply nitrogen and energy (Fig. 2). Furthermore, by removing ACC, the bacteria reduce the deleterious effect of ethylene, ameliorating plant stress and promoting plant growth (Glick 2007). Saleem and others (2007) have reviewed the role of microbes containing ACC deaminase in stress agriculture. Inoculation with ACC deaminase-containing bacteria induced longer roots which might be helpful in the uptake of relatively more water from deep soil under drought stress conditions, thus increasing water use efficiency of the plants under drought conditions (Zahir and others 2008).

Microbial polysaccharides can bind soil particles to form microaggregates and macroaggregates. Plant roots and fungal hyphae fit in the pores between microaggregates and thus stabilize macroaggregates. Plants treated with exopolysaccharide (EPS)-producing bacteria display increased resistance to water stress due to improved soil structure (Sandhya and others 2009). EPS can also bind to cations including Na^+ thus making it unavailable to plants under saline conditions. Chen and others (2007) correlated proline accumulation with drought and salt tolerance in plants. Introduction of proBA genes derived from *Bacillus subtilis* into *A. thaliana* resulted in production of higher levels of free proline resulting in increased tolerance to osmotic stress in the transgenic plants. Increased production of proline along with decreased electrolyte leakage, maintenance of relative water content of leaves, and selective uptake of K^+ ions resulted in salt tolerance in *Zea mays* coinoculated with *Rhizobium* and *Pseudomonas* (Bano and Fatima 2009). Accumulation of proline buffers cellular redox potential under environmental stresses (Wahid and Close 2007). Trehalose metabolism in PGPB a is key for signaling plant growth, yield, and adaptation to abiotic stress and its manipulation had a major agronomical impact on plants (Suarez and others 2008; Duan and others 2013). Figueiredo and others (2008) reported increased plant growth, N content, and nodulation of *Phaseolus vulgaris* L. under drought stress due to coinoculation of *Rhizobium tropici* and *P. polymyxa*. *Phaseolus vulgaris* (common bean) plants inoculated with *Rhizobium etli* overexpressing the trehalose-6-phosphate synthase gene had more nodules with increased nitrogenase activity and high biomass compared with plants inoculated with wild-type *R. etli*. Three-week-old plants subjected to drought stress fully recovered whereas plants inoculated with a wild-type *R. etli* died. Microarray analysis of 7200 expressed sequence tags from nodules of plants inoculated with a strain of over expressing trehalose-6-phosphate synthase gene revealed upregulation of genes involved in stress tolerance, suggesting a signaling mechanism for trehalose (Figueiredo and others 2008).

Some of the volatiles organic compounds (VOCs) emitted from *Bacillus* (Ryu and others 2004) are bacterial determinants involved in IST. The volatiles emitted by PGPB down regulate hkt1 (high-affinity k^+ transporter1) expression in roots but upregulates it in shoots, orchestring lower Na^+ levels and recirculation of Na^+ in the whole plant under salt conditions (Zhang and others 2008). Root colonization of *A. thaliana* by *Pseudomonas chlororaphis* O6 induced tolerance in the plants against biotic and

Table 1 PGPB-mediated IST against abiotic stress

Stress type	Bacterial inoculate	Plant species	Reference
Salt	*Pseudomonas spp.*	Soybean (*Glycine max.* L)	Kasotia and others (2012)
	Agrobacterium tumefaciens, Zhinguelliuella, Brachybacterium	*Arachis hypogaea*	Shukla and others (2012)
	Saurashtrense, Vibrio, Brevibacterium casei, and *Haererohalobacter*		
	Pseudomonas pseudoalcaligenes, Bacillus pumilus	Rice (*Oryza sativa*)	Jha and others (2010)
	Azospirillum brasilense	Barley (*Hordeum vulgare*)	Omar and others (2009)
	Pseudomonas mendocina	Lettuce (*L. sativa* L. cv. Tafalla)	Kohler and others (2009)
	Azospirillum sp.	Pea (*Phaseolus vulgaris*)	Dardanelli and others (2008)
	Bacillus subtilis	*Arabidopsis thaliana*	Zhang and others (2008)
	Pseudomonas syringae, Pseudomonas fluorescens, Enterobacter aerogenes	Maize (*Zea maize*)	Nadeem and others (2007)
	P. fluorescens	Groundnut (*Arachis hypogaea*)	Saravanakumar and Samiyappan (2007)
	Azospirillum	Lettuce (*Lactuca sativa)*	Barassi and others 2006a, b
	Achromobacter piechaudii	Tomato (*Lycopersicon esculentum*)	Mayak and others (2004b)
Drought	*Bacillus cereus, Bacillus*	Cucumber (*Cucumis sativus* L.)	Wang and others (2012)
	Subtilis, and *Serratia*		
	Burkholderia phytofirmans	Wheat (*T. aestivum*)	Naveed and others (2013a, b)
	Pseudomonas spp.	Maize (*Zea mays* L. cv. Kaveri)	Sandhya and others (2010)
	Pseudomonas spp.	Asparagus (*Asparagus officinalis* L.)	Liddycoat and others (2009)
	Pseudomonas mendocina	Lettuce (*Lactuca sativa* L.)	Kohler and others (2008)
	Rhizobium tropici, Paenibacillus polymyxa	Common bean *(Phaseolus vulgaris* L.)	Figueiredo and others (2008)
	Bacillus	Lettuce (*Lactuca sativa* L.)	Arkhipova and others (2007)
	Pseudomonas chlororaphis	*Arabidopsis thaliana*	Cho and others (2008)
	Ensifer meliloti bv.mediterranense	Bean (*Phaseolus vulgaris* cv. Flamingo)	Mnasri and others (2007)
	Bradyrhizobium elkanii	Flat crown (*Albizia adianthifolia*)	Swaine and others (2007)
	Achromobacter piechaudii	Tomato (*L. esculentum*), pepper (*Capsicum annuum*)	Mayak and others (2004a, 2004b)
Osmotic stress	*Bacillus*	Potato (*Solanum tuberosum*)	Gururani and others (2013)
	Bacillus subtilis	*Arabidopsis*	Zhang and others (2010)
	A. brasilense	Rice (*Oryza sativa* L.)	Cassan and others (2009)
	Arthrobacter sp., Bacillus sp.	Pepper (*C. annuum*)	Sziderics and others (2007)
	Azospirillum	Wheat (*T. aestivum*)	Pereyra and others (2006)
Temperature	*Bacillus Amyloliquefaciens* and *Azospirillum brasilense*	Wheat (Triticum aestivum)	Abd El-Daim and others (2014)
	Burkholderia phytofirmans	*Vitis vinifera* L.	Theocharis and others (2012)
	Burkholderia phytofirmans	Grapevine (*Vitis vinifera*)	Barka and others (2006)
	Pseudomonas fluorescens, Pantoea agglomerans, Mycobacterium sp.	Wheat (*Triticum aestivum*)	Egamberdiyeva and Hoflich (2003)
Nutrient deficiency	*Azospirillum sp., Azotobacter chroococcum, Mesorhizobium ciceri, Pseudomonas fluorescens*	Chickpea (*Cicer arietinum* L.)	Rokhzadi and Toashih (2011)
	Azotobacter chroococcum, Azospirillum brasilense, Pseudomonas putida, Bacillus lentus	Zea maize L.	Yazdani and others (2009)
	Bacillus sp., Burkholderia sp., Streptomyces platensis	*Zea maize* L.	Oliveira and others (2009)
	Bacillus sp.,	*Zea maize* L.	Adesemoye and others (2008)

Table 1 continued

Stress type	Bacterial inoculate	Plant species	Reference
	Bacillus polymyxa, Mycobacterium phlei, Pseudomonas alcaligenes	*Zea maize* L. (*Zea maize* cv. Felix)	Egamberdiyeva (2007)

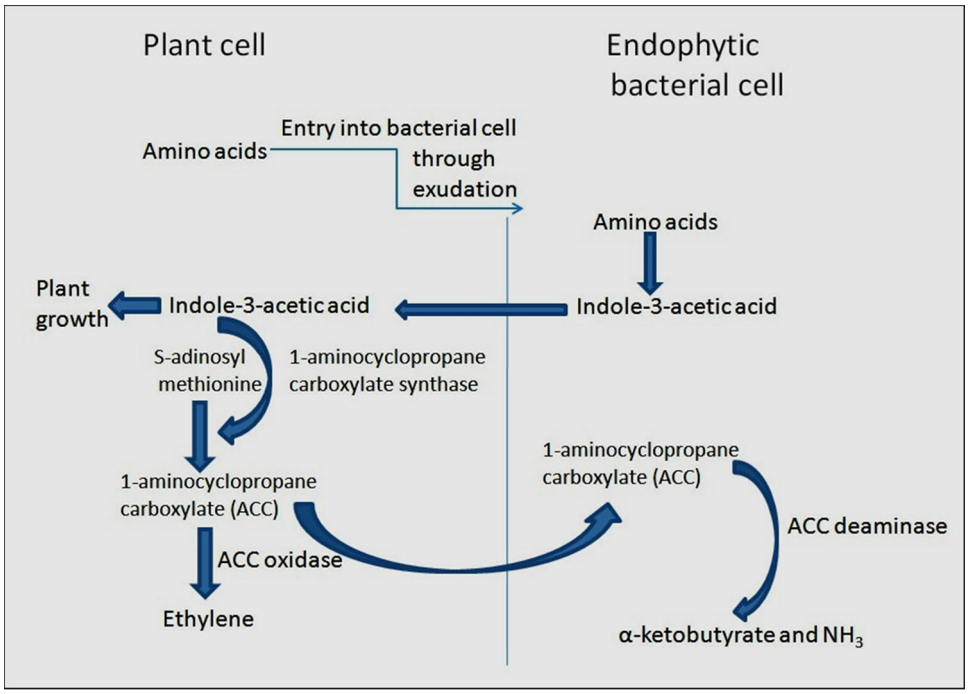

Fig. 2 ACC deaminase activity shown by endophyte at interface between plant and bacterial cell

abiotic stresses due to the production of a volatile metabolite, 2R, 3R-butanediol. Studies with *Arabidopsis* mutant lines indicated that induced drought tolerance requires salicylic acid (SA), ethylene, and jasmonic acid-signaling pathways (Cho and others 2008). Higher temperatures influence photosynthetic rate, plant water relations, flowering, and fruit set in tropical and temperate crops. Similarly, low temperature is a major factor limiting the productivity and geographical distribution of many species, including important agricultural crops. Srivastava and others (2008) isolated a thermotolerant *Pseudomonas putida* NBRI0987 from drought-affected rhizosphere of chickpea. Over production of stress sigma (S) (RpoS) was observed by this microorganism when grown under high temperature stress at 40 °C compared with 30 °C. A thermotolerant *Pseudomonas* sp. strain AMK-P6 induced thermotolerance in sorghum seedlings due to synthesis of high molecular weight protein in leaves and improved plant biomass as well as biochemical status in terms of proline, sugar, amino acid, and chlorophyll contents (Ali and others 2009). A plant growth-promoting bacterium *Burkholderia phytofirmans* PsJN, capable of epiphytic and endophytic colonization of grapevine tissue and organs (Compant and others 2005), could protect the plants against heat as well as chilling stress (Ait Bakra and others 2006). The bacterized plantlets showed significantly increased levels of starch, proline, and phenolics. PsJN is also reported for the higher expression of 1-aminocyclopropane-1-carboxylate deaminase which hydrolyzes the ethylene precursor 1-aminocyclopropane-1-carboxylate into ammonia and α-ketobutyrate, thereby reducing the destructive effects of cold and drought by lowering the production of ethylene in plants (Sessitsch and others 2005; Theocharis and others 2012; Naveed and others (2013a, b)).

The role of abscisic acid (ABA) had been suggested behind AM-mediated stress response of plants (Aroca and others 2008). The addition of exogenous ABA considerably enhanced the ABA content in shoots of non-AM plants, concomitant with the expression of the stress marker genes *Lsp5cs* and *Ls1ea* and the gene *Lsnced*. By contrast, the addition of exogenous ABA decreased the content of ABA in shoots of AM plants and did not produce any further enhancement of the expression. Coinoculation of lettuce with PGPB *Pseudomonas mendocina* and *G. intraradices* or *G. mosseae* augmented an antioxidative catalase under severe drought conditions, suggesting that they could be used in inoculants to alleviate the oxidative damage (Kohler and others 2008). A 14-3-3 protein-

encoding gene from *Glomus intraradices* growing in vitro and subjected to drought stress was identified (Porcel and others 2006). The role of these proteins that regulate both signaling pathways and also effector proteins was suggested as imparting protection to the host plants against drought stress. Glutathione and ascorbate have an important role in conferring protection and maintain metabolic function of plants under water deficit conditions. Low accumulation of these compounds in lavender plants colonized by the autochthonous drought tolerant *Glomus intraradices* and *Glomus* sp. strain indicated high drought tolerance in plants (Marulanda and others 2007). Mycorrhized lavender plants showed improved water content, root biomass, and N and K contents. AM symbiosis has frequently increased resilience of host plants to salinity stress, perhaps with greater consistency than to drought stress. Growth in saline soils was increased by inoculation with *Glomus* spp., with AM plants having increased phosphate and decreased Na^+ concentrations in shoots compared to uninoculated controls (Giri and Mukerji 2004). Salt resistance was improved by AM colonization in maize (Feng and others 2002) and clover (Ben Khaled and others 2003) with AM effect correlated with improved osmoregulation or proline accumulation. AM inoculation also improved NaCl resistance in tomato, with the extent of improvement related to salt sensitivity of the cultivar (Al-Karaki and others 2001).

Salinity is the major constraint for enhancing agricultural productivity in arid and semiarid regions of the world. Saline soils occupy 7 % of the earth's land surface (Ruiz-Lozano and others 2001) and increased salinization of arable land will result in 50 % land loss by the middle of the 21st century (Wang and others 2003). Precisely, secondary salinity developed from irrigation is widely responsible for reducing water and soil quality, edging crop growth, and leading to the rejection of agricultural land (Egamberdiyeva and others 2007). Salt stress disrupts ion homeostasis in plant cells whereby plants have adopted some strategies to attain ion homeostasis that include two main mechanisms for maintenance of ion homeostasis: exclusion and compartmentalization of ions accomplished by a salt-inducible enzyme, Na^+/H^+ antiporter (Parida and Das 2005). Ion concentrations in the cytosol are maintained in balance by various ion channels. Removal of sodium from the cytoplasm or compartmentalization in the vacuoles is done by a salt-inducible enzyme, Na^+/H^+ antiporter (Apse and others 1999). Na^+ extrusion from plant cells is powered by the operation of the plasma membrane H^+-ATPase generating an electrochemical H^+ gradient that allows the plasma membrane Na^+/H^+ antiporter to couple the passive movement of H^+ inside the cells, along its electrochemical potential, to the active extrusion of Na^+ (Yamaguchi and Blumwald 2005). Molecular genetic analysis of *Arabidopsis sos* mutants has led to the identification of a plasma membrane Na^+/H^+ antiporter, SOS1, which plays a role in salt stress sensing. The SOS1 transcript level is upregulated under salt stress. Sodium efflux through SOS1 under salinity is regulated by the SOS3–SOS2 kinase complex (Chinnusamy and others 2005). Na^+ sequestration into the vacuole depends not only on expression and activity of Na^+/H^+ antiporters, but also on V-type H^+-ATPase and H^+-PPase. These phosphatases generate the necessary proton gradient required for activity of Na^+/H^+ antiporters. The tonoplast Na^+/H^+ antiporter *NHX1* gene is induced by both salinity and ABA in *Arabidopsis* (Shi and Zhu 2002) and rice (Fukuda and others 1999; Horie and Schroeder 2004). Another ion carrier channel, *AtHKT1*, has been shown to function as a selective Na + transporter in Arabidopsis (Yamaguchi and Blumwald 2005). *AtHKT1* was identified as a putative regulator of Na^+ influx in plant roots. Based on various research results, *AtHKT1* was proposed to play a role in long-distance Na^+ transport and Na^+ circulation in the plant, with *AtHKT1* mediating Na^+ loading into the leaf phloem and Na^+ unloading from the root phloem sap (Berthomieu and others 2003). *Bacillus* sp. and *Arthrobacter pascens* sp. isolated from rhizospheric soil of halophyte regions showed reliability in growth promotion of maize by increasing osmolytes including sugar and proline and elevating antioxidant enzyme activity including superoxide dismutase, peroxidase, catalase, and ascorbate peroxidase (Ullah and Bano 2015). Another PGPB, *Pseudomonas koreensis* strain AK-1, -inoculated soybean plant showed growth promotion in salinity by reducing Na^+ levels but increased K^+ levels in leaves and roots in comparison with the non-inoculated salt-treated plants. AK-1-treated plants also had increased stress enzyme activity along with proline content as compared to nontreated plants (Kasotia and others 2015).

In addition, salinity alters the normal homeostasis of cells because of disruption of photosynthesis and increased photorespiration, and generates high levels of reactive oxygen species (ROS) such as the super oxide radical, hydrogen peroxide, and hydroxyl radical (Miller and others 2010). Under optimal growth conditions, ROS are mainly produced at low levels in organelles such as chloroplasts, mitochondria, and peroxisomes (Apel and Hirt 2004). The enhanced production of ROS during stress can pose a threat to cells but it is thought that ROS also act as signals for the activation of stress response and defense pathways (Pitzschke and others 2006). The damage caused by ROS to the biological membrane can be modulated by regulation of membrane structures by adaptive mechanisms such as alteration of composition and organization of lipids inside the bilayer, in a way that prevents lipid peroxidation, modification of the degree of polyunsaturated fatty acid

(PUFA) unsaturation, mobility of lipids within the bilayer and preventive antioxidant systems (Blokhina and others 2003). ROS also attack other macromolecules such as proteins and DNA, with the formation of nucleotide peroxides especially at the level of thymine (Cullis and others 1987). Oxidative attack on proteins results in site-specific amino acid modifications, fragmentation of the peptide chain, aggregation of cross-linked reaction products, and altered electrical charge. After oxidative modification, proteins become sensitive to proteolysis and/or may be inactivated, or may show reduced activity. ROS-induced DNA damage includes single- and double-strand breaks, abasic sites, and base damages. Furthermore, mitochondrial DNA is more sensitive to oxidative damage than nuclear DNA, in particular because of the absence of chromatin organization and lower mitochondrial DNA repair activities (Yakes and Van Houten 1997). As a major site of ROS production both in animal and plant cells is the mitochondrial electron transport chain (ETC), the importance of ROS dependent damage on mitochondrial proteins such as ETC proteins and mitochondrial DNA becomes clearer. Because ROS are toxic but also participate in signaling events, plant cells require at least two different mechanisms to regulate their intracellular ROS concentrations by scavenging of ROS: one that will enable the fine modulation of low levels of ROS for signaling purposes, and one that will enable the detoxification of excess ROS, especially during stress (Mittler 2002). Plants have evolved both non-enzymatic and enzymatic mechanisms to cope with deleterious effects of ROS in the cells. To control the level of ROS and to protect cells under stress conditions, plant tissues contain several enzymes that scavenge ROS such as superoxide dismutase [SOD; E.C. 1.15.1.1], ascorbate peroxidase [APX; E.C. 1.1.1.11], catalase [CAT; E.C. 1.11.1.6], glutathione reductase [GR; E.C. 1.6.4.2], monodehydroascorbate reductase [MDHAR; E.C. 1.6.5.4], glutathione peroxidase, alternative oxidase, and dehydroascorbate reductase [DHAR; E.C. 1.8.5.1], and detoxifying lipid peroxidation products (glutathione S-transferase, and phospholipid-hydroperoxide glutathione peroxidase) (Blokhina and others 2003).

PGPB are likely associated with most plant species and are commonly present in many environments (Gray and Smith 2005). These PGPB have the potential to improve crop production under stress conditions solely and/or in combination with other microbes. Multi-strain bacterial consortia have proven to be useful for enhancing plant growth and development particularly in conditions in which single inoculation was not so effective; however, the compatibility of strains with each other is a very important aspect to obtain better results. The literature showed that genetically engineered bacteria can also be used effectively for promoting plant growth under normal and stress conditions (Nadeem and others 2015). More interestingly, the combined inoculation of PGPBs and *Rhizobia* allowed a longer and more persistent exudation of nod-gene-inducing flavonoids that, ultimately, improve the performance of symbiotic nitrogen fixation (SNF). The combined interaction of PGPBs and *Rhizobia* with legume plants also supports the establishment of seedlings and improves the vitality of legumes during metal phytostabilization and phytoextraction strategies (Gómez-Sagasti and Marino 2015).

PGPB can improve plant performance under stress environments and, consequently, enhance yield both directly and indirectly (Dimkpa and others 2009). Some PGPB may exert a direct stimulation on plant growth and development by providing plants with fixed nitrogen, phytohormones, and iron that has been sequestered by bacterial siderophores, and soluble phosphate (Rodrìguez and Fraga 1999; Hayat and others 2010). Others do this indirectly by protecting the plant against soil-borne diseases, most of which are caused by pathogenic fungi (Lutgtenberg and Kamilova 2009). Common adaptation mechanisms of plants exposed to environmental stresses, such as temperature extremes, high salinity, drought and nutrient deficiency, or heavy metal toxicity, include changes in root morphology (Potters and others 2007), a process in which phytohormones are known to play a key role (Spaepen and Vanderleyden 2010). The majority of root-associated bacteria that display beneficial effects on plant growth have been shown to produce IAA, and inoculation of various plant species with such bacteria has resulted in increased root growth and/or enhanced formation of lateral roots and root hairs (Patten and Glick 2002). According to Glick and others (1999), PGPB expressed an indole-3-pyruvate decarboxylase enzyme that converts tryptophan to indole-3-acetic acid via indole-3-pyruvic acid. Bioassay experiments of canola seeds and mung bean cuttings inoculated with *Pseudomonas putida* strain GR12-2 resulted in a significant increase of lateral root development and adventitious roots, respectively, compared to uninoculated controls (Mayak and others 1999). Bacterial IAA production also stimulates the activity of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, by a signaling cascade, which hydrolyzes the ethylene precursor ACC to ammonia and α-ketobutyrate (Glick 2005). In the signaling events, IAA activates the transcription of ACC synthase that results in the production of high level of ethylene which feedback inhibits IAA signal transduction, thereby limiting the extent that IAA can further activate ACC synthase transcription (Glick and others 2007; Prayitno and others 2006; Stearns and others 2012). In the presence of ACC deaminase, there is much less ethylene and subsequent ethylene feedback inhibition of IAA signals transduction so that the bacterial IAA can continue to both

promote plant growth and increase ACC synthase transcription. However in this case, a large portion of the additional ACC is cleaved by bacterial ACC deaminase. The net result of this cross-talk between IAA and ACC deaminase is that by lowering plant ethylene levels, ACC deaminase facilitates the stimulation of plant growth by IAA (Glick 2014).

It was also observed that inoculation with PGPB containing ACC deaminase was effective in increasing water use efficiency in peas under drought stress conditions (Zahir and others 2008). Mayak and others (2004a, b) also reported that inoculation with PGPB containing ACC deaminase confers resistance against drought stress in tomatoes and peppers. According to Yang (1987), ACC is the precursor of ethylene and the last step of ethylene biosynthesis is catalyzed by 1- aminocyclopropane-1-carboxylic acid oxidase (ACO), which converts ACC into ethylene. In this study, inoculated plants showed low expression of the ACC oxidase gene as compared to non-inoculated plants. This verifies that ACC deaminase breakdowns the ACC level which results in the low expression of the ACC oxidase gene. ACC deaminase activity could be helpful in sustaining plant growth and development under stress conditions by reducing stress-induced ethylene production. ACC levels and, consequently, ethylene synthesis increases in plants under drought stress conditions have been frequently reported (Mayak and others 2004a, b; Arshad and others 2008). Therefore, the inhibitory effects of ethylene induced by drought stress might have been eliminated through ACC deaminase activity of the PGPB. Shah and others (1998) isolated the strains UW1, UW2, and UW3 of *P. putida* from the rhizosphere of bean, corn, and clover, which possessed the ACC deaminase capacity. Mayak and others (2004a, 2004b) reported that *A. pie-chaudii* ARV8 contains ACC deaminase activity and thus should be able to lower ethylene production in inoculated host plants.

Modulation of other major plant hormones could improve crop salt tolerance by reducing the toxic effects of salinity (Bianco and Defez 2009). When plants are subjected to environmental stress conditions such as those listed above, the balance between the production of ROSs and the quenching activity of the antioxidants is upset, often resulting in oxidative damage (Jubani-Marì and others 2010; Miller and others 2010). Plants with high levels of antioxidants, either constitutive or induced, have been reported to have greater resistance to this oxidative damage (Ahmad and others 2008; Kohler and others 2008). The activities of the antioxidative enzymes such as CAT, APX, guaiacol peroxidase (POX), GR, and SOD increase under salt stress in plants, and a correlation between these enzyme levels and salt tolerance has been described (Apel and Hirt 2004). It has been found that *Medicago* plants infected with IAA-overproducing PGPB strains showed high antioxidant enzyme activity which contributed to enhance plant protection against salt stress (Bianco and Defez 2009). Drought, salt, and temperature stress induce metabolic rearrangements and regulatory networks, which can delay plant growth and development, reduce productivity, and in extreme cases cause plant death (Krasensky and Jonak 2012). This can be alleviated by use of endophytic PGPB which moreover provide abiotic stress tolerance (Choudhary 2012).

The EPS production of PGPB was found to be higher under stress conditions, indicating that EPS production in bacteria occurs as a response to the stress (Roberson and Firestone 1992). Probably EPS can provide a microenvironment that holds water and dries more slowly than the surrounding microenvironment, thus protecting bacteria from drying and fluctuations in water potential (Hepper 1975; Wilkinson 1958). Production of EPS by bacteria improved RAS permeability by increasing soil aggregation and maintaining higher water potential around the roots; in this way, there was an increase in the uptake of nutrients by plant, with an increase in plant growth; in addition, the bacteria protected the seedlings from drought stress (Sandhya and others 2009; Alami and others 2000; Bezzate and others 2000). Higher EPS content and better aggregation of RAS could help the plants to take up a higher volume of water and nutrients from rhizosphere soil (Miller and Wood 1996), resulting in better growth of plants, and also, this was useful to counteract the negative effects of drought stress (Munns 2002). ABA accumulation is one of the most important responses of a plant to water stress. It plays a key role in plant water maintenance under stress conditions by inducing stomatal closure (Leung and Giraudat 1998). It has been reported that NO serves as a signaling component for ABA accumulation in plants (Garcia-Mata and Lamattina 2001, 2002). A consortium culture applied with SNP (0.1 mM) decreased a high amount of LWL under drought conditions. This reduced LWL correlated with smaller stomatal aperture. Smaller size was found in SNP-treated plants, approx. 2.8 µm. These results suggest that NO plays an important role in leaf water maintenance under osmotic stress. Similar results were reported in a previous study (Garcia-Mata and Lammattina 2001).

There are many reports that rhizobacteria containing ACC deaminase can decrease salinity-induced shoot growth inhibition (Mayak and others 2004b). Although the simplest interpretation of these data is that rhizobacterial reduction of root ACC concentrations (Penrose and Glick 2001) diminished long-distance ACC signaling (Belimov and others 2009) and hence foliar ethylene evolution (Else and Jackson 1998), alternative explanations should also be

considered. Rhizobacterial inoculation with *Achromobacter piechaudii* AVR8 had no effect on leaf relative water content of tomato seedlings grown with 207 mM NaCl, and actually decreased the relative water content of plants growth with 120 Mm NaCl (Mayak and others 2004b). Such evidence that foliar water relations are not responsible for the improved growth of inoculated plants is not surprising in view of evidence that preventing a salinity-induced decrease in foliar turgor (via root pressurization) has no long-term (days to weeks) influence on plant growth (Munns and others 2000). However, *Achromobacter piechaudii* increased foliar K and P concentrations by 24, and 62 %, respectively, while decreasing Ca^2 and Mg^{+2} concentrations by 21 and 14 %, respectively (averaged over two salt concentrations). Interestingly, although rhizobacterial inoculation decreased foliar Na concentrations (by 24 %) when plants were grown with 120 mM NaCl, there was no significant effect at a higher salt concentration (207 mM). Although further work is required to substantiate whether these nutritional changes are a universal response to the presence of ACC deaminase-containing bacteria in the rhizosphere, changes in tissue nutrient ratios may also be physiologically important in regulating growth under salinity (Rodrıguez-Rosales and others 2008).

In plants, ROS are continuously produced as byproducts of various metabolic pathways localized in different cellular compartments. A common feature of these species is their capacity to cause oxidative damage to proteins, DNA, and lipids. Under physiological steady-state conditions, these molecules are scavenged by different antioxidative defense components that are often confined to particular compartments (Apel and Hirt 2004). Under normal growth conditions, the production of ROS in cells is low, whereas during stress, their rate of production is enhanced. ROS accumulation during stress results from the imbalance between production and scavenging of ROS. Major ROS-scavenging mechanisms of plants include SOD, APX, and CAT enzymes. Antioxidants such as ascorbic acid and glutathione, which are found in high concentrations in chloroplasts and other cellular compartments, are also crucial for plant defense against oxidative stress (Miller and others 2010). For the detoxification of excess ROS in plants, the overall balance between different antioxidants is crucial for determining the steady-state level of superoxide radicals and hydrogen peroxide, and has to be tightly controlled (Mittler 2002). *Bacillus amyloliquefaciens* UCMB5113 and *Azospirillum brasilense* NO40 showed higher heat tolerance in young seedlings of wheat. The enhancement of heat tolerance by bacteria seems to be associated with reduced generation of reactive oxygen species (and consequently less cell damage), small changes in the metabolome and preactivation of certain heat shock transcription factors (Abd El-Daim and others 2014).

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

Several studies correlated accumulation of nitrogen-containing compounds (NCC) with drought and salt tolerance in plants (Parida and Das 2005). The most frequently accumulating NCC include amino acids, amides, imino acids, proteins, quaternary ammonium compounds, and polyamines. Very high accumulation of cellular proline (up to 80 % of the amino acids pool under stress and 5 % under normal conditions) due to increased synthesis and decreased degradation under a variety of stress conditions such as salt and drought has been documented in many plant species (Szabados and Savourè 2009). Several comprehensive studies using transgenic plants or mutants demonstrate that proline metabolism has a complex effect on development and stress responses. Proline has been proposed to act as a compatible osmolyte and to be a way to store carbon and nitrogen. Saline and drought are known to induce oxidative stress. Several studies showed that proline may have an antioxidant activity acting as a ROS scavenger. Proline may also function as a molecular chaperone able to stabilize the structures of proteins and enhance the activity of different enzymes, and its accumulation plays a role in maintenance of cytosolic pH and regulation of intracellular redox potential (Hare and Cress 1997; Kavi Kishor and others 2005; Verbruggen and Hermans 2008). Under abiotic stress conditions, increased proline biosynthesis was observed for various plant species inoculated with different PGPB (Barka and others 2006; Jha and others 2010; Kohler and others 2009; Sandhya and others 2010; Vardharajula and others 2011). The synthesis of proline as well as other compatible solutes requires an energy cost (41 mol of ATP) and occurs at the expense of plant growth, but may allow the plant to survive and recover from the presence of high external salt concentrations (Munns and Tester 2008).

A key factor limiting plant growth is excessive Na^+, a harmful mineral element not required by most plants. High Na^+ tissue content is often considered as the most critical factor responsible for salt toxicity. A possible survival strategy of plants under saline conditions was to sequester absorbed Na^+ in roots. Although toxic ions such as Na^+ and Cl^- can benefit plant adaptation to salinity by contributing to vacuolar osmotic adjustment, it is generally accepted that salt tolerance in glycophyte species is mostly related to the exclusion of these ions from the leaves thereby avoiding or delaying toxic effects (Munns and Tester 2008). Hence, any contribution of the soil biota toward maintaining the homeostasis of toxic ions must benefit plant growth under salinity. Microbes can alter root uptake of toxic ions and nutrients by altering host physiology (by regulating ion transporter expression and/or activity) and modifying physical barriers around the roots (more extensive rhizosheaths formed by bacterial exopolysaccharides), or by directly reducing foliar accumulation of toxic ions (Na^+, Cl^-) while improving the nutritional status of both macro- (N, P, and K) and micronutrients (Zn, Fe, Cu, and Mn), mostly via unknown mechanisms. Nutrients may also become more accessible to the plant due to microbial-induced changes in rhizosphere pH (organic acid excretion) and/or chelation with organic molecules (siderophores) exuded by microbes. Particular importance has been attached to microbial enhancement of in planta K^+/Na^+ ratios (Giri and others 2007; Sharifi and others 2007) in beneficial plant/microbe interactions.

In the case of PGPB, decreased plant Na^+ accumulation could be explained by the excretion of bacterial exopolysaccharides, which bind cations (especially Na^+) in roots, thus preventing their transfer to leaves and helping alleviate salt stress in plants (Ashraf and others 2004). The authors suggested that a higher proportion of the root zone of inoculated seedlings was covered in soil sheaths, which reduced apoplastic flow of sodium ions into the stele. Furthermore, ACC deaminase-containing PGPB increased plant N, P, and K uptake, resulting in higher K^+:Na^+ ratios in salinized maize plants and increased P, K^+, and Ca^{2+} uptake at the expense of Mg^{2+} and Na^+ uptake in salinized tomatoes (Mayak and others 2004b). Although these studies suggest that PGPB can mediate plant ionic relations by alterations of the radix processes, exposing *Arabidopsis* plants to bacterial volatile organic compounds from *Bacillus subtilis* decreased root transcriptional expression of a high-affinity K^+ transporter (*AtHKT1*) but upregulated it in the shoots, not only decreasing root Na^+ import but facilitating Na^+ exclusion from the shoot by retrieving Na^+ from the xylem and facilitating root-to-root Na^+ recirculation (Zhang and others 2008). As *AtHKT1* differentially adjusts Na^+ and K^+ levels depending on the plant tissue, the induction of this transporter may explain the reduced Na^+ accumulation in the plants and the improved salt tolerance, as supported by the typical salt stress phenotype and inhibited growth observed when exposing an *AtHKT1* mutant to bacterial volatile organic compounds (Zhang and others 2008).

However, the beneficial effect of PGPB under salinity has been also related to the alleviation of osmotic stress by maintaining higher stomatal conductance and photosynthetic activities (del Amor and Cuadra-Crespo 2012). In turn, this could lower accumulation of toxic ions (Na^+ and Cl^-) and improve the leaf K^+:Na^+ ratio, thus delaying toxic effects through both growth and/or energetic maintenance of ion-exclusion mechanisms (Pérez-Alfocea and others 2010). Bacteria-triggered induced systemic tolerance fortifies plant cell wall strength and alters host physiology and metabolic responses, leading to an enhanced synthesis of plant defense chemicals upon challenge by pathogens and/or abiotic stress factors (Broetto and others 2005).

Bacterial-Elicited Induced Systemic Resistance

PGPB-mediated resistance in plants completely overcomes the effect of a pathogen and/or related damaging factors (Agrios 1988; Vaan loon 1997). Plants possess a powerful immune system as a protective guard against microbial pathogens and parasites, which is coordinated by a complex signaling network. According to the types of molecules recognized by plants as indicators of a pathogen attack, they have two types of immune systems, termed PAMP-triggered immunity (PTI) and effector-triggered immunity (ETI) (Vleesschauwer and HöFte 2009; Eulgem and Somssich 2007; Jones and Dangl 2006). A schematic presentation of plant immune systems is shown in Fig. 3. PTI is triggered by recognition of pathogen- or microbe-associated molecular patterns (PAMPs/MAMPs). PAMPs/MAMPs are referred to as small molecular motifs conserved within a class of microbes, hence characteristic of microbes, and recognized by pattern recognition receptors (PRRs) which are localized in the plant cell membrane, leading to activation of a basal level of resistance (Vleesschauwer and HöFte 2009; Chisholm and others 2006). But some microbial pathogens have the ability to escape PTI through secretion of effector molecules (Vleesschauwer and HöFte 2009; Göhre and Robatzek 2008). For these type of pathogens, plants adapted themselves to produce cognate R (resistance) proteins which are typically localized inside the plant cell that recognize, either directly or indirectly, these pathogen-specific effector proteins, resulting in a superimposed layer of defense variably termed ETI, gene-for-gene resistance, or R gene-

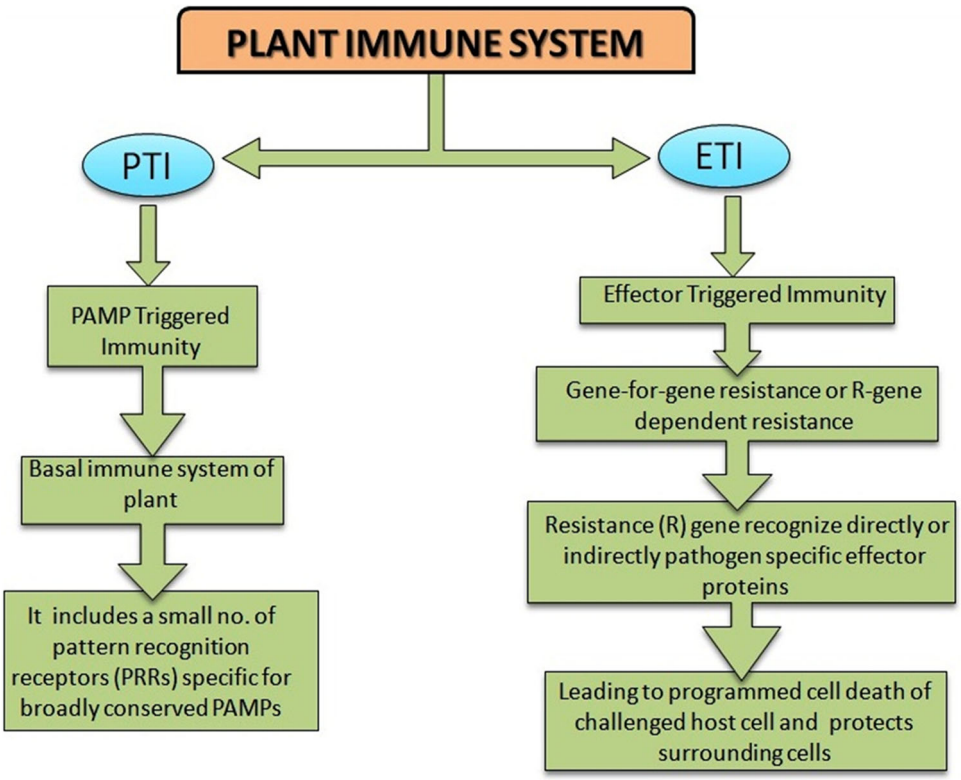

Fig. 3 Role of PTI and ETI in induced resistance. *PTI* PAMP-triggered immunity, *ETI* effector-triggered immunity

dependent resistance (Vleesschauwer and HöFte 2009; Jones and Dangl 2006). After recognition of effector molecules, a limited number of host cells culminate in programmed cell death restricting further growth or spread of the infection. This hypersensitive response (HR) is thought to benefit the plant by restricting pathogen access to water and nutrients and is correlated with an integrated set of physiological and metabolic alterations that are instrumental in impeding further pathogen ingress, among which exists a burst of oxidative metabolism leading to the massive generation of ROS (Vleesschauwer and HöFte 2009; Glazebrook 2005). Despite having such a strong immune system, sometimes plants are affected by infectious microbes. These microbes have the capability to escape the plant's immune system and that is how they can infect plants and lead to reduced quality and quantity of the product. For this type of microbe, plants require an enhanced level of resistance and this resistance is provided by PGPB (Choudhary and Johri 2009).

An enhanced defensive capacity in plants developed when appropriately stimulated by specific environmental stimuli whereby plants can resist biotic stress. There are mainly two forms of induced resistance, SAR (systemic acquired resistance) and ISR (induced systemic resistance) wherein plant defenses are preconditioned by biotic stimuli through prior infection and/or treatment that results in resistance upon challenge. Induction and expression of genes involved in SAR and ISR are dependent on the nature of the elicitor and the regulatory pathways involved. These pathways are activated by a specific signaling molecule or elicitor which activates different intermediate molecules in a cascading manner and forms a network of interconnected signaling pathways which regulate induced defense in plants against pathogens (Jain and others 2013; Choudhary and others 2007). Induction of SAR involves exposing the plant to various types of biotic stimuli wherein a specific time period is required for the establishment of SAR which depends on the type of plant and elicitors. Accumulation of pathogenesis-related (PR) proteins and salicylic acid (SA) is induced in SAR, whereas ISR is triggered by PGPB and does not involve accumulation of PR proteins and/or SA and it relies on pathways regulated by jasmonates (JA) and ethylene (ET) (Choudhary and others 2007; Pieterse and others 2001; Yan and others 2002). Moreover, PGPBs elicit a range of defense-responsive activities in plants including activation of antioxidant status by reprogramming defense-related enzymes, modulation of quorum sensing phenomenon, and activation of the phenylpropanoid pathway leading to phenolic production, lignin deposition, and transgenerational defense response to combat the pathogen challenge (Mishra and others 2015).

Studies on plant microbe interactions showed PGPB-elicited ISR against various pathogens to reduce

susceptibility to respective concerned diseases, for example, carnation (*Dianthus caryophyllus*) with reduced susceptibility to wilt caused by pathogenic fungus *Fusarium* sp. and cucumber (*Cucumis sativus*) with reduced susceptibility to the foliar disease caused by *Colletotrichum orbiculare*, respectively (Compant and others 2005). A huge diversity of PGPB have been obtained that induce resistance against different pathogens, diseases, and insects (Table 2). ISR and SAR both induce resistance in plants by activating different sets of genes, products of which make plants resistant against any further pathogen attack. *Arabidopsis*, a model of the plant world, has been widely used for plant–microbe interactions. Expressions of a specific set of pathogen-inducible defense-related genes have been reported in *Arabidopsis* after induction of the SA, JA, and ET pathways. As previously described, whenever plants get affected by any pathogen, accumulation of SA takes place in the infected region and formation of a phloem-mobile signal is also induced. Subsequently, in the distal part of the plant, the SA concentration increases and volatile methyl salicylate (MeSA) is released. The accumulation of SA in SAR has been proven by using the *Arabidopsis* SA-nonaccumulating mutant plant NahG which expresses the bacterial salicylate hydroxylase (*nahG*) gene responsible for conversion of SA into catechol and therefore is unable to express SAR (Pieterse and others 1998). SA is the primary molecule for SAR which activates further signaling cascades to activate the genes responsible for resistance against a pathogen, called a pathogenesis-related (PR) gene which encodes different PR proteins of families PR-2, PR-5, and PR-1. All of these PRs in plants have some antimicrobial properties primarily against fungal pathogens (vanWees, Luijendijk, Smoorenburg, van Loon and Pieterse 1999; Uknes and others 1992; Kombrink and Somssich 1997). NPR-1 protein encoded by *npr-1* gene allowed SAR establishment as it activates PRs genes after getting a signal from SA accumulation (Pieterse and others 1998). Therefore, the sequence of the signaling event in SAR is in such a way that after recognition of a pathogen, SA accumulation takes place which activates the *npr-1* gene followed by activation of PRs genes. It has been proven that the volatile MeSA is released as a long-distance mobile signal for SAR wherein MeSA itself appears to be biologically inactive, but in the systemic tissue, MeSA is hydrolyzed to SA by the MeSA-esterase activity of SA-binding protein-2 (Park and others 2007; Vlot and others 2008a, b; Heil and Ton 2008; Vleesschauwer and HöFte 2009).

On the other hand, ISR has a more diverse and complex route to establish a higher degree of prior resistance without any infection. In place of the PRs gene, defense-related gene activation takes place in ISR by employing JA- and ET-mediated signaling. In JA signaling defense-related protein thionin is expressed after induction of JA (Epple and others 1995; Wasternack and Parthier 1997; Pieterse and others 1998), including that of proteinase inhibitors, whereas pathogen-inducible genes are induced in ET signaling (Saskia and others 1999). Unlike SAR, ISR is elicited by nonpathogenic rhizobacteria or PGPB and there is no need for initial infection as required in SAR. After elicitation from PGPB, transient synthesis of JA and ET takes place and formation of a phloem-mobile signal moves these signals toward the distal part of the plant, and after challenge inoculation, JA and ET response activates *npr-1* gene expression, which encodes the NPR-1 protein followed by activation of defense-related genes. NPR-1 protein is known as a master regulator of both defense pathways, as upon receiving the signal it activates expression of either the PR gene or defense-related gene for the establishment of SAR and ISR, respectively. Like MeSA, methyl jasmonate (MeJA) also works as a volatile signal for the distal part of the plant. Expression of different defense-related genes depends on the fact that NPR -1 is getting a signal from JA or ET or from both in concert. vanWees, Luijendijk, Smoorenburg, van Loon, and Pieterse (1999) have elaborately described different defense-related gene activations by JA and ET. Expression of the pathogen-inducible genes, *Hel* (encoding a hevein-like protein), *ChiB* (encoding a basic chitinase), and *Pdf1.2* (encoding a plant defensin) and proteins encoded by all of these three genes showed antifungal activity through ET signaling (Samac and others 1990; Potter and others 1993; Penninckx and others 1996). Likewise, the activation of the *Hel*, *ChiB*, and *Pdf1.2* genes was also mediated by JA signaling (Penninckx and others 1996; Thomma and others 1998). For the expression of plant defense proteins exhibiting antagonistic and proteinase inhibitory activities, ET- and JA-mediated signalings are required in a cohort manner (Penninckx and others 1998). The *Pal1* gene that encodes phenylalanine ammonia-lyase (PAL) played an important regulatory role in the synthesis of lignin and SA in *Arabidopsis*, and was also found to be induced by JA (Mauch-Mani and Slusarenko 1996; McConn and others 1997). Besides, JA is also involved in plant protection from insects and herbivory, for example, tomato produced JA-induced expression of the *Pin* gene which encoded for the proteinase inhibitor proteins (Farmer and Ryan 1992) and protects the plant against herbivory (Heitz and others 1999). Expression of the *Atvsp* gene (encoding vegetative storage protein) is also induced by JA signaling in *Arabidopsis*. Vegetative storage protein (VSP) possesses acid phosphates activity and by using this activity it retards development of insects and increases the mortality rate. In this way, by activation of such a wide range of different defense-related genes, PGPB-elicited ISR helps protect plants against a broad range of pathogens, insects, and

Table 2 PGPB-mediated biocontrol of different plant diseases, pathogens, and insects

PGPBs	Crops	Disease/pathogen/insect	References
*Carnobacterium Spp.*SJ-5	Soybean	*Fusarium oxysporum*	Jain and Choudhary (2014)
Burkholderia tropica	Maize	*Colletotrichum Gloeosporioides*, *Fusarium culmorum*, *Fusarium oxysporum* and *Sclerotium rolfsii*	Tenorio-Salgado and others (2013)
Bacillus amyloliquefaciens	Bell pepper	*Myzus persicae* (Sulzer)	Herman and others (2008)
Enterobacter sp	Chickpea	*Fusarium avenaceum*	Hynes and others (2008)
Azospirillum brasilense	*Prunus cerasifera* L.	Rhizosphere fungi	Russo and others (2008)
Paenibacillus polymyxa E681	Sesame	Fungal disease	Ryu and others (2006)
Bacillus cereus MJ-1	Red pepper	*Myzus persicae*	Joo and others (2005)
Bacillus subtilis and *Bacillus Amyloliquefaciens*	*Arabidopsis*	*Erwinia carotovora*	Ryu and others (2004)
Bacillus licheniformis	Pepper	*Myzus persicae*	Lucas and others (2004)
Streptomyces marcescens 90–116	Tobacco	Blue mold	Zhang and others (2002)
Bacillus pumilus SE 34	Tobacco	Blue mold	Zhang and others (2002)
Pseudomonas sp	Groundnut	*Rhizoctonia bataticola*	Gupta and others (2002)
Bacillus sp.	Cucumber	Cotton aphids	Stout and others (2002)
Bacillus subtilis G803	Pepper	*Myzus persicae*	Kokalis-Burelle and others (2002)
Pseudomonas aeruginosa	Mung bean	Root rot	Siddiqui and others (2001)
Bacillus amyloliquefaciens	Tomato	Tomato mottle virus	Murphy and others (2000)
Pseudomonas fluorescens	Tobacco	Tobacco necrosis virus	Park and Kloepper (2000)

herbivores (Berger and others 1995). There are a number of bioactive natural chemicals known as allelochemicals produced during plant–microbe and microbe–microbe interactions. Allelochemicals are a subset of metabolites, which are not required for growth, development, and reproduction of the organism. Some PGPB are also for production of different allelochemicals such as siderophore, antibiotics, volatiles, and so on, which can be used as a weapon against plant pathogens and thereby PGPB protect plants from diseases. Allelochemicals may work in a competitive manner such as siderophores for the acquisition of iron or may directly cause damage by inhibiting the gene machinery of the target pathogen such as antibiotics and volatiles (Choudhary and others 2007).

Siderophore

The transition metal iron is one of the most important and essential micronutrients for the animal and plant worlds, as it is crucial for some life-holding processes such as respiration, photosynthesis, N_2-fixation, and so on. Despite being the fourth most frequent element on earth, it is not readily available in many environments because of the very low solubility of the Fe^{3+} ion. In such iron-limiting environments, it is difficult for plants and microbes to survive and be productive. For the survival of self and the host plant in such environments, PGPB secrete iron-binding ligands called "siderophores," which form complexes with Fe^{3+} ion and make it available to the host organism (Gupta and Gopal 2008). Siderophores are low molecular weight organic compounds with a very high and specific affinity to chelate iron (Boukhalfa and Crumbliss 2002). Although a wide range of siderophores are produced by different plant growth promoting microorganism' pseudobactines, also known as pyoverdin or fluorescein, are the most important that exhibit a distinctive phenotypic trait of the rRNA homology group I species of the genus *Pseudomonas* (Visca and others 2007). Siderophores produced by different PGPB decrease the growth of pathogenic fungi in the vicinity by sequestering Fe^{3+} ions and showed heterologous siderophores produced by co-inhabitants (Compant and others 2005; Loper and Henkels 1999; Whipps 2001). Although fungi also produce siderophores, they have lower affinity for ferric ions (Compant and others 2005; Loper and Henkels 1999; O'Sullivan and O'Gara 1992.). In addition to protection by siderophores via ferric iron between biocontrol bacteria and plant deleterious microorganisms, it also triggers an immune response in plants (Höfte and Bakker 2007). A lot of research has been done on pseudobactines in the past decade demonstrating

their role in triggering resistance in plants. For instance, pseudobactines produced by *Pseudomonas putida* WCS358 were reported to suppress *Ralstonia solanacearum* in *Eucalyptus urophylla* (Ran and others 2005), *Erwinia carotovora* in tobacco (Van Loon and others 2008), and *Botrytis cinerea* in tomato (Meziane and others 2005). Pseudobactines are also effective against viral pathogens, such as pseudobactines produced by *Pseudomonas fluorescens* WCS374r make *Arabidopsis* plants resist against turnip crinkle virus (TCV) (Djavaheri 2007), whereas *Pseudomonas fluorescens* CHA0 produced by pseudobactines protect Tobacco plant from Tobacco necrosis virus(TNV) (Maurhofer and others 1994). Recently, Arora and others (2001) have isolated two strains of PGPB *Rhizobium meliloti*, RMP_3 and RMP_5, from *Mucuna pruriens* which produce siderophores and showed strong antagonism against the pathogen *Macrophomina phaseolina.*

Antibiotics

Discovery of the characteristic of PGPB to produce antibiotics has significantly increased our knowledge about biocontrol of diseases. Fluorescent *pseudomonads* produce a wide range of antibiotics that include 2, 4-diacetylphloroglucinol (DAPG), pyoluteorin (PLT), pyrrolnitrin (PRN), phenazine-1-carboxylic acid (PCA), 2-hydroxy phenazines, and phenazine-1-carboxamide (PCN) which have different structural configurations. Beside *Pseudomonas*, a wide range of bacteria produce different types of antibiotics which target different pathogens and protect plant from respective diseases (Fernando and others 2005; Raaijmakers and Weller 1998).

Among the aforesaid antibiotics, DAPG is most frequently reported in PGPB-mediated disease control and is produced by *Pseudomonas fluorescens* CHA0 that induce resistance against oomycete *Hyaloperonospora arabidopsidis* (Iavicoli and others 2003) and the root knot nematode *Meloidogyne javanica* (Siddiqui and Shaukat 2003). DAPG-mediated ISR was shown by *Pseudomonas chlororaphis* Q2-87 in *Arabidopsis* against the leaf pathogen *Pseudomonas syringae* pv. tomato (Vleesschauwer and HöFte 2009). Several bacterial strains have the ability to produce a huge array of antibiotics and help suppress diverse microbial competitors, for example, *Bacilluscereus* strain UW85 produced zwittermycin (Pal and Gardener 2006; Silo-Suh and others 1994) and kanosamine (Milner and others 1996). By studying a set of *Arabidopsis* mutants and transgenic lines implicated in defense-signaling pathways, it was found that DAPG-induced resistance follows a different signaling route in comparison to ISR. This pathway does not depend on the master regulator NPR-1 or functional JAR1 protein but is regulated by the *eir1* (ethylene-insensitive root-1) gene, which is ET insensitive in the roots only (Vleesschauwer and HöFte 2009; Roman and others 1995). The absence of ISR expression after exogenous exposure of DAPG on the *eir1* mutant suggested that an intact ET signaling pathway is required for the establishment of DAPG-inducible resistance (Vleesschauwer and HöFte 2009; Iavicoli and others 2003). PCA, a green-pigmented heterocyclic nitrogenous compound, produced extracellularly by several PGPB with antagonistic activity coupled with the accumulation of toxic superoxide radicals in the target cells (Hassett and others 1992, 1993; Chin-A-Woeng and others 1998; Fernando and others 2005). PCA produced by *Pseudomonas fluorescens* 2-79 and *Pseudomonas aureofaciens* 30–84 exhibited antagonism against *Gaeumannomyces graminis* var. *tritici* (Thomashow and others 1990). *S*tem rot disease of canola caused by *Sclerotinia* was suppressed by activity of the *Pseudomonas chlororaphis* strain PA-23 (Zhang and Fernando 2004). Hu and others (2005) have isolated Strain M-18 from the rhizosphere soil of sweet melon, using 1-aminocyclopropane-1-carboxylate (ACC) as a sole nitrogen source and it was found that this strain is capable of production of PCA and pyoluteorin antibiotics.

Volatiles

n context to plant defense, PGPB production of volatile organic compounds (VOCs) eliciting plant growth promotion and inducing systemic resistance provides a new insight in PGPB–plant interactions. Several different types of VOCs produced by bacteria have been reported, which play a crucial role in plant defense. Some of the most common VOCs include dodecane, 2-undecanone, 2-tridecanone, 2-tridecanol, tetramethyl pyrazine 2, 3- butanediol, and 3-hydroxy-2-butanone (acetoin). Among these, 2, 3-butanediol and 3-hydroxy-2-butanone are the most important and recent research on bacterial-produced VOCs confirmed their role in elicitation of ISR (Ryu and others 2003). Two bacterial strains namely, *Bacillus subtilis* GB03 and *Bacillus amyloliquefaciens* IN937a, were found to consistently release 2,3-butanediol and 3-hydroxy-2-butanone, and *A. thaliana* plants treated with these strains have shown significant resistance against the challenge inoculation of *Erwinia carotovora* subsp. Carotovora SCC1. The priming activity of such VOCs to induce resistance against diseases was reported with a genetically modified *Bacillus* strain which is unable to produce VOCs (Ryu and others 2003). Besides *Bacillus,* several strains of *Pseudomonas fluorescens* were also reported for the production of VOCs and were shown to be more effective in controlling root and seedling diseases (Duffy and Défago 1997; Schnider and others 1995; Cronin and others 1995; Raaijmakers and Weller 2001; Raaijmakers and others

1997, 1999; Raaijmakers and Weller 1998; Landa and others 2002).

Studies on mechanisms of induced systemic resistance (ISR) are suggested to be valuable in extension of microbial-elicited ISR to practical agriculture. Choudhary and others (2007, 2008) elaborately described induced resistance and its mechanism of action in plants. Plants have the ability to acquire an enhanced level of resistance to pathogens after exposure to biotic stimuli provided by many different PGPB. These in association with plant roots elicit a steady state of defense or ISR in plants. This is often referred to as rhizobacteria-mediated ISR. PGPB-elicited ISR was initially observed in carnation, common bean, and in cucumber with reduced susceptibility to *Fusarium* wilt, halo blight, and *Colletotrichum orbiculare*, respectively. Several PGPB that colonize root systems with seed applications protect plants against foliar diseases, which include *Pseudomonas fluorescens, P. putida, Bacillus pumilus*, and *Serratia marcescens*. Induced resistance is a physiological "state of enhanced defensive capacity" elicited by specific environmental stimuli, whereby the plant's innate defenses are potentiated against subsequent biotic challenges. This enhanced state of resistance is effective against a broad range of pathogens and parasites (van Loon 2000).

PGPB can suppress diseases through antagonism between bacteria and soil-borne pathogens, as well as by inducing a systemic resistance in the plant against both root and foliar pathogens. The induced resistance constitutes an increase in the level of basal resistance to several pathogens simultaneously, which is of benefit under natural conditions in which multiple pathogens exist (Van Loon and Glick 2004). Plants possess a range of active defense apparatuses that can be actively expressed in response to biotic stresses (pathogens and parasites) of various scales (ranging from microscopic viruses to phytophagous insect). The timing of this defense response is critical and reflects the difference between coping and succumbing to such biotic challenged of necrotizing pathogens/parasites (Choudhary and others 2007). Pathogenic microorganisms affecting plant health are major and chronic threats to food production and ecosystem stability worldwide. Despite inconsistency in field performance, biological control is considered an alternative or supplemental means of reducing root diseases in agro-ecosystems (Sharma and Johri 2003). The widely recognized mechanism of biocontrol mediated by PGPB is competition for an ecological niche/substrate, production of inhibitory allelochemicals, and ISR in host plants to a broad spectrum of pathogens. Earlier attempts to commercialize products containing fluorescent pseudomonad strains of PGPB generally failed due to lack of long-term viability of these asporogenous bacteria. Although commercialization of PGPB is mainly proceeding with *Bacillus* spp. rather than pseudomonads, the preponderance of research on PGPB as elicitors of growth promotion or ISR employs PGPB strains that are fluorescent pseudomonads. Compared to plant growth-promoting *Pseudomonas* rhizobacteria, relatively little is known about the lifestyle of plant-associated *Bacillus* spp., which was originally considered as typical soil bacteria, despite their well-established advantages for beneficial action on plant growth and biocontrol (Kloepper and others 2004).

In the literature on elicitation of ISR by pseudomonads, the most often investigated component of mechanisms accounting for ISR is the study of signaling pathways in the plant *Arabidopsis thaliana* (Van Loon and Glick 2004). Fewer published accounts of ISR by *Bacillus* spp. are available which showed that specific strains of the species *B. amyloliquefaciens*, *B. subtilis*,*B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* elicit significant reductions in the incidence or severity of various diseases on a diversity of hosts. One aspect of mechanisms is to determine which compounds associated with plant defense against pathogens are produced during PGPB-elicited ISR. Elicitation of ISR in sugar beet was associated with enhanced peroxidase activity and increased production of one chitinase isozyme and two isozymes of β-1,3-glucanase that was produced by the *B. mycoides* strain Bac J, and *B. pumilus* strains 203-6 and 203-7 (Bargabus and others 2004), respectively. In the tobacco blue mold system, Zhang and others (2002) reported that plants treated with *B. pumilus* strain SE34 had greatly increased levels of salicylic acid, compared with that of nontreated plants or plants treated with two gram-negative bacteria, 1 day after challenge inoculation with the pathogen. In the tomato late blight system reported by Yan and others (2002), elicitation of ISR by *B. pumilus* SE34 on tomato lines with various mutations in signaling pathways was tested. ISR was elicited on *nah*G lines, which breakdown endogenous salicylic acid, but not in the ethylene-insensitive NR/NR line or in the jasmonic acid insensitive *df*1/*df*1 line. These results are consistent with studies on several strains of *Pseudomonas* spp. that elicit ISR in *Arabidopsis thaliana* (Van Loon and Glick 2004) where ISR is typically independent of salicylic acid and does not result in activation of the PR1a gene that encodes production of the pathogenesis-related (PR) protein PR1a. Similar results were reported by Zhang and others (2002). In the tobacco blue mold system, SE34 as well as two strains of gram-negative bacteria elicited ISR on both wild-type and *nah*G transgenic tobacco lines evidenced by significant reductions in the severity of blue mold on bacterized plants compared with that on nonbacterized plants. The conclusion that SE34 elicits ISR

via salicylic acid-independent pathways confirms the model with ISR elicited by *Pseudomonas* spp. in *A. thaliana* (van Loon and Glick 2004).

Various results were found with *B. pumilus* strain T4 (Park and Kloepper 2000) that elicited ISR in tobacco against wildfire, caused by *Pseudomonas syringae* pv. *tabaci*. In this system, a bacterized transgenic line of tobacco (*Nicotiana tabacum* cv. Xanthi-nc) with a GUS reporter gene fused to the PR1a promoter had significantly reduced severity of wildfire compared with nonbacterized controls. Elicitation of ISR by strain T4 was associated with a significant increase in GUS activity in microtiter-plate and whole-plant bioassays. Hence, with strain T4, elicitation of ISR results in activation of PR1a, which is activated during the salicylic acid-dependent signaling pathway (Van Loon and Glick 2004). In another study of signaling pathways, Ryu and others (2003) found different results with strain T4 in *Arabidopsis* spp. In this study, *B. pumilus* T4 and SE34, *B. amyloliquefaciens* IN937a, and *B. subtilis* GB03 were evaluated for elicitation of ISR against two different pathovars of *Pseudomonas syringae* (pvs. *tomato* and *maculicola*). Strains T4 and SE34 elicited ISR against both pathogens, whereas strains IN937a and GB03 did not elicit protection against either pathovar. When tested on NahG plants, both T4 and SE34 elicited ISR against *Pseudomonas syringae*pv. *maculicola*. However, against *Pseudomonas syringae*pv. *tomato*, ISR was elicited by T4 but not by SE34. Hence, although a salicylic acid-independent pathway was dominant in the tests, a salicylic acid-dependent pathway appeared to be activated during ISR elicited by strain SE34 against one pathovar. Additional tests of T4 and SE34 on various mutant lines of *Arabidopsis* spp. (Ryu and others 2003) revealed that in agreement with results on signaling during ISR elicited by *Pseudomonas* spp., ISR elicited by strain SE34 was dependent on NPR1, jasmonic acid, and ethylene, whereas ISR elicited by strain T4 was dependent on ethylene. In contrast to results on signaling during ISR elicited by *Pseudomonas* spp., ISR elicited by strain T4 was independent of NPR1 and jasmonic acid.

The observed increases in lipoxygenase (LOX) activity in plant tissue expressing resistance in diverse pathosystems have been reported (Croft and others 1990). The activities of plant peroxidase (POD) and phenylammonialyase (PAL) enzymes are known as stress indicators. POD participates in the cell wall polysaccharides processes such as oxidation of phenols, suberization, and lignification of host plant cells during the defense reaction against pathogenic agents (Ray and others 1998). The high peroxidase activities detected in treatments are linked to lignification and generation of hydrogen peroxides that inhibit pathogens directly or generate other free radicals with antimicrobial effects (Hammerschmidt 1999). The peroxidase activity results reported in this study are in agreement with those of Podile and Lakshmi (1998), who observed an increase in POD activity in pea plants treated with *B. subtilis* 7 days after inoculation with *Fusarium udum*. PAL plays a key role in the phenylpropanoid pathway wherein lignin is one of the major products. Deposition of lignin is an inducible defense mechanism employed for protection against pathogen invasion (Liang and others 1989). The type of bacterized plant response induced after challenge with a pathogen resulted in the formation of structural barriers, such as thickened cell wall because of the deposition of callose and the accumulation of phenolic compounds at the site of pathogen attack (Benhamou and others 1998). PAL activity was higher in plants grown from microbiolized seeds that were challenge inoculated with charcoal rot pathogen. PAL activity is reflective of disease proliferation and consequent stress. Studies with different plant species showed that PAL activity increases with the biotic and abiotic stresses including bacterial infection (Hammerschmidt 1999; Yan and others 2002).

The role of volatiles of microbial origin as signal molecules for plant defense has come to light recently. A comparison has been drawn between herbivore-induced plant volatiles (HIPVs) as an elicitor of plant defenses and two other classes of signaling molecules, C6 green-leaf volatiles (GLVs) and C4 bacterial volatiles which appear to prime plant defenses, thereby enhancing the capacity to mobilize cellular defense responses when plants are faced with herbivore/pathogen attacks (Choudhary and others 2008). Volatile signals generated by certain nonpathogenic bacteria have also been shown to trigger defense responses in *Arabidopsis* (Ryu and others 2003). Ryu and others (2004) examined the role of airborne bacterial metabolites in triggering ISR by growing PGPB and *Arabidopsis* seedlings on separate sides of divided Petri dishes. ISR was activated by exposure of *Arabidopsis* seedlings to volatile organic compounds (VOCs) from the *Bacillus* sp. on continuous exposure for as short as 4 days by a significant reduction in symptomatic leaves inoculated with the soft rot-causing pathogen *Erwinia carotovora*. VOCs collected from growth-promoting bacteria *B. subtilis* GB03 and *B.amyloliquefaciens* IN937a showed consistent difference in the composition of volatile blends compared to VOCs which were recovered from the non-growth-promoting bacterial strain DH5α. Strains GB03 and IN937a consistently released two of the most abundant compounds, 2, 3-butanediol and 3-hydroxy-2-butanone (acetoin), whereas these metabolites were not released from DH5α or water-treated MS media (Ryu and others 2003). Several other VOCs were also observed, including dodecane, 2-undecanone, 2-tridecanone, 2-tridecanol, and tetramethyl pyrazine from a complex bacterial bouquet that did not exhibit ISR priming activity. Bacteria employ different mechanisms

to produce VOCs; for example, in the *Bacillus* sp. strain GB03 and IN937a, 2,3-butanediol and acetoin were produced under low atmospheric O_2 partial pressure to provide an alternative electron sink for the regeneration of NAD^+ when usual respiration was not possible (Ryu and others 2004).

No disease protection was observed when *Bacillus* strains were genetically blocked for the production of 2, 3-butanediol; this confirmed the priming activity of the compound to induce resistance against disease. The involvement of known signaling pathways in *Arabidopsis* was screened by exposing defined mutants and transgenic plant lines to bacterial emissions containing VOCs especially 2, 3-butanediol. ISR triggered by GB03 VOC was independent of SA, NPR1, and the JA signaling pathway but was more or less mediated by ethylene. Interestingly, ISR activation by the strain IN937a was independent of all the signaling pathways and this opens up the possibility of involvement of additional VOCs which utilize alternative pathways to trigger ISR. From a more general perspective, the diversity within populations of antagonistic microorganisms with a common biocontrol trait is a means to improving biocontrol. This approach builds on existing knowledge of mechanisms while exploiting genetic differences that have evolved to enable microbial populations to compete successfully in diverse soil and rhizosphere environments. Understanding the diversity within populations of biocontrol agents holds the promise of pairing specific genotypes with their most supportive plant hosts or soil environments to maximize root colonization and disease suppression. In addition, agricultural management practices as well as the "history" of cultivation in a crop rotation cycle may be supportive or contra-productive for the successful establishment of biocontrol active Bacilli in a given crop. PGPBs also serve as biocontrol agents by the biopriming method. Biopriming is a popular approach of seed treatment which includes inoculation of seed with beneficial microorganisms to protect the seed from various seed- and soil-borne diseases. Seed priming is commonly being used in many horticultural crops to facilitate uniform seed germination and amplify growth. Therefore, PGPBs are becoming a viable alternative for inorganic chemicals (Bisen and others 2015).

Conclusion

Increased incidences of abiotic and biotic stresses impacting productivity in principal crops are being witnessed all over the world. Extreme events like prolonged droughts, intense rains, and flooding, heat waves, and frost damage are likely to further increase in the future due to climate change. A wide range of adaptations and mitigation strategies are required to cope with such impacts. The development of stress tolerant crop varieties through genetic engineering and plant breeding can help to overcome stresses to some extent. However, because such strategies are time-consuming and cost intensive, there is a need to develop simple and low cost biological methods for the management of stresses, which can be used on a short-term basis. The above-discussed review indicates the role of PGPB in plant protection against biotic stresses ranging from microorganisms and parasites to nematodes and insects, and in tolerance to biotic stresses by the production of different osmoprotectants. Due to effective root colonization and their interaction with plant and other microbial populations, PGPB have great potential for improving root growth, enhancing biomass yield, and increasing crop yields. In addition to normal growth-promoting traits, PGPB also protect the plant from certain biotic and abiotic stresses by using some particular mechanisms; for example, the presence of the ACC deaminase enzyme and the production of EPS are one of the very important mechanisms that play a key role for reducing the negative impact of salinity and drought. PGPB enhance defense-related enzymes, phenolic production, and elicit jasmonic and ethylene pathways in plants to combat biotic stress. Through these and other mechanisms, PGPB not only promote plant biomass yield in normal conditions but also create a favorable environment that is conducible for microbes themselves as well as for plant growth in adverse conditions.

Acknowledgments Some of the research in the present review has partially been supported by DBT and SERB Grant No. BT/PR1231/AGR/021/340/2011 and SR/FT/LS-129/2012, respectively, to DKC.

References

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

Adesemoye AO, Torbert HA, Kloepper JW (2008) Enhanced plant nutrient use efficiency with PGPR and AMF in an integrated nutrient management system. Can J Microbiol 54:876–886

Agrios GN (1988) Plant pathology, 3rd edn. Academic Press Inc., San Diego

Ahmad P, Sarwat M, Sharma S (2008) Reactive oxygen species, antioxidants and signalling in plants. Plant Biol 51:167–173

Ait bakra E, Nowak J, Clement C (2006) Enhancement of chilling resistance of inoculated grapevine plantlets with a plant growth promoting rhizobacterium, *Burkholderia phytofirmans* strain PsJN. Appl Environ Microbiol 72(11):7246–7252

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

Ali Sk Z, Sandhya V, Grover M, Kishore N, Rao LV, Venkateswarlu B (2009) *Pseudomonas* sp. strain AKM-P6 enhances tolerance of

sorghum seedlings to elevated temperatures. Biol Fert Soil 46:45–55

Al-Karaki GN, Ammad R, Rusan M (2001) Response of two tomato cultivars differing in salt tolerance to inoculation with mycorrhizal fungi under salt stress. Mycorrhiza 11:43–47

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

Apse MP, Aharon GS, Snedden WA, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar Na +/H + antiport in Arabidopsis. Science 285:1256–1258

Arkipova 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

Aroca R, Vernieri P, Ruiz-Lozano JM (2008) Mycorrhizal and non-mycorrhizal *Lactuca sativa* plants exhibit contrasting responses to exogenous ABA during drought stress and recovery. J Exp Bot 59(8):2029–2041

Arora NK, Kang SC, Maheshweri DK (2001) Isolation of siderophore producing strain of *Rhizobium meliloti* and their biocontrol potential against *Macrophomina phaseolina* that causes charcoal rot of groundnut. Curr Sci 81:673–677

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.). Pedosphere 18:611–620

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

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, Sobero MT (2006a) Seed inoculation with *Azospirillum mitigates* NaCl effects on lettuce. Sci Hortic 109:8–14

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

Barea JM, Azcon R, Azcón-Aguilar C (2004) Mycorrhizal fungi and plant growth promoting rhizobacteria. In: Varma A, Abbott L, Werner D, Hampp R (eds) Plant surface microbiology. Springer, Heidelberg, pp 351–371

Bargabus RL, Zidack NK, Sherwood JW, Jacobsen BJ (2004) Screening for the identification of potential biological control agents that induce systemic acquired resistance in sugar beet. Biol Control 30:342–350

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

Barraquio WL, Segubre EM, Gonzalez MAS, Verma SC, James EK, Ladha JK, Tripathi AK (2000) Diazotrophic entetrobacteria: what is their role in the rhizosphere of rice? In: Ladha JK, Reddy PM (eds) The quest for nitrogen fixation in rice. IRRI, Los Banos, pp 93–118

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 grow in drying soil via both local and systemic hormone signaling. New Phytol 181:413–423

Ben Khaled L, Gomez AM, Ourraqi EM, Oihabi A (2003) Physiological and biochemical responses to salt stress of mycorrhized and/or nodulated clover seedlings (*Trifolium alexandrinum* L.). Agronomie 23:571–580

Benhamou N, Kloepper JW, Tuzun S (1998) Induction of resistance against *Fusarium* wilt of tomato by combination of chitosan with an endophytic bacterial strain: ultrastructure and cytochemistry of the host response. Planta 204:153–168

Berger S, Bell E, Sadka A, Mullet JE (1995) *Arabidopsis thaliana AtVsp* is homologous to soybean *VspA* and *VspB*, genes encoding vegetative storage protein acid phosphatases, and is regulated similarly by methyl jasmonate, wounding, sugars, light and phosphate. Plant Mol Biol 27:933–942

Berthomieu P, Coné jé ro G, Nublat A, Brackenbury WJ, Lambert C, Savio C, Uozumi N, Oiki S, Yamada K, Cellier F, Gosti F, Simonneau T, Essah PA, Tester M, Véry A-A, Sentenac H, Casse F (2003) Functional analysis of AtHKT1 in Arabidopsis shows that Na + recirculation by the phloem is crucial for salt tolerance. EMBO J 22:2004–2014

Bezzate S, Aymerich S, Chambert R, Czarnes S, Berge O, Heulin T (2000) Disruption of the *Paenibacillus polymyxa*levansucrase gene impairs its ability to aggregate soil in the wheat rhizosphere. Environ Microbiol 2:333–342

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(11):3097–3107

Bisen K, Keswani C, Mishra S, Saxena A, Rakshit A, Singh HB (2015) Unrealized potential of seed biopriming for versatile agriculture. In: Rakshit A, Singh HB, Sen A (eds) Nutrient use efficiency: from basics to advances. Springer, Berlin pp 193–206

Blokhina O, Virolainen E, Fagerstedt KV (2003) Antioxidants, oxidative damage and oxygen deprivation stress: a review. Ann Bot 91:179–194

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

Broetto F, Marchese JA, Leonardo M, Regina M (2005) Fungal elicitor-mediated changes in polyamine content, phenylalanine ammonia-lyase and peroxidase activities in bean cell culture. Gen Appl Plant Physiol 31:235–246

Buscot F (2005) What are soils? In: Buscot F, Varma S (eds) Microorganisms in soils: roles in genesis and functions. Springer, Heidelberg, pp 3–18

Cassan F, Maiale S, Masciarelli O, Vidal A, Luna V, Ruiz O (2009) Cadaverine production by *Azospirillum brasiliense* and its possible role in plant growth promotion and osmotic stress mitigation. Eur J Soil Biol 45:12–19

Chen M, Wei H, Cao J, Liu R, Wang Y, Zheng C (2007) Expression of *Bacillus subtilis* proAB genes and reduction of feedback inhibition of proline synthesis increases proline production and confers osmotolerance in transgenic *Arabidopsis*. J Biochem Mol Biol 40:396–403

Chin-A-Woeng TFC, Bloemberg GV, van der Bij AJ, van der Drift KMGM, Schripsema J, Kroon B, Scheffer RJ, Keel C, Bakker PAHM, De Bruijn FJ, Thomas- Oates JE, Lugtenberg BJJ (1998) Biocontrol by phenazine-1-carboxamide producing *Pseudomonas chlororaphis* PCL1391 of tomato root rot caused by *Fusarium oxysporum* f.sp. *radicis-lycopersici*. Mol Plant-Microbe Interact 10:79–86

Chinnusamy V, Jagendorf A, Zhu J-K (2005) Understanding and improving salt tolerance in plants. Crop Sci 45:437–448

Chisholm ST, Coaker G, Day B, Staskawicz BJ (2006) Host-microbe interactions: shaping the evolution of the plant immune response. Cell 124:803–814

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

Choudhary DK (2011) Plant growth-promotion (PGP) activities and molecular characterization of rhizobacterial strains isolated from soybean (*Glycine* max) plants against charcoal rot pathogen, *Macrophomina phaseolina*. Biotechnol Lett 33:2287–2295

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

Choudhary DK, Johri BN (2009) Interactions of *Bacillus* spp. and plants-with special reference to induced systemic resistance (ISR). Microbiol Res 164:493–513

Choudhary DK, Prakash A, Johri BN (2007) Induced systemic resistance (ISR) in plants: mechanism of action.Indian. J Microbiol 47:289–297

Choudhary DK, Johri BN, Prakash A (2008) Volatiles as priming agent that initiate plant growth and defense responses. Curr Sci 94:595–604

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

Croft KPC, Voisey CR, Slusarenkl AJ (1990) Mechanism of hypersensitive cell collapse: correlation of increase lipoxygenase activity with membrane damage in leaves of *Phaseolus vulgaris* cv. Red Mexican inoculated with avirulent race/cells of *Pseudomonas syringae* pv. Phaseolicola. Physiol Mol Plant Pathol 36:49–62

Cronin D, Moënne-Loccoz Y, Fenton A, Dunne C, Dowling DN, O'Gara F (1997) Role of 2, 4-diacetylphloroglucinol in the interaction of the biocontrol pseudomonad strain F113 with the potato cyst nematode Globodera rostochiensis. Appl Environ Microbiol 63:1357–1361

Cullis PM, Jones GD, Symons MC, Lea JS (1987) Electron transfer from protein to DNA in irradiated chromatin. Nature 330(6150):773–774

Dardanelli MS, Fernández de Córdoba FJ, Rosario Espuny M, Rodríguez Carvajal MA, Soria Díaz ME, Gil Serrano AM, Okon Y, Megías M (2008) Effect of *Azospirillum brasilense* coinoculated with *Rhizobium* on *Phaseolus vulgaris* flavonoids and Nod factor production under salt stress. Soil Bio Biochem 40:2713–2721

Del Amor F, Cuadra-Crespo P (2012) Plant growth-promoting bacteria as a tool to improve salinity tolerance in sweet pepper. Funct Plant Biol 39:82–90

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

Djavaheri M (2007) Iron-regulated metabolites of plant growth-promoting *pseudomonas fluorescens* WCS374: their role in induced systemic resistance. Ph.D. Thesis, Utrecht University, Utrecht

Duan J, Jiang W, Cheng Z, Heikkila JJ, Glick BR (2013) The complete genome sequence of the plant growth promoting bacterium Pseudomonas sp. UW4. Plos One 8(3):1–19

Duffy BK, Défago G (1997) Zinc improves biocontrol of *Fusarium* crown and root rot of tomato by *Pseudomonas fluorescens* and represses the production of pathogen metabolites inhibitory to bacterial antibiotic biosynthesis. Phytopath 87:1250–1257

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

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

Egamberdiyeva D, Hoflich G (2003) Influence of growth-promoting bacteria on the growth of wheat in different soils temperatures. Soil Biol Biochem 35:973–978

Egamberdiyeva D, Gafurova L, Islam KR (2007) Salinity effects on irrigated soil chemical and biological properties in the Syr Darya Basin of Uzbekistan. In: Lal R, Sulaimanov M, Stewart B, Hansen D, Doraiswamy P (eds) Climate change and terrestrial C sequestration in Central Asia. Taylor- Francis, New York, pp 147–162

Else MA, Jackson MB (1998) Transport of 1-aminocyclopropane-1-carboxylic acid (ACC) in the transpiration stream of tomato (*Lycopersicon esculentum*) in relation to foliar ethylene production and petiole epinasty. Aus J Plant Physiol 25(4):453–458

Epple P, Apel K, Bohlmann H (1995) An *Arabidopsis thaliana* thionin gene is inducible via a signal transduction pathway different from that for pathogenesis-related proteins. Plant Physiol 109:813–820

Eulgem T, Somssich IE (2007) Networks of WRKY transcription factors in defense signaling. Curr Opin Plant Bio 10:366–371

Farmer EE, Ryan CA (1992) Octadecanoid precursors of jasmonic acid activate the synthesis of wound-inducible proteinase inhibitors. Plant Cell 4:129–134

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

Fernando WGD, Nakkeeran S, Zhang Y (2005) In: Siddiqui ZA (ed) PGPR: biocontrol and biofertilization. Springer, Dordrecht, pp 67–109

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

Fukuda A, Nakamura A, Tanaka Y (1999) Molecular cloning and expression of the Na^+/H^+ exchanger gene in *Oryza sativa*. Biochim Biophys Acta 1446(1–2):149–155

Garcia-Mata C, Lammattina L (2001) Nitric oxide induces stomatal closure and enhances the adaptive plant responses against drought stress. Plant Physiol 126:1196–1204

Garcia-Mata C, Lammattina L (2002) Nitric oxide and abscisic acid cross talk in guard cells. Plant Physiol 128:790–792

Geng SM, Yan DH, Zhang TX, Weng BS, Zhang ZB, Qin TL (2015) Effects of drought stress on agriculture soil. Nat Hazards 75:1997–2011

Giri B, Mukerji KG (2004) Mycorrhizal inoculant alleviate salt stress in *Sesbania aegyptiaca* and *Sesbania grandiflora* under field conditions: evidence for reduced sodium and improved magnesium uptake. Mycorrhiza 14:307–312

Giri B, Kapoor R, Mukherji KG (2007) Improved tolerance of *Acacia nilotica* to salt stress by *Arbuscular mycorrhiza*, *Glomus fasciculatum* may be partly related to elevated K^+/Na^+ ratios in root and shoot tissues. Microb Ecol 54:753–760

Glazebrook J (2005) Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. Annu Rev Phytopathol 43:205–227

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

Glick BR (2007) Promotion of plant growth by bacterial ACC deaminase. Crit Rev Plant Sci 26:227–242

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

Glick BR, Patten C, Holguin G, Penrose D (1999) Biochemical and genetic mechanisms used by plant growth promoting bacteria. Imperial College Press, London

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

Göhre V, Robatzek S (2008) Breaking the barriers: microbial effector molecules subvert plant immunity. Annu Rev Phytopathol 46:189–215

Gómez-Sagasti M, Marino D (2015) PGPRs and nitrogen fixing legumes: a perfect team for efficient Cd phytoremediation? Front Plant Sci 81(6):1–9

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

Gryndler M (2000) Interactions of *Arbuscular mycorrhizal* fungi with other soil organisms. In: Kapulnik Y, Douds DD Jr (eds) Arbuscular mycorrhizas: physiology and functions. Kluwer Academic Publishers, Dordrecht, pp 239–262

Gupta A, Gopal M (2008) siderophore production by plant growth promoting rhizobacteria. Ind J Agric Res 42:153–156

Gupta CP, Dubey RC, Maheshwari DK (2002) Plant growth enhancement and suppression of Macrophomina phaseolina causing charcoal rot of peanut by fluorescent *Pseudomonas*. Biol Fertil Soil 35:399–405

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

Hammerschmidt R (1999) Induced disease resistance: how do induced plants stop pathogens? Physiol Mol Plant Pathol 55:77–84

Hardoim PR, van Overbeek SV, van Elsas JD (2008) Properties of bacterial endophytes and their proposed role in plant growth. Trends Microbiol 16:463–471

Hare PD, Cress WA (1997) Metabolic implications of stress-induced proline accumulation in plants. Plant Growth Regul 21:79–102

Hassett DJ, Charniga L, Bean K, Ohman DE, Cohen MS (1992) Response of *Pseudomonas aeruginosa* to pyocyanin: mechanisms of resistance, antioxidant defenses, and demonstration of manganese-cofactored superoxide dismutase. Infect Immu 60:328–336

Hassett DJ, Woodruff WA, Wozniak DJ, Vasil ML, Cohen MS, Ohman DE (1993) Cloning of *sodA* and *sodB* genes encoding manganese and iron superoxide dismutase in *Pseudomonas aeruginosa*: demonstration of increased manganese superoxide dismutase activity in alginate-producing bacteria. J Bacteriol 175:7658–7665

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

Heil M, Ton J (2008) Long-distance signalling in plant defense. Trend Plant Sci 13:264–272

Heitz T, Geoffroy P, Fritig B, Legrand M.(1999) The PR-6 family: proteinase inhibitors in plant-microbe and plant-insects interactions. In: Datta SK and Muthukrishnan S (Eds.); Pathogenesis-related proteins in plants. CRC Press, Boca Raton, pp 131–155

Hepper CM (1975) Extracellular polysaccharides of soil bacteria. In: Walker N (ed) Soil microbiology, a critical review. Wiley, New York, pp 93–111

Herman MAB, Nault BA, Smart CD (2008) Effects of plant growth promoting rhizobacteria on bell pepper production and green peach aphid infestations in New York. Crop Prot 27:996–1002

Höfte M, Bakker PAHM (2007) Competition for iron and induced systemic resistance by siderophores of plant growth-promoting rhizobacteria. In: Varma A, Chincholkar SB (eds) Microbial siderophores. Springer, Berlin, pp 121–134

Horie T, Schroeder JI (2004) Sodium transporters in plants. Diverse genetic and physiological functions. Plant Physiol 136:2457–2462

Hu HB, Xu YQ, Chen F, Zhang XH, Hur BK (2005) Isolation and characterization of a new fluorescent *Pseudomonas* strain that produces both phenazine 1-carboxylic acid and pyoluteorin. J Microbiol Biotechnol 15:86–90

Hynes RK, Leung GC, Hirkala DL, Nelson LM (2008) Isolation, selection, and characterization of beneficial rhizobacteria from pea, lentil and chickpea grown in western Canada. Can J Microbiol 54:248–258

Iavicoli A, Boutet E, Buchala A, Métraux J-P (2003) Induced systemic resistance in *Arabidopsis thaliana* in response to root inoculation with *Pseudomonas fluorescens* CHA0. Mole Plant-Microbe Interact 16:851–858

Jain S, Choudhary DK (2014) Induced defense-related proteins in soybean (*Glycine max* L. Merrill) plants by *Carnobacterium* sp. SJ-5 upon challenge inoculation of *Fusarium oxysporum*. Planta. doi:10.1007/s00425-014-2032-3

Jain S, Vaishnav A, Kasotia A, Kumari S, Gaur RK, Choudhary DK (2013) Bacterium-induced systemic resistance and growth promotion in Glycine max L. Merrill upon challenge inoculation with Fusarium oxysporum. Proc Natl Acad Sci, India, Sect. B Biol Sci 83(4):561–567

Jeffries P, Barea JM (2001) *Arbuscular mycorrhiza*: a key component of sustainable plant soil ecosystems. In: Hock B (ed) The Mycota: fungal associations, vol 9. Springer, Berlin, pp 95–113

Jha Y, Subramanian RB, Patel S (2010) Combination of endophytic and rhizospheric plant growth promoting rhizobacteria in *Oryza sativa* shows higher accumulation of osmoprotectant against saline stress. Acta Physiol Plant 33(3):797–802

Jones JDG, Dangl JL (2006) The plant immune system. Nature 444:323–329

Joo GJ, Kin YM, Kim JT, Rhee IK, Kim JH, Lee IJ (2005) Gibberellins-producing rhizobacteria increase endogenous gibberellins content and promote growth of red peppers. J Microbiol 43:510–515

Jubani-Marì T, Munné-Bosch S, Alegre L (2010) Redox regulation of water stress responses in field-grown plants. Role of hydrogen peroxide and ascorbate. Plant Physiol Biochem 48:351–358

Kasotia A, Jain S, Vaishnav A, Kumari S, Gaur RK, Choudhary DK (2012) Soybean growth promotion by *Pseudomonas* sp. strain VS-1 under salt stress. Pak J Biol Sci 15:698–701

Kasotia A, Varma A, Choudhary DK (2015) *Pseudomonas* mediated mitigation of salt stress and growth promotion in *Glycine max*. Agric Res 4(1):31–41

Kavi Kishor PB, Sangam S, Amrutha RN, Sri Laxmi P, Naidu KR, Rao KRSS, Rao S, Reddy KJ, Theriappan P, Sreenivasulu N (2005) Regulation of proline biosynthesis, degradation, uptake and transport in higher plants: its implications in plant growth and abiotic stress tolerance. Curr Sci 88:424–438

Kloepper JW, Ryu C-M, Zhang S (2004) Induced systemic resistance and promotion of plant growth by *Bacillus* spp. Phytopathology 94:1259–1266

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

Kohler J, Hernandez JA, Caravaca F, Roldàn 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

Kohler J, Caravaca F, Roldàn A (2010) An AM fungus and a PGPR intensify the adverse effects of salinity on the stability of rhizosphere soil aggregates of *Lactuca sativa*. Soil Biol Biochem 42:429–434

Kokalis-Burelle N, Vavrina CS, Rosskopf EN, Shelby RA (2002) Field evaluation of plant growth-promoting rhizobacteria amended transplant mixes and soil solarization for tomato and pepper production in Florida. Plant Soil 238:257–266

Kombrink E, Somssich IE (1997) Pathogenesis-related proteins and plant defense. In: Carroll G, Tudzynski P (eds) The Mycota V, part A plant relationships. Springer, Berlin, pp 107–128

Krasensky J, Jonak C (2012) Drought salt, and temperature stress-induced metabolic rearrangement and regulatory net-works. J Exp Bot 4:1593–1608

Landa BB, Mavrodi OV, Raaijmakers JM, Gardene BBM, Thomashow LS, Weller DM (2002) Differential ability of genotypes of 2,4-diacetylphloroglucinol-producing *Pseudomonas fluorescens* strains to colonize the roots of pea plants. Appl Environ Microbiol 68:3226–3237

Leung J, Giraudat J (1998) Abscisic acid signal transduction. Annu Rev Plant Physiol Plant Mol Biol 49:199–222

Liang X, Dron M, Schmid J, Dixon R, Lamb C (1989) Developmental and environmental regulation of a phenylalanine ammonia-lyase-β-glucuronidase gene fusion in transgenic tobacco plants. Proc Natl Acad Sci USA 86:9284–9288

Liddycoat SM, Greenberg BM, Wolyn DJ (2009) The effect of plant growth-promoting rhizobacteria an asparagus seedling and germinating seeds subjected to water stress under greenhouse conditions. Can J Microbiol 55:388–394

Loper JE, Henkels MD (1999) Utilization of heterologous siderophores enhances levels of iron available to *Pseudomonas putida* in the rhizosphere. Appl Environ Microbiol 65:5357–5363

Lucas GJA, Probanza A, Ramos B, Palomino MR, Gutierrez Manero FJ (2004) Effect of inoculation of *Bacillus licheniformis* on tomato and pepper. Agronomie 24:169–176

Lutgtenberg B, Kamilova F (2009) Plant-growth-promoting rhizobacteria. Annu Rev Microbiol 63:541–556

Marulanda A, Porcel R, Barea JM, Azcon R (2007) Drought tolerance and antioxidant activities in lavender plants colonized by native drought tolerant or drought sensitive *Glomus* species. Microb Ecol 54(3):543–552

Mauch-Mani B, Slusarenko AJ (1996) Production of salicylic acid precursors is a major function of phenylalanine ammonialyase in the resistance of *Arabidopsis* to *Peronospora parasitica*. Plant Cell 8:203–212

Maurhofer M, Hase C, Meuwly P, Métraux J-P, Défago G (1994) Induction of systemic resistance of tobacco to tobacco necrosis virus by the root colonizing *Pseudomonas fluorescens* strain CHA0: influence of the gacA gene and of pyoverdine production. Phytopath 84:139–146

Mayak S, Tirosh T, Glick B (1999) Effect of wild-type and mutant plant growth-promoting rhizobacteria on the rooting of mung bean cuttings. Plant Growth Regul 18:49–53

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

Mayak S, Tirosh T, Glick BR (2004b) Plant growth-promoting bacteria confer resistance in tomato plants to salt stress. Plant Physiol Bioch 42:565–572

McConn M, Creelman RA, Bell E, Mullet JE, Browse J (1997) Jasmonate is essential for insect defense in *Arabidopsis*. Proc Natl Acad Sci USA 94:5473–5477

Meziane H, Van der Sluis I, Van Loon LC, Höfte M, Bakker PAHM (2005) Determinants of *Pseudomonas putida* WCS358 involved in inducing systemic resistance in plants. Mole Plant Path 6:177–185

Miller RM, Jastrow JD (2000) Mycorrhizal fungi influence soil structure. In: Kapulnik Y, Douds D (eds) *Arbuscular Mycorrhizas*: physiology and function. Kluwer Academic Publishers, Dordrecht, pp 4–18

Miller KJ, Wood JM (1996) Osmoadaptation by rhizosphere bacteria. Annu Rev Microbiol 50:101–136

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

Milner JL, Silo-Suh L, Lee JC, He HY, Clardy J, Handelsman J (1996) Production of kanosamine by *Bacillus cereus* UW85. Appl Environ Microbiol 62:3061–3065

Miransari M (2014) Use of microbes for the alleviation of soil stresses. Springer, Berlin

Mishra S, Singh A, Keswani C, Saxena A, Sarma BK, Singh HB (2015) Harnessing plant-microbe interactions for enhanced protection against phytopathogens. In: Arora N (eds) plant microbes symbiosis: applied facets. Springer, Berlin, pp 111-125

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Mnasri B, Aouani ME, Mhamdi R (2007) Nodulation and growth of common bean (*Phaseolus vulgaris*) under water deficiency. Soil Bio Biochemi 39:1744–1750

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

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

Munns R, Guo JM, Passioura JB, Cramer GR (2000) Leaf water status controls day-time but not daily rates of leaf expansion in salt treated barley. Aust J Plant Physiol 27:949–957

Murphy JF, Zehnder GW, Schuster DJ, Sikora EJ, Polston JE, Kloepper JW (2000) Plant growth-promoting rhizobacterial mediated protection in tomato against tomato mottle virus. Plant Dis 84:779–784

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, Naveed M, Ahmad M, Zahir ZA (2015) Rhizosphere bacteria for crop production and improvement of stress tolerance: mechanisms of action, applications, and future prospects. In: Arora N (eds) plant microbes symbiosis: applied facets. Springer, Berlin, pp 1–36

Nannipieri P, Ascher J, Ceccherini MT, Landi L, Pietramellara G, Renella G (2003) Microbial diversity and soil functions. Eur J Soil Sci 54:655–670

Naveed M, Hussain MB, Zahir ZA, Mitter B, Sessitsch A (2013a) Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. Plant Growth Regul. doi:10.1007/s10725-013-9874-8

Naveed M, Hussain MB, Zahir ZA, Mitter B, Sessitsch A (2013b) Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. Plant Growth Regul. doi:10.1007/s10725-013-9874-8

O'Sullivan DJ, O'Gara F (1992) Traits of fluorescent *Pseudomonas* spp. involved in suppression of plant root pathogens. Microbiol Rev 56:662–676

Oliveira CA, Alves VMC, Marriel IE, Gomes EA, Scotti MR, Carneiro NP, Guimaraes CT, Schaffert RE, Scotti MR (2009) Phosphate solubilizing microorganisms isolated from rhizosphere of maize cultivated in an oxisol of the Brazilian Cerrado Biome. Soil Biol Biochem 41:1782–1787

Omar MNA, Osman MEH, Kasim WA, Abd El-Daim IA (2009) Improvement of salt tolerance mechanisms of barley cultivated under salt stress using *Azospirillum brasiliense*. Task Veget Sci 44:133–147

Pal KK, Gardener BM (2006) Biological Control of Plant Pathogens. T Plant Healt Instruct. doi:10.1094/PHI-A-2006-1117-02

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

Park KS, Kloepper JW (2000) Activation of PR-1a promoter by rhizobacteria that induce systemic resistance in tobacco against *Pseudomonas syringae pv. tabaci*. Biol Control 18:2–9

Park S-W, Kaimoyo E, Kumar D, Mosher S, Klessig DF (2007) Methyl salicylate is a critical mobile signal for plant systemic acquired resistance. Science 318:113–116

Patten CL, Glick BR (2002) Role of *Pseudomonas putida* indole acetic acid in development of the host plant root system. Appl Environ Microbiol 68:3795–3801

Pé rez-Alfocea F, Albacete A, Ghanem ME, Dodd IC (2010) Hormonal regulation of source sink relations to maintain crop productivity under salinity: a case study of root-to-shoot signalling in tomato. Funct Plant Biol 37:592–603

Penninckx IAMA, Eggermont K, Terras FRG, Thomma BPHJ, De Samblanx GW, Buchala A, Métraux J-P, Manners JM, Broekaert WF (1996) Pathogen-induced systemic activation of a plant defensin gene in *Arabidopsis* follows a salicylic acid-independent pathway. Plant Cell 8:2309–2323

Penninckx IAMA, Thomma BPHJ, Buchala A, Métraux J-P, Broekaert WF (1998) Concomitant activation of jasmonate and ethylene response pathways is required for induction of a plant defensin gene in *Arabidopsis*. Plant Cell 10:2103–2113

Penrose DM, Glick BR (2001) Levels of 1-aminocyclopropane-1-carboxylic acid (ACC) in exudates and extracts of canola seeds treated with plant growth-promoting bacteria. Can J Microbiol 47:368–372

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

Pieterse CMJ, van Wees SCM, van Pelt JA, Knoester M, Laan R, Gerrits H, Weisbeek PJ, van Loon LC (1998) A novel signalling pathway controlling induced systemic resistance in *Arabidopsis*. Plant Cell 10:1571–1580

Pieterse CMJ, Ton J, van Loon LC (2001) Cross-talk between plant defense signaling pathways: boost or burden? Agri Biotech Net 3:1–18

Pitzschke AM, Forzani C, Hirt H (2006) Reactive oxygen species signalling in plants. Antioxi Redox Sign 8:1757–1764

Podile AR, Lakshmi VDV (1998) Seed bacterization with *Bacillus subtilis* increases phenylalanine ammonia-lyase and reduces the incidence of fusarium wilt of pigeonpea. Phytopathology 146:255–259

Porcel R, Aroca R, Cano C, Bago A, Ruiz-Lozano JM (2006) Identification of a gene from the arbuscular mycorrhizal fungus *Glomus intraradices* encoding for a 14–3-3 protein that is up-regulated by drought stress during the AM symbiosis. Micro Ecol 52(3):575–582

Potter S, Uknes S, Lawton K, Winter AM, Chandler D, DiMaio J, Novitzky R, Ward E, Ryals J (1993) Regulation of a hevein-like gene in *Arabidopsis*. Mol. Plant-Microbe Interact 6:680–685

Potters G, Pasternak TP, Guisez Y, Palme KJ, Jansen MAK (2007) Stress-induced morphogenic responses, growing out of trouble? Trends Plant Sci 12:98–105

Prayitno J, Rolfe BG, Mathesius U (2006) The ethylene-insensitive sickle mutant of *Medicago truncatula* shows altered auxin transport regulation during nodulation. Plant Physiol 142:168–180

Raaijmakers JM, Weller DM (1998) Natural plant protection by 2,4-diacetyl-phloroglucinol-producing *Pseudomonas* spp. in take-all decline soils. Mol Plant-Microbe Interact 11:144–152

Raaijmakers JM, Weller DM (2001) Exploiting genotypic diversity of 2,4-diacetylphloroglucinol-producing *Pseudomonas* spp.: characterization of superior root-colonizing *P. fluorescens* strain Q8r1–96. Appl Environ Microbiol 67:2545–2554

Raaijmakers JM, Weller DM, Thomashow LS (1997) Frequency of antibiotic-producing *Pseudomonas* spp. in natural environments. Appl Environ Microbiol 63:881–887

Raaijmakers JM, Bonsall RF, Weller DM (1999) Effect of population density of *Pseudomonas fluorescens* on production of 2,4-diacetylphloroglucinol in the rhizosphere of wheat. Phytopath 89:470–475

Raghothama KG (2005) Phosphorus. In: Broadly MR, White PJ (eds) Plant nutritional genomics. Blackwell, Oxford, pp 112–126

Ran LX, Li ZN, Wu GJ, Van Loon LC, Bakker PAHM (2005) Induction of systemic resistance against bacterial wilt in Eucalyptusurophylla by fluorescent *Pseudomonas* spp. Euro J Plant Pathol 113:59–70

Ray H, Douches DS, Hammerschmidt R (1998) Transformation of potato with cucumber peroxidase: expression and disease response. Physiol Mol Plant Pathol 53:93–103

Requena N, Perez-Solis E, Azcon-Aguilar C, Jeffries P, Barea JM (2001) Management of indigenous plant-microbe symbioses aids restoration of desertified. App Environ Microbiol 67:495–498

Roberson EB, Firestone MK (1992) Relationship between desiccation and exopolysaccharide production in soil *Pseudomonas* sp. Appl Environ Microbiol 58:1284–1291

Rodrìguez H, Fraga R (1999) Phosphate solubilizing bacteria and their role in plant growth promotion. Biotechnol Adv 17:319–339

Rodriguez-Rosales MP, Jiang X, Gá lvez FJ, Aranda MN, Cubero B, Venema K (2008) Overexpression of the tomato K^+/H^+ antiporter LeNHX2 confers salt tolerance by improving potassium compartmentalization. New Phytol 179:366–377

Roesti D, Gaur R, Johri BN, Imfeld G, Sharma S, Kawaljeet K, Aragno M (2006) Plant growth stage, fertilizer management and bio-inoculation of *Arbuscular mycorrhizal* fungi and plant growth promoting rhizobacteria affect the rhizobacterial community structure in rain-fed wheat fields. Soil Biol Biochem 38:1111–1120

Rokhzadi A, Toashih V (2011) Nutrient uptake and yield of chickpea (*Cicer arietinum* L.) inoculated with plant growth-promoting rhizobacteria. Aust J Cop Scienc 5:44–48

Roman G, Lubarsky B, Kieber JJ, Rothenberg M, Ecker JR (1995) Genetic analysis of ethylene signal transduction in *Arabidopsis thaliana*: five novel mutant loci integrated into a stress response pathway. Genetic 139:1393–1409

Ruiz-Lozano JM, Collados C, Barea JM, Azcón R (2001) Arbuscular mycorrhizal symbiosis can alleviate drought induced nodule senescence in soybean plants. Plant Physiol 82:346–350

Russo A, Vettori L, Felici C, Fiaschi G, Morini S, Toffanin A (2008) Enhanced micropropagation response and biocontrol effect of Azospirillum brasilense Sp245 on *Prunus cerasifera* L. clone Mr.S 2/5 plants. J Biotechnol 134:312–319

Ryu C-M, Hu C-H, Reddy MS, Kloepper JW (2003) Different signaling pathways of induced resistance by rhizobacteria in Arabidopsis thaliana against two pathovars of Pseudomonas syringae. New Phytol 160:413–420

Ryu CM, Farag MA, Hu CH, Reddy MS, Wei HX, Kloepper JW, Paré PW (2004) Bacterial volatiles induce systemic resistance in *Arabidopsis*. Plant Physiol 134:1017–1026

Ryu CM, Kim J, Choi O, Kim SH, Park CS (2006) Improvement of biological control capacity of *Paenibacillus polymyxa* E681 by seed pelleting on sesame. Bio Contl 39:282–289

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

Samac DA, Hironaka CM, Yallaly PE, Shah DM (1990) Isolation and characterization of the genes encoding basic and acidic chitinase in *Arabidopsis thaliana*. Plant Physiol 93:907–914

Sandhya V, Ali SKZ, Grover M, Reddy G, Venkateswarlu B (2009) Alleviation of drought stress effects in sunflower seedlings by

exopolysaccharides producing *Pseudomonas putida* strain P45. Biol Fertil Soil 46:17–26

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

Saravanakumar D, Samiyappan R (2007) ACC deaminase from Pseudomonas fluorescens mediated saline resistance in groundnut (*Arachis hypogea*) plants. J Appl Microbiol 102:1283–1292

Saskia CM, Wees V, Luijendijk M, Smoorenburg I, van Loon LC, Pieterse CMJ (1999) Rhizobacteria-mediated induced systemic resistance (ISR) in *Arabidopsis* is not associated with a direct effect on expression of known defense-related genes but stimulates the expression of the jasmonate inducible gene *Atvsp* upon challenge. Plant Mol Biol 41:537–549

Schnider U, Keel C, Blumer C, Troxler J, Défago GHaas D (1995) Amplification of the housekeeping sigma factor in *Pseudomonas fluorescens* CHA0 enhances antibiotic production and improves biocontrol abilities. J Bacteriol 177:5387–5392

Sessitsch A, Coenye T, Sturz AV, Vandamme P, Ait Barka E, Faure D, Reiter B, Glick BR, Wang-Pruski G, Nowak J (2005) *Burkholderia phytofirmans* sp. nov., a novel plant-associated bacterium with plant beneficial properties. Int J Syst Evol Microbiol 55:1187–1192

Shah S, Li J, Moffatt B, Glick B (1998) Isolation and characterization of ACC deaminase genes from two different plant growth-promoting rhizobacteria. Can J Microbiol 44:833–843

Shahzad SM, Arif MS, Ashraf M, Abid M, Ghazanfar MU, Riaz M, Yasmeen T, Zahid MA (2015) Alleviation of abiotic stress in medicinal plants by PGPR. Plant-growth-promoting rhizobacteria (PGPR) and medicinal plants. Springer, Berlin, pp 135–166

Sharifi M, Ghorbanli M, Ebrahimzadeh H (2007) Improved growth of salinity-stressed soybean after inoculation with salt pretreated mycorrhizal fungi. J of Plant Physiol 164:1144–1151

Sharma A, Johri BN (2003) Combat of iron-deprivation through a plant growth promoting fluorescent *Pseudomonas* strain GRP3A in mung bean. Microbiol Res 158:77–81

Shi H, Zhu JK (2002) Regulation of expression of the vacuolar Na +/H + antiporter gene AtNHX1 by salt stress and ABA. Plant Mole Biol 50:543–550

Shukla PS, Agarwal PK, Jha B (2012) Improved salinity tolerance of *Arachis hypogaea* (L.) by the interaction of halotolerant plant-growth-promoting rhizobacteria. J Plant Growth Regul 31:195–206

Siddiqui IA, Ehteshamul-Haque S, Shaukat SS (2001) Use of rhizobacteria in the control of root rot-root knot disease complex of mungbean. J Phytopathol 149:337–346

Siddiqui MA, Shaukat SS (2003) Suppression of root-knot disease by *Pseudomonas fluorescens* CHA0 in tomato: importance of bacterial secondary metabolite, 2,4-diacetylpholoroglucinol. Soil Biol Biochem 35:1615–1623

Silo-Suh LA, Lethbridge BJ, Raffel SJ, He H, Clardy J, Handelsman J (1994) Biological activities of two fungistatic antibiotics produced by *Bacillus cereus* UW85. Appl Environ Microbiol 60:2023–2030

Spaepen S, Vanderleyden J (2010) Auxin and plant-microbe interactions. Cold Spring Harb Perspect Biol. doi:10.1101/cshperspect.a001438

Srivastava S, Yadav A, Seem K, Mishra S, Chaudhary V, Srivastava CS (2008) Effect of high temperature on *Pseudomonas putida* NBRI0987 biofilm formation and expression of stress sigma factor RpoS. Curr Microbiol 56(4):453–457

Stearns JC, Woody OZ, McConkey BJ, Glick BR (2012) Effects of bacterial ACC deaminase on *Brassica napus* gene expression measured with an *Arabidopsis thaliana* microarray. Mol Plant-Microb Interact 25:668–676

Stout MJ, Zehnder GW, Baur ME (2002) Potential for the use of elicitors of plant defence in arthropod management programs. Arch Insect Biochem Physiol 51:222–235

Suarez R, Wong A, Ramirez M, Barraza A, OrozcoMdel C, Cevallos MA, Lara M, Hernandez G, Iturriaga G (2008) Improvement of drought tolerance and grain yield in common bean by overexpressing trehalose-6-phosphate synthase in rhizobia. Mol Plant Microbe Interact 21:958–966

Swaine EK, Swaine MD, Killham K (2007) Effects of drought on isolates of *Bradyrhizobium elkanii* cultured from *Albizia adianthifolia* seedlings on different provenances. Agroforest Syst 69:135–145

Szabados L, Savouré A (2009) Proline: a multifunctional amino acid. Trends Plant Sci 15:89–97

Sziderics AH, Rasche F, Trognitz F, Sessitsch A, Wilhelm E (2007) Bacterial endophytes contribute to abiotic stress adaptation in pepper plants (*Capsicum annum* L.). Can J Microbiol 53:1195–1202

Tenorio-Salgado S, Tinoco R, Vazquez-Duhalt R, Caballero-Mellado J, Perez-Rueda E (2013) Identification of volatile compounds produced by the bacterium Burkholderia tropica that inhibit the growth of fungal pathogens Bioengine 4:236–243

Theocharis A, Bordiec S, Fernandez O, Paquis S, Dhondt-Cordelier S, Baillieul F, Clément C, Barka EA (2012) Burkholderia phytofirmans PsJN primes Vitis vinifera L. and confers a better tolerance to low nonfreezing temperatures. Mole Plant-Microbe Interact 25(2):241–249

Thomashow LS, Weller DM, Bonsall RF, Pierson LS (1990) Production of the antibiotic phenazine-1-carboxylic acid by fluorescent *Pseudomonas* species in the rhizosphere of wheat. Appl Environ Microbiol 56:908–912

Thomma BPHJ, Eggermont K, Penninckx IAMA, Mauch-Mani B, Cammue BPA, Broekaert WF (1998) Separate jasmonate-dependent and salicylic acid-dependent defense response pathways in *Arabidopsis* are essential for resistance to distinct microbial pathogens. Proc Natl Acad Sci USA 95:15107–15111

Tilak KVBR, Ranganayaji N, Pal KK, De R, Saxena AK, Nautiyal CS, Mittal S, Tripathi AK, Johri BN (2005) Diversity of plant growth and soil health supporting bacteria. Curr Sci 89:136–150

Toal ME, Yeomans C, Killham K, Meharg AA (2000) A review of rhizosphere carbon flow modelling. Plant Soil 222:263–281

Uknes S, Mauch-Mani B, Moyer M, Potter S, Williams S, Dincher S, Chandler D, Slusarenko A, Ward E, Ryals J (1992) Acquired resistance in *Arabidopsis*. Plant Cell 4:645–656

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

Vaan loon LC (1997) Induced resistance in plants and the role of pathogenesis-related proteins. Euro J Plant Pathol 103:753–765

Van Loon LC (2000) Systemic induced resistance. In: Slusarenko AJ, Fraser RSS, van Loon LC (eds) Mechanisms of resistance to plant diseases. Kluwer, Dordrecht, pp 521–574

Van Loon LC, Glick BR (2004) Increased plant fitness by rhizobacteria. In: Sandermann H (ed) Molecular ecotoxicology of plants. Springer, Berlin, pp 177–205

Van Loon LC, Bakker PAHM, Van der Heijdt WHW, Wendehenne D, Pugin A (2008) Early responses of tobacco suspension cells to rhizobacterial elicitors of induced systemic resistance. Mole Plant-Microbe Interact 21:1609–1621

van Wees SCM, Luijendijk M, Smoorenburg I, van Loon Leendert C, Pieterse CMJ (1999) Rhizobacteria-mediated induced systemic resistance (ISR) in *Arabidopsis* is not associated with a direct effect on expression of known defense-related genes but stimulates the expression of the jasmonate-inducible gene *Atvsp upon challenge*. Plant Mole Biol 41:537–549

Vardharajula S, Ali SZ, Grover M, Reddy G, Bandi V (2011) Drought-tolerant plant growth promoting Bacillus spp.: effect on growth, osmolytes, and antioxidant status of maize under drought stress. J Plant Interact 6:1–14

Verbruggen N, Hermans C (2008) Proline accumulation in plants: a review. Amino Acids 35:753–759

Visca P, Imperi F, Lamont IL (2007) Pyoverdine siderophores: from biogenesis to biosignificance. Trends Microbiol 15:22–30

Vleesschauwer D, HöFte M (2009) Rhizobacteria-Induced Systemic Resistance. Advanc Bot Res 51:223–281

Vlot AC, Klessig DF, Park SW (2008a) Systemic acquired resistance: the elusive signal(s). Curr Opin Plant Biol 11:436–442

Vlot AC, Liu P-P, Cameron RK, Park S-W, Yang Y, Kumar D, Zhou F, Padukkavidana T, Gustafsson C, Pichersky E, Klessig DF (2008b) Identification of likely orthologs of tobacco salicylic acid-binding protein 2 and their role in systemic acquired resistance in *Arabidopsis thaliana*. The Plant J 56:445–456

Wahid A, Close TJ (2007) Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. Biol Plant 51:104–109

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 Y, Li L, Cui W, Xu S, Shen W, Wang R (2012) Hydrogen sulfide enhances alfalfa (*Medicago sativa*) tolerance against salinity during seed germination by nitric oxide pathway. Plant Soil 351:107–119

Wasternack C, Parthier B (1997) Jasmonate-signaled plant gene expression. Trends Plant Sci 2:302–307

Whipps JM (2001) Microbial interactions and biocontrol in the rhizosphere. J Exp Bot 52:487–511

White PJ (2003) Ion Transport. In: Thomas B, Murphy DJ, Murray BG (eds) Encyclopaedia of applied plant sciences. Academic Press, London, pp 625–634

Wilkinson JF (1958) The extracellular polysaccharides of bacteria. Bacteriol Rev 22:46–73

Yakes FM, Van Houten B (1997) Mitochondrial DNA damage is more extensive and persists longer than nuclear DNA damage in human cells following oxidative stress. PNAS 94:514–549

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

Yan Z, Reddy MS, Ryu CM, Mc Inroy JA, Wilson M, Kloepper JW (2002) Induced systemic protection against tomato late blight elicited by plant growth-promoting rhizobacteria. Phytopathology 92:1329–1333

Yang SF (1987) The biosynthesis and metabolism of 1-(malonylamino)cyclopropane-1-carboxylic acid in relation to ethylene production. In Schreiber K, Schütte HR, Sembdner G (eds) Conjugated Plant Hormones: Structure, Metabolism, and Function. VEB Deutscher Verlag der Wissenschaaften, Berlin, pp 92–101

Yazdani M, Bahmanyar MA, Pirdashti H, Esmaili MA (2009) Effect of phosphate solubilization microorganisms (PSM) and plant growth promoting rhizobacteria (PGPR) on yield and yield components of corn (*Zea mays*, L.). World Acd Sci Engi Technol 49:90–92

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

Zahir ZA, Munir A, Asghar HN, Shaharoona B, Arshad M (2008) Effectiveness of rhizobacteria containing ACC deaminase for growth promotion of peas (*Pisum sativum*) under drought conditions. J Microbiol Biotechnol 18(5):958–963

Zhang Y, Fernando WGD (2004) Presence of biosynthetic genes for phenazine-1-carboxylic acid and 2,4-diacetylphloroglucinol and pyrrolnitrin in *Pseudomonas chlororaphis* strain PA-23. Can J Plant Pathol 6:430–431

Zhang S, Moyne A-L, Reddy MS, Kloepper JW (2002) The role of salicylic acid in induced systemic resistance elicited by plant growth-promoting rhizobacteria against blue mold of tobacco. Biol Control 25:288–296

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

Zhang H, Murzello C, Sun Y, Mi-Seong Kim, Xie X, Jeter RM, Zak JC, Dowd SE, Paré PW (2010) Choline and osmotic-stress tolerance induced in *Arabidopsis* by the soil microbe *Bacillus subtilis* (GB03). Mole Plant-Microbe Interact 23:1097–1104