The Potential of Rhizobacteria for Plant Growth and Stress Adaptation

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Abstract

Plants host a very rich microbiome comprising fungi, bacteria, and protozoa. Bacteria proliferate inside tissues or around roots, where carbon-rich compounds exert positive chemotaxis. Many physiological functions in crops are related to symbiotic events with Gram-positive or Gram-negative bacteria, which influence growth, development, nutrition, and immunity and fine-tune root tropisms. This potentiates the exploration of the substrate and may confer stress tolerance. The production of secondary metabolites and volatile compounds has been thoroughly investigated in Gram-positive bacteria in recent years, and a few of these info-chemicals increase the endogenous auxin levels and/or response, whereas Gram-negative species releases quorum-sensing signals of the *N*-acyl-homoserine type that are recognized by roots to strengthen root branching and immunity. This chapter reviews the contributions of rhizobacteria to enhance crop fitness in the field to make agriculture safer and more sustainable and highlights a few examples of how cross-kingdom signaling influences root behavior.

11.1 Introduction

Agriculture is the primary economic activity enabling food supply worldwide. Starting from the so-called "green revolution" driven by Dr. Norman Borlaug and his coworkers, through the development of crops more efficient to take up nutrients and water and more resistant to environmental challenges along with industrial

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production of fertilizers, now we may have access to fruits and fiber to satisfy world's demand in the few following years. Nevertheless, continuous population growth has led to the undesirable situation of the opening of natural ecosystems to agriculture, despite these lands may not be adequate to support plantations in the long term (Gomiero 2016). Another challenging trend is that the excessive use of agrochemicals has led to soil salinity, water contamination, and environmental risks (Atafar et al. 2008). Recent approaches to make agriculture more sustainable take advantage of the mutualistic relationships that plants establish with microorganisms, mainly bacteria and fungi. The root microbiome contains a great diversity of rhizobacteria that positively impact plant growth, help in phytoremediation, nutrient solubilization, or prevent diseases (Alori et al. 2017; Köhl et al. 2019; Jiang and Fan 2008). Besides, through chemical communication with root cells, rhizobacteria amplify host responses associated with the tolerance to biotic and abiotic challenges (Bano and Muqarab 2017; Chiappero et al. 2019).

The establishment of rhizobacterial populations is promoted by root exudates, which are mainly constituted of carbohydrates, amino acids, organic acids, and secondary metabolites. Changes in the chemical composition of the rhizosphere influence the microbiome and, consequently, modify the overall plant adaptive responses (Sasse et al. 2018). The competition of soil microorganisms for space along roots drives the association between different bacterial taxa (Philippot et al. 2013). Consortia establishment allows the integration of diverse traits related to the growth of the host and health maintenance (Kumar et al. 2016). Recent studies have identified compatible rhizobacteria for consortia formulation and farming practices. Here, we present an overview of the rhizobacterial mechanisms that benefit crops and how these can be modulated when bacteria coexist within plant roots.

11.2 Rhizobacterial Functions in Plant Growth and Development

Plant developmental processes such as embryogenesis, germination, growth, flowering, and reproduction are regulated by a wide range of compounds named phytohormones, many of which can be produced by rhizobacteria. Indole-3-acetic acid (IAA) is the most widely distributed auxin in plants and microorganisms that stimulates root growth and organogenesis (Perrot-Rechenmann 2010). Through changes in the configuration of the root system, bacteria improve soil exploration and, therefore, nutrient uptake (Fig. 11.1). *Pseudomonas*, *Bradyrhizobium*, *Streptomyces*, *Azospirillum*, *Sphingomonas*, and *Acinetobacter* species that actively produce IAA constitute important options to enhance crop performance (Chouyia et al. 2020; Hashmi et al. 2019; Ijaz et al. 2019; Kumawat et al. 2019; Molina-Romero et al. 2017).

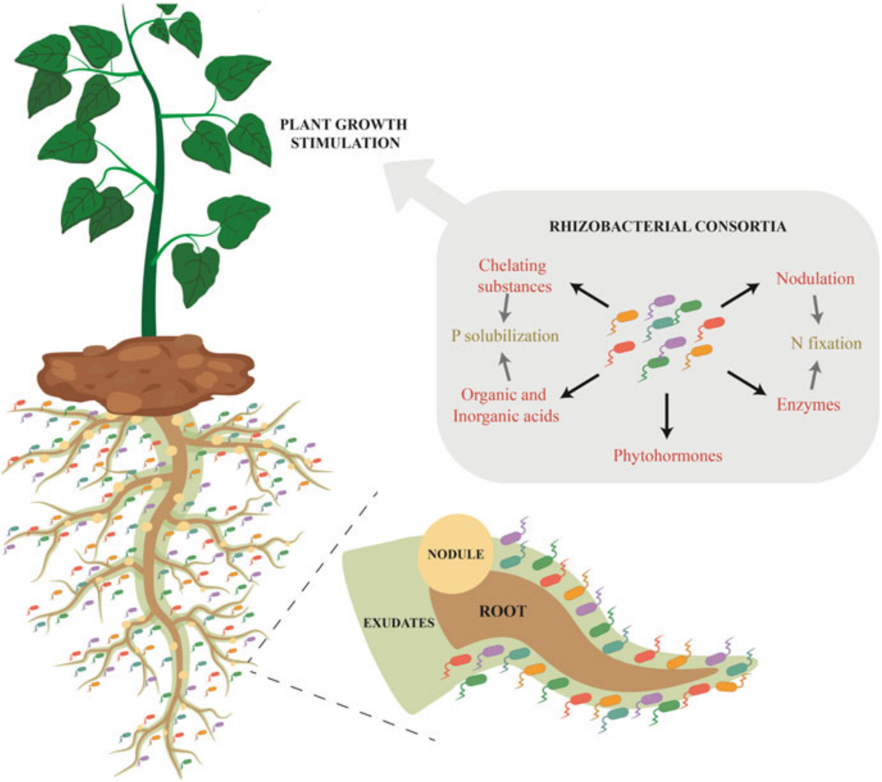

Fig. 11.1 Plant growth enhancement by rhizobacterial species. Soil bacteria can improve plant growth and development contributing to P solubilization by the production of chelating substances and organic acids. The enzymatic machinery of some rhizobacteria allows to convert the atmospheric nitrogen into assimilable N forms for plants. Phytohormones produced by rhizobacteria reconfigure the root system architecture in a way that improves its ability to explore the soil and therefore boosts the uptake of nutrients

11.3 Enhanced Nutrient Uptake

Plants rely on an adequate supply of minerals for growth and development. When a given soil lacks any macro- or micronutrients, various physiological processes are altered, decreasing their productivity. Phosphorus (P) and nitrogen (N) are the most limiting elements for the success of crops due to their structural, metabolic, and signaling functions. Most nutrients should be supplied in their ionic forms as part of chemical fertilizers or as part of organic amendments that farmers use to warrant high productivity (Maathuis 2009). Phosphorus commonly remains in the soil as insoluble phosphate complexes, not easily available for uptake by the root system. The production of organic acids, chelating substances, and enzymes from rhizobacterial species promotes solubilization of organic and inorganic P forms, which can be taken up by root hairs and lateral roots (Alori et al. 2017). Such ability to solubilize P is an interesting trait of bacteria that increases the growth and yield parameters in tomatoes and maize (Bradáčová et al. 2019, 2020) and supports growth in P-deficient soils (Bradáčová et al. 2019). Noteworthy, a mixture of *Pseudomonas* sp., *Burkholderia* sp., *Enterobacter* sp., and *Serratia* sp. improved both the available P content in soil and its uptake in aloe plants (Gupta et al. 2012).

Rhizobacteria may support N reduction to form nitrate (NO_3^-) and ammonium (NH_4^+) for plant nutrition. Particularly, the *Rhizobium* genus stimulates the growth of legumes through N fixation in root nodules (Vargas et al. 2017). The mineralization of organic matter contributes to enriching the pool of available N in the soil by the activity of lytic enzymes from saprophytic bacteria and fungi (Geisseler et al. 2010). Soybean and common bean seeds inoculated with *Bradyrhizobium* sp. and co-inoculated with *Azospirillum* sp. generated the same yield under N deficiency conditions as in fertilized soils. This consortium is an example of alternatives less expensive for farmers to support productivity (Hungria et al. 2013). Integration of rhizobia species including *Bradyrhizobium* sp., *R. leguminosarum*, and *Sinorhizobium meliloti* synergistically increased the nodule number, biomass, and the N uptake in soybean and pigeon pea (Kumar et al. 2016; Kumawat et al. 2019; Pandey and Maheshwari 2007).

Plant nutrition also demands several trace elements that play critical roles in redox reactions and function as cofactors of several enzymes such as RNA polymerase, cytochromes, and superoxide dismutase (Nagajyoti et al. 2010). Bacteria can help plants, either by solubilizing these micronutrients through acidifying the soil or by releasing siderophores that act as metal chelators (Abbaszadeh-Dahaji et al. 2016; Scavino and Pedraza 2013). Wheat plants whose seeds were treated with *Bacillus* sp., *Providencia* sp., and *Brevundimonas* sp. mixtures showed better content of Fe, Zn, Cu, and Mn (Rana et al. 2012). Another triple consortium (*B. megaterium*, *Arthrobacter chlorophenolicus*, and *Enterobacter* sp.) applied to wheat seeds increased the content of microelements in the harvested grains (Kumar et al. 2014).

11.4 Tolerance to Abiotic Stress

Soil pollution caused by natural or anthropogenic factors and extreme weather conditions are detrimental to agriculture. Heavy metals, salinity, drought, and drastic temperature fluctuations are the principal abiotic stresses that negatively impact crop growth and productivity (Farooq et al. 2012; Nagajyoti et al. 2010; Parihar et al. 2015; Mathur and Jajoo 2014). Physiological consequences of abiotic stress reside in overproduction of reactive oxygen species (ROS) and the emission of the gaseous phytohormone ethylene (Kumar and Verma 2018). ROS include free radicals that act as messengers in cell signaling through the so-called oxidative stress response. Disturbed ROS homeostasis compromises cell integrity and may cause cell death (Sharma et al. 2012). ROS affect membrane stability via lipoperoxidation and damage proteins and nucleic acids, and thus plants employ scavenging enzymes such as peroxidase, superoxide dismutase, catalase, polyphenol oxidase, and

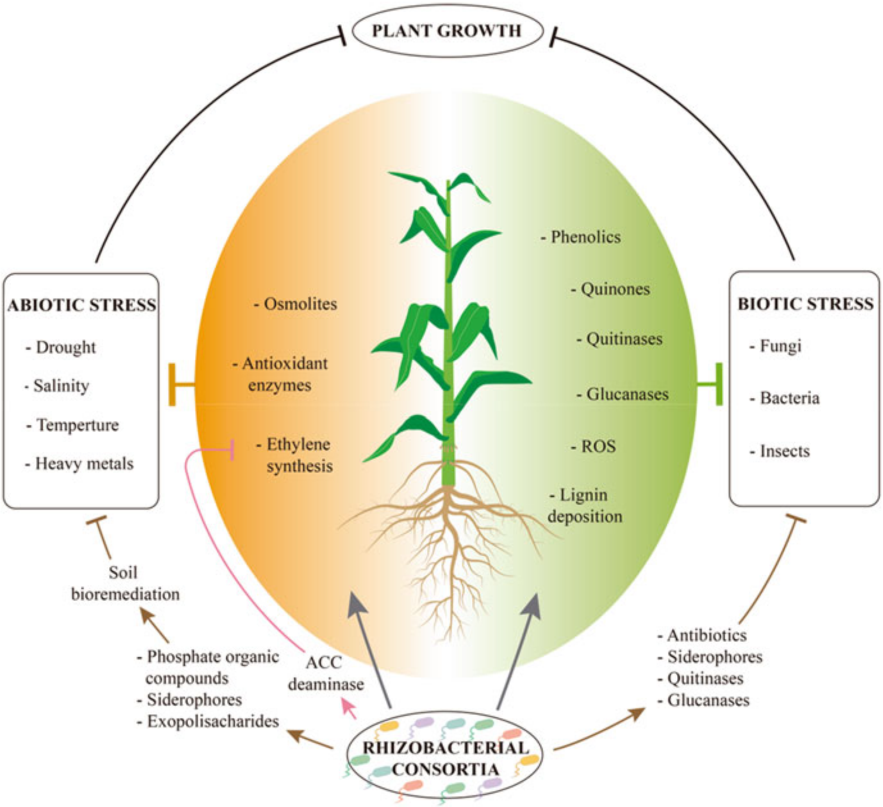

Fig. 11.2 Rhizobacteria mitigate abiotic and biotic stress in plants. Arrows represent positive or negative regulation. Soil bacteria produce numerous enzymes and compounds that directly reduce the soil pollution caused by heavy metals and eliminate the soilborne phytopathogens (brown arrows). The induced systemic tolerance and the induced systemic resistance in plants, which involve components that attenuate the impact of abiotic and biotic stresses, can be activated by rhizobacteria (grey arrows). ACC deaminase from bacteria can decrease ethylene overproduction triggered in plants in response to several stresses (pink arrows). Overall, growth/defense trade-offs are finely modulated in symbiotic interactions

antioxidant compounds including proline, glutathione, ascorbic acid, carotenoids, vitamins, and flavonoids to diminish the oxidative stress (Mehla et al. 2017). Also, as part of adaptive strategies, plants maintain a precise balance in the amount of ethylene synthesized from aminocyclopropane-1-carboxylic acid (AAC) through ACC deaminase enzyme activity that degrades ACC to α-ketobutyrate and ammonia (Shi et al. 2012; Singh et al. 2015).

A practical and eco-friendly strategy to mitigate these nonbiological stresses is the use of probiotic microbes (Fig. 11.2). Rhizobacteria can restore soil fertility by eliminating contaminants and inducing morphological, physiological, and gene expression changes in plants to improve their resistance through a mechanism termed induced systemic tolerance (IST) (Etesami and Maheshwari 2018). Indeed, rhizobacteria provide a combination of different and potential properties that reinforce the plant tolerance to abiotic stresses (Rajput et al. 2018; Saikia et al. 2018; Silambarasan et al. 2019).

11.4.1 Heavy Metals

Fe, Zn, Mn, Mo, Cu, and Ni are heavy metals considered micronutrients for plants in low micromolar or nanomolar concentrations. However, higher concentrations of these minerals (i.e., millimolar range) or other nonessential metals led to adverse effects on germination and shoot and root development not only by oxidative damage, but also by causing enzymatic dysfunction, chlorosis, and senescence (Nagajyoti et al. 2010).

Heavy metal pollution in soils represents a problem for agriculture and human health, and its origin can be natural (i.e., volcanic eruptions and rocks) or industrial (mining and smelting) (Alloway 2013; Ma et al. 2019; Wei et al. 2018). Long-term application of fertilizers and pesticides may also pollute the soils with heavy metals (Atafar et al. 2008). The use of microorganisms is one of the cheapest and most ecological alternatives for the restoration of contaminated soils. Certain bacteria can precipitate, methylate, reduce, oxidize, and chelate heavy metals to attenuate their toxicity (Jiang and Fan 2008; Ojuederie and Babalola 2017). Phosphate organic compounds, as well as siderophores, can interact and bind heavy metals. Shilev et al. (2020) isolated a bacterial consortium (*Pseudomonas* spp. and *Bacillus* sp.) tolerant to heavy metals and inoculated it to spinach seeds in soils contaminated with Pb, Zn, and Cd. The consortium showed the capacity to precipitate or immobilize heavy metals forming insoluble complexes and at the same time increased phosphate solubilization and siderophore production. Plants treated with the bacterial mixture had less accumulation of heavy metals in leaves, stems, and roots and sustained remarkable growth. Another bacterial consortium supported the Pb and Cd immobilization, increasing the phosphate solubilization (Yuan et al. 2017). Through interaction with their functional groups, exopolysaccharides from bacteria also retain various heavy metals (Morillo Pérez et al. 2008). Phosphate solubilizing activity, siderophore, and exopolysaccharide production are traits of *B. megaterium* and *Pantoea agglomerans* that enhance the growth of mung bean plants in soils polluted with Al reducing its concentration in tissues (Silambarasan et al. 2019).

Plants possess mechanisms to counteract the toxicity of heavy metals. For instance, compounds from root exudates such as organic acids, carbohydrates, and siderophores retain toxic elements by chelation, avoiding their absorption by crops (Nagajyoti et al. 2010). These mechanisms can be over-induced by rhizobacteria, allowing the plants to continue growing, even at high concentrations of heavy metals (Silambarasan et al. 2019).

11.4.2 Salinity

Salinization is a severe problem for plant development that has spread to 20% of irrigated lands. Unlike halophytes, most crops exhibit physiological problems when grown in soils with moderate or high salt concentrations (Abogadallah 2010; Farooq et al. 2015). Saline stress increases the Na^+ and Cl^- levels in the cytoplasm and chloroplasts, provoking an osmotic imbalance that stimulates ROS and ethylene overproduction and affects photosynthesis and plant growth (Amjad et al. 2014; Dar et al. 2017; Farooq et al. 2015). Cellular responses to salinity imply the production of osmoregulatory solutes, increased antioxidant activity, and improved selectivity of ions (Ahanger et al. 2017; Amjad et al. 2014). Highly efficient mechanisms are employed by rhizobacteria isolated from halophytes to improve the host adaptation to saline soils (Abbas et al. 2019; Jiménez-Vázquez et al. 2020). These microbes regulate the rhizosphere osmolality and promote adaptation through counteracting saline shock (Bharti et al. 2016; Sarma et al. 2012). Halotolerant rhizobacteria such as *Achromobacter* sp., *Serratia* sp., and *Enterobacter* sp., which presented ACC deaminase activity and IAA production, were found to increase the length of the shoot and root system in avocado plants exposed to saline stress conditions. The consortium intensified the superoxide dismutase activity and diminished lipoperoxidation (Barra et al. 2017). Halotolerant *Aeromonas* spp. mixture protected wheat plants from saline stress improving the root and leaf biomass and increasing the grain yield under half chemical fertilization (Rajput et al. 2018).

11.4.3 Drought

Comparable to salt toxicity, drought increases osmotic stress. The main physiological processes altered by drought are photosynthesis and the uptake and transport of nutrients (Farooq et al. 2012). Therefore, the germination, growth, and development of plants are drastically disrupted under this adverse condition (Asrar and Elhindi 2011; Liu et al. 2011; Samarah and Alqudah 2011). Under drought, plants raise the synthesis of abscisic acid, a phytohormone that induces stomatal closure and prevents water loss through transpiration (Tombesi et al. 2015). Rhizobacteria may support plant growth in water-deficient conditions via decreasing stomatal aperture and reducing ethylene levels (Chiappero et al. 2019; Cho et al. 2008; Mayak et al. 2004). Rhizobacterial consortia alleviated the growth repression of common bean and mung bean triggered by drought stress (Figueiredo et al. 2008; Silambarasan et al. 2019). Crops exposed to drought and grown under pretreatments with bacteria showed more superoxide dismutase, peroxidase, and catalase activity (Barra et al. 2017; Kohler et al. 2008). The mixture of *Ochrobactrum* sp., *Pseudomonas* sp., and *Bacillus* sp. had a synergic effect on the growth of different plant species exposed to drought. Also, they reduce the ACC levels in plants (Saikia et al. 2018).

11.4.4 Temperature

Extreme temperatures either heat or cold affect crop productivity. Production of ROS, heat shock proteins, and abscisic acid and the activation of mitogen-activated protein kinases (MAPKs) are part of the signaling mechanisms triggered by heat stress (Andrási et al. 2019; Evrard et al. 2013; Guo et al. 2016; Link et al. 2002; Yu et al. 2019). Elevated temperatures impair water content, photosynthesis, and membrane stability (Liu and Huang 2000; Mathur et al. 2011; Wassie et al. 2019). Thermotolerant rhizobacteria can enhance plant mechanisms associated with tolerance to heat stress, such as the production of osmolytes, activation of antioxidant enzymes, and reduction of ethylene levels (Ali et al. 2011; Khan et al. 2020; Mukhtar et al. 2020; Sarkar et al. 2018).

The foliage is very sensitive to cold stress and is one of the organs more impacted by chilling, exhibiting wilting, necrosis, chlorosis, and deformation, which affect early leaf growth and flowering (Kumar et al. 2010; Rymen et al. 2007; Yadav 2010). Acclimation to low temperatures is regulated positively by abscisic acid since mutants altered in the signaling of this phytohormone are hypersensitive to cold stress (Shi and Yang 2014). Adverse effects of cold stress can be attenuated by an overproduction of solutes such as sugars and amino acids, whose accumulation is stimulated through interaction with rhizobacteria (Ait Barka et al. 2006; Fernandez et al. 2012; Mishra et al. 2011). Tomato plants grown in soil inoculated with *B. cereus*, *B. subtilis*, and *Serratia* sp. were exposed to cold stress and showed a high level of hydrogen peroxide (H_2O_2) than non-inoculated plants. After days, the consortium moderated the oxidative stress caused by low temperatures mainly through the activation of superoxide dismutase and peroxidase activities. Besides, rhizobacteria increased the production of osmoprotectants such as proline and sugars. These effects helped to reach almost 100% plant survival (Wang et al. 2016). Kakar et al. (2016) applied a combination of *Bacillus* sp. and *Brevibacillus* sp. in rice seedlings and then applied cold stress treatment. The bacteria improved cold tolerance, upregulated the activity of antioxidant enzymes, and increased the proline content of plants, stimulating their growth and survival.

11.5 Biotic Challenges

Considerable crop losses occur due to nematode, viral, bacterial, oomycete, and fungal pathogens, which cause damage at each developmental stage (Savary et al. 2019). The control of plant diseases has been possible in the last decades by applying biocides that pollute air, water, and soil, damage pollinators, and ultimately enter the food chain (Popp et al. 2013; He et al. 2016). Thus, an important goal to achieving sustainable productivity is to develop new alternatives based on understanding plant-microbe interactions in an ecological context (Fig. 11.2).

Plants manifest constitutive and inducible defenses to protect themselves from pathogens. The properties of their immune system can be further modulated by abiotic and biotic stresses (Jain et al. 2016; Miura and Tada 2014). Detailed information on how plant defense is mounted has been gathered in leaves, and until recently little was known about how roots react under attack. It has become evident that damaged roots unlock a protective mechanism in coordination with probiotic bacteria surrounding them that boosts the defense reaction (Berendsen et al. 2012; Hematy et al. 2009).

11.5.1 Disease Suppressive Soils

Some soils have the property to suppress plant diseases because their microbiomes inhibit the spread of phytopathogens. On the other hand, the so-called conducive soils favor the incidence of plant diseases (Schlatter et al. 2017). Abiotic factors and certain farming practices can influence the growth of microorganisms related to the balance required for plants to survive and thrive (Jansson and Hofmockel 2020; Mehta et al. 2014). Continuous cropping is a practice that diminishes rhizobacterial diversity, generating a higher vulnerability to the root rot disease (Tan et al. 2017). In contrast, monocropping systems triggered the reduction of take-all disease, a phenomenon linked to the rising of *P. fluorescens* (Sanguin et al. 2009). The release of root exudates attracts specific groups of bacteria, causing changes in the soil microbial composition that reinforces defensive barriers (Berendsen et al. 2012). Proteobacteria, Firmicutes, Acidobacteria, and Actinobacteria strains predominate in the bacterial community of suppressive soils associated with tolerance to distinct crop diseases (Cha et al. 2016; Kyselkova et al. 2009; Sanguin et al. 2009). Mendes et al. (2011) dissected the rhizobacterial microbiome of sugar beet cultivated in suppressive soils of damping-off disease, concluding that the bacterial taxa contribute to disease mitigation. Seven rhizobacterial strains delayed the *Fusarium verticillioides* mycelial growth on maize seeds and decreased the blight disease incidence in seedlings. Each bacterial strain had a biocontrol effect on spreading the fungus and disease incidence, but not to the same degree as the consortium did (Niu et al. 2017). Other rhizobacteria showed a synergistic biocontrol on the blast disease in rice and collar rot disease in betelvine (Lucas et al. 2009; Singh et al. 2003). This protective capacity could persist for more than one season (Zhang et al. 2019). Therefore, multiple mechanisms depending on the composition of the microbial consortia account for the natural root antagonism to soilborne pathogens.

11.5.2 Fighting Plant Diseases

The production of antibiotics such as 2,4-diacetylphloroglucinol (2,4-DAPG), phenazine-1-carboxylic acid, pyrrolnitrin, oomycin, aerugine, and kanosamine is an important mechanism used by rhizobacteria to suppress the growth of phytopathogens (Kenawy et al. 2019). These compounds damage cell membranes, interfere with the electron transport chain, and affect enzymatic activity (Janiak and Milewski 2001; Raaijmakers et al. 2009; Troppens et al. 2013). Santhanam et al. (2019) evaluated biofilm development during the colonization of tobacco roots by

Bacillus sp., *Pseudomonas* sp., and *Arthrobacter* sp. This consortium increased plant survival against the sudden wilt disease, and one of the factors associated with the resistance was the production of surfactin, an antifungal compound. A single antibiotic can control diverse phytopathogens; for example, 2,4-DAPG, produced by several *Pseudomonas* strains, suppressed take-all, root rot, and damping-off fungal diseases and crown gall caused by *Agrobacterium tumefaciens* (Weller et al. 2007).

Cell wall degrading enzymes can be secreted by rhizobacteria that affect fungal phytopathogens. Chitinase and glucanase production is one of the desirable determinants to select rhizobacteria for biocontrol (Pliego et al. 2011). In this manner, the attenuation of *F. oxysporum* in maize was made possible, and at the same time plant growth and yield increases were obtained upon applying a quadruple bacterial inoculum composed of *B. megaterium*, *P. aeruginosa*, *Serratia* sp., and *P. fluorescens* (Akhtar et al. 2018).

Micronutrient availability is an ecological determinant for plant-microbe interactions. Under deficiency of Fe, an essential micronutrient, specific bacteria produce and secrete siderophores to chelate the available iron, rendering it unavailable for phytopathogens (Kramer et al. 2020). Treatments of *Pseudomonas* sp. or its siderophores protected plants against *Gaeumannomyces graminis* and *F. oxysporum* (Kloepper et al. 1980). Besides, some consortia had suppressive effects related to the activity of siderophores (Akhtar et al. 2018; Estevez de Jensen et al. 2002; Santhanam et al. 2019).

11.5.3 Plant Defensive Reactions

The plant immune system is reinforced by gene expression related to lytic enzymes and the production of antimicrobial compounds (Jain et al. 2016). Two main pathways control the defense reactions, the first involves systemic acquired resistance (SAR), stimulated after an attack of pathogens and dependent on the phytohormone salicylic acid. SAR induces pathogenesis-related (PR) genes, and it is initially manifested in the damaged site but later spreads systemically to distant tissues (Klessig et al. 2018). In the second pathway, the so-called induced systemic resistance (ISR) involves plant interactions with nonpathogenic rhizobacteria, which promote defense-related gene expression through signaling of the phytohormones ethylene and jasmonic acid. ISR has been reported to occur in the aerial and root system and also in leaves, keeping the plant defense machinery ready and alert to respond quickly to single and multiple biotic stimuli (Pieterse et al. 2014).

Berendsen et al. (2018) isolated three bacterial strains from the *Arabidopsis thaliana* rhizosphere, which prevailed during foliage infection caused by the oomycete *Hyaloperonospora arabidopsidis*. The plants grown in soil previously inoculated with these rhizobacteria showed less incidence of the oomycete in leaves. Besides, a combination of rhizobacteria and plant growth-promoting fungi (PGPF) protected cucumber plants against *F. oxysporum* infection in stems, enhancing the expression of genes encoding chitinases, glucanases, and enzymes involved in the synthesis of antifungal compounds (Alizadeh et al. 2013). Peroxidase is another defense component of plants that limits the pathogen spread as it mediates the establishment of physical barriers such as lignin and suberin in cells (Passardi et al. 2005). Adjusting the levels of reactive oxygen species, both peroxidase and superoxide dismutase, can create a toxic environment for pathogens in plant cells (Torres et al. 2006). *Bacillus* spp. diminished the bacterial and fungal infection in tomato and pepper apparently by induction of the peroxidase and superoxide dismutase activity (Jetiyanon 2007).

The plant phenylpropanoid pathway directs the production of phenolic compounds with antimicrobial properties. Phenylalanine ammonia-lyase converts L-phenylalanine into *trans*-cinnamic acid, a precursor for the synthesis of phenolics (Cheynier et al. 2013). Indeed, polyphenol oxidase oxidizes phenols to generate quinones, which also inhibit phytopathogen growth (Jukanti 2017). *Pseudomonas* sp., *Rhizobium* sp., and *Trichoderma* sp. reduced the mortality in chickpea plants infected by *Sclerotium rolfsii*. The triple microbial consortium enhanced the gene expression of peroxidase and superoxide dismutase and increased phenylalanine ammonia-lyase, polyphenol oxidase activity, and lignin deposition (Singh et al. 2013).

11.5.4 Quorum-Sensing-Mediated Antagonistic Activity

Colonization of roots, either by beneficial microorganisms or by plant pathogens, initiates a complex interrelationship where root exudates and mineral nutrients play an essential role. The formation of biofilms mainly composed of bacteria is a biological barrier that extends beyond the root epidermis. This process is under the control of a cell-to-cell chemical communication program termed quorum sensing (QS). In Gram-negative bacteria, QS controls the transcription of genes by producing small molecules, mainly the *N*-acyl-L-homoserine lactones (AHL) (Dwivedi et al. 2017). These compounds have strong activity not only in bacteria but also in roots, which suggests that they modulate the inter-kingdom plant-bacteria language (Ortíz-Castro et al. 2008).

Mutants of *P. chlororaphis* deficient in QS regulation lost their ability to inhibit the growth of plant pathogens. These variants exhibited low expression of *phzA*/*prnA* genes related to the production of two broad-spectrum antibiotics phenazine-1-carboxylic acid and pyrrolnitrin. AHL supplements induced the *prnA* expression, indicating that the QS compounds directly trigger pyrrolnitrin synthesis (Selin et al. 2012; Shah et al. 2020). Kim et al. (2017) concluded that the QS in *Chromobacterium* sp. supports its capacity to suppress fungal diseases in plants since the mutation of the gene encoding homoserine lactone synthetase reduced its chitinolytic activity. Other rhizobacterial enzymes attenuated the virulence of phytopathogenic bacteria by degrading QS molecules. For instance, Actinobacteria releases lactonases, which degrade AHLs in *Pectobacterium carotovorum* and affect its virulence (Vesuna and Nerurkar 2020). The interaction between bacterial communities also upregulated or downregulated the production of siderophores via QS signals (Shah et al. 2020; Stintzi et al. 1998; Whiteley et al. 1999).

11.6 Perspectives

Plants and microorganisms have developed inter-kingdom relations, which have been gaining special attention in agriculture since they improve crop yields and may reduce fertilization and pest control costs. The combination of selected traits from two or more bacteria further intensifies the probiotic effects on crops. Competition for energy and nutrient sources from exudates has led rhizobacteria to influence the host defense responses against bacteria and fungi that could be a threat. Therefore, it is crucial to identify and understand the mechanisms that define rhizobacteria compatibility and antagonism to develop successful inoculants.

Exploration of natural ecosystems has proven to be a valuable strategy to identify novel traits in both bacteria and plants useful to resist stress. The search for halophyte bacteria in a largely untouched sink hole termed the “Poza Salada,” located in the Chihuahua Desert, enabled the identification of a group of plant beneficial bacteria living in association with roots of well-adapted plant species, which grow healthy despite the very high salt concentrations. Three bacterial isolates typified molecularly as *Bacillus* sp., *P. lini*, and *Achromobacter* sp. promoted the growth of *A. thaliana*, *Cucumis sativus*, and *Citrullus lanatus* in vitro and in soil under standard and saline growth conditions (Jiménez-Vázquez et al. 2020; Palacio-Rodríguez et al. 2017). Noteworthy, *Achromobacter* sp. interfered with the root gravity response and caused the formation of waves and circles called coils, which primed roots for enhanced branching through the proliferation of lateral roots (Jiménez-Vázquez et al. 2020). The mechanisms underlying the beneficial properties of halophytes to plants are far from being understood; however, their protection from salinity in different plant species opens new avenues for agriculture. Regardless of the plant growth-promoting traits that rhizobacteria have in their natural niche, their survival should be tested under different environmental conditions to warrant their prevalence on crops. Generating more knowledge about the ways rhizobacteria interact with plants will facilitate access to biological tools for more productive and sustainable agriculture.

References

Abbas R, Rasul S, Aslam K, Baber M, Shahid M, Mubeen F, Naqqash T (2019) Halotolerant PGPR: a hope for cultivation of saline soils. J King Saud Univ Sci 31:1195–1201. https://doi.org/10.1016/j.jksus.2019.02.019

Abbaszadeh-Dahaji P, Omidvari M, Ghorbanpour M (2016) Increasing phytoremediation efficiency of heavy metal-contaminated soil using PGPR for sustainable agriculture. In: Choudhary DK, Varma A, Tuteja N (eds) Plant-microbe interaction: an approach to sustainable agriculture. Springer Singapore, Singapore

Abogadallah GM (2010) Antioxidative defense under salt stress. Plant Signal Behav 5:369–374. https://doi.org/10.4161/psb.5.4.10873

Ahanger MA, Tomar NS, Tittal M, Argal S, Agarwal RM (2017) Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. Physiol Mol Biol Plants 23:731–744. https://doi.org/10.1007/s12298-017-0462-7

Ait Barka E, Nowak J, Clément C (2006) Enhancement of chilling resistance of inoculated grapevine plantlets with a Plant Growth-Promoting Rhizobacterium, *Burkholderia phytofirmans* strain PsJN. Appl Environ Microbiol 72:7246–7252. https://doi.org/10.1128/AEM.01047-06

Akhtar N, Naveed M, Khalid M, Ahmad N, Rizwan M, Siddique S (2018) Effect of bacterial consortia on growth and yield of maize grown in *Fusarium* infested soil. Soil Environ 37:35–44. https://doi.org/10.25252/SE/18/872

Ali SZ, Sandhya V, Grover M, Linga VR, Bandi V (2011) Effect of inoculation with a thermotolerant plant growth promoting *Pseudomonas putida* strain AKMP7 on growth of wheat (*Triticum* spp.) under heat stress. J Plant Interact 6:239–246. https://doi.org/10.1080/17429145.2010.545147

Alizadeh H, Behboudi K, Ahmadzadeh M, Javan-Nikkhah M, Zamioudis C, Pieterse CMJ, Bakker PAHM (2013) Induced systemic resistance in cucumber and *Arabidopsis thaliana* by the combination of *Trichoderma harzianum* Tr6 and *Pseudomonas* sp. Ps14. Biol Control 65:14–23. https://doi.org/10.1016/j.biocontrol.2013.01.009

Alloway B (2013) Sources of heavy metals and metalloids in soils. In: Alloway BJ (ed) Heavy metals in soils: trace metals and metalloids in soils and their bioavailability. Springer Netherlands, Dordrecht

Alori ET, Glick BR, Babalola OO (2017) Microbial phosphorus solubilization and its potential for use in sustainable agriculture. Front Microbiol 8:971. https://doi.org/10.3389/fmicb.2017.00971

Amjad M, Akhtar J, Anwar-ul-Haq M, Yang A, Akhtar SS, Jacobsen S-E (2014) Integrating role of ethylene and ABA in tomato plants adaptation to salt stress. Sci Hortic 172:109–116. https://doi.org/10.1016/j.scienta.2014.03.024

Andrási N, Rigó G, Zsigmond L, Pérez-Salamó I, Papdi C, Klement E, Pettkó-Szandtner A, Baba AI, Ayaydin F, Dasari R, Cséplő Á, Szabados L (2019) The mitogen-activated protein kinase 4-phosphorylated heat shock factor A4A regulates responses to combined salt and heat stresses. J Exp Bot 70:4903–4918. https://doi.org/10.1093/jxb/erz217

Asrar A-WA, Elhindi KM (2011) Alleviation of drought stress of marigold (*Tagetes erecta*) plants by using arbuscular mycorrhizal fungi. Saudi J Biol Sci 18:93–98. https://doi.org/10.1016/j.sjbs.2010.06.007

Atafar Z, Mesdaghinia A, Nouri J, Homaee M, Yunesian M, Ahmadimoghaddam M, Mahvi AH (2008) Effect of fertilizer application on soil heavy metal concentration. Environ Monit Assess 160:83. https://doi.org/10.1007/s10661-008-0659-x

Bano A, Muqarab R (2017) Plant defence induced by PGPR against *Spodoptera litura* in tomato (*Solanum lycopersicum* L.). Plant Biol 19:406–412. https://doi.org/10.1111/plb.12535

Barra PJ, Inostroza NG, Mora ML, Crowley DE, Jorquera MA (2017) Bacterial consortia inoculation mitigates the water shortage and salt stress in an avocado (*Persea americana* Mill.) nursery. Appl Soil Ecol 111:39–47. https://doi.org/10.1016/j.apsoil.2016.11.012

Berendsen RL, Pieterse CM, Bakker PA (2012) The rhizosphere microbiome and plant health. Trends Plant Sci 17:478–486. https://doi.org/10.1016/j.tplants.2012.04.001

Berendsen RL, Vismans G, Yu K, Song Y, de Jonge R, Burgman WP, Burmølle M, Herschend J, Bakker PAHM, Pieterse CMJ (2018) Disease-induced assemblage of a plant-beneficial bacterial consortium. ISME J 12:1496–1507. https://doi.org/10.1038/s41396-018-0093-1

Bharti N, Pandey SS, Barnawal D, Patel VK, Kalra A (2016) Plant growth promoting rhizobacteria *Dietzia natronolimnaea* modulates the expression of stress responsive genes providing protection of wheat from salinity stress. Sci Rep 6:34768. https://doi.org/10.1038/srep34768

Bradáčová K, Florea AS, Bar-Tal A, Minz D, Yermiyahu U, Shawahna R, Kraut-Cohen J, Zolti A, Erel R, Dietel K, Weinmann M, Zimmermann B, Berger N, Ludewig U, Neumann G, Poşta G

(2019) Microbial consortia versus single-strain inoculants: an advantage in PGPM-assisted tomato production? Agronomy 9:105. https://doi.org/10.3390/agronomy9020105

Bradáčová K, Kandeler E, Berger N, Ludewig U, Neumann G (2020) Microbial consortia inoculants stimulate early growth of maize depending on nitrogen and phosphorus supply. Plant Soil Environ. https://doi.org/10.17221/382/2019-PSE

Cha JY, Han S, Hong HJ, Cho H, Kim D, Kwon Y, Kwon SK, Crusemann M, Bok Lee Y, Kim JF, Giaever G, Nislow C, Moore BS, Thomashow LS, Weller DM, Kwak YS (2016) Microbial and biochemical basis of a *Fusarium* wilt-suppressive soil. ISME J 10:119–129. https://doi.org/10.1038/ismej.2015.95

Cheynier V, Comte G, Davies KM, Lattanzio V, Martens S (2013) Plant phenolics: recent advances on their biosynthesis, genetics, and ecophysiology. Plant Physiol Biochem 72:1–20. https://doi.org/10.1016/j.plaphy.2013.05.009

Chiappero J, Cappellari LR, Sosa Alderete LG, Palermo TB, Banchio E (2019) Plant growth promoting rhizobacteria improve the antioxidant status in *Mentha piperita* grown under drought stress leading to an enhancement of plant growth and total phenolic content. Ind Crop Prod 139: 111553. https://doi.org/10.1016/j.indcrop.2019.111553

Cho SM, Kang BR, Han SH, Anderson AJ, Park JY, Lee YH, Cho BH, Yang KY, Ryu CM, Kim YC (2008) 2R,3R-butanediol, a bacterial volatile produced by *Pseudomonas chlororaphis* O6, is involved in induction of systemic tolerance to drought in *Arabidopsis thaliana*. Mol Plant Microbe Interact 21:1067–1075. https://doi.org/10.1094/mpmi-21-8-1067

Chouyia FE, Romano I, Fechtali T, Fagnano M, Fiorentino N, Visconti D, Idbella M, Ventorino V, Pepe O (2020) P-solubilizing *Streptomyces roseocinereus* MS1B15 with multiple plant growth-promoting traits enhance barley development and regulate rhizosphere microbial population. Front Plant Sci 11:1137. https://doi.org/10.3389/fpls.2020.01137

Dar MI, Naikoo MI, Khan FA, Rehman F, Green ID, Naushin F, Ansari AA (2017) An introduction to reactive oxygen species metabolism under changing climate in plants. In: Khan MIR, Khan NA (eds) Reactive oxygen species and antioxidant systems in plants: role and regulation under abiotic stress. Springer Singapore, Singapore

Dwivedi D, Khare M, Chaturvedi H, Singh V (2017) Plant pathogenic bacteria: role of quorum sensing and biofilm in disease development. In: Ahmad I, Husain FM (eds) Biofilms in plant and soil health. Wiley, Hoboken, NJ. https://doi.org/10.1002/9781119246329.ch20

Estevez de Jensen C, Percich JA, Graham PH (2002) Integrated management strategies of bean root rot with *Bacillus subtilis* and *Rhizobium* in Minnesota. Field Crops Res 74:107–115. https://doi.org/10.1016/S0378-4290(01)00200-3

Etesami H, Maheshwari DK (2018) Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture: action mechanisms and future prospects. Ecotoxicol Environ Saf 156:225–246. https://doi.org/10.1016/j.ecoenv.2018.03.013

Evrard A, Kumar M, Lecourieux D, Lucks J, von Koskull-Döring P, Hirt H (2013) Regulation of the heat stress response in *Arabidopsis* by MPK6-targeted phosphorylation of the heat stress factor HsfA2. PeerJ 1:e59. https://doi.org/10.7717/peerj.59

Farooq M, Hussain M, Wahid A, Siddique KHM (2012) Drought stress in plants: an overview. In: Aroca R (ed) Plant responses to drought stress: from morphological to molecular features. Springer Berlin Heidelberg, Berlin, Heidelberg

Farooq M, Hussain M, Wakeel A, Siddique KHM (2015) Salt stress in maize: effects, resistance mechanisms, and management. A review. Agron Sustain Dev 35:461–481. https://doi.org/10.1007/s13593-015-0287-0

Fernandez O, Vandesteene L, Feil R, Baillieul F, Lunn JE, Clément C (2012) Trehalose metabolism is activated upon chilling in grapevine and might participate in *Burkholderia phytofirmans* induced chilling tolerance. Planta 236:355–369. https://doi.org/10.1007/s00425-012-1611-4

Figueiredo MVB, Burity HA, Martínez CR, Chanway CP (2008) Alleviation of drought stress in the common bean (*Phaseolus vulgaris* L.) by co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. Appl Soil Ecol 40:182–188. https://doi.org/10.1016/j.apsoil.2008.04.005

Geisseler D, Horwath WR, Joergensen RG, Ludwig B (2010) Pathways of nitrogen utilization by soil microorganisms – a review. Soil Biol Biochem 42:2058–2067. https://doi.org/10.1016/j.soilbio.2010.08.021

Gomiero T (2016) Soil degradation, land scarcity and food security: reviewing a complex challenge. Sustainability 8:1–41. https://doi.org/10.3390/su8030281

Guo M, Liu J-H, Ma X, Luo D-X, Gong Z-H, Lu M-H (2016) The plant heat stress transcription factors (HSFs): structure, regulation, and function in response to abiotic stresses. Front Plant Sci 7:114. https://doi.org/10.3389/fpls.2016.00114

Gupta M, Kiran S, Gulati A, Singh B, Tewari R (2012) Isolation and identification of phosphate solubilizing bacteria able to enhance the growth and aloin-A biosynthesis of *Aloe barbadensis* Miller. Microbiol Res 167:358–363. https://doi.org/10.1016/j.micres.2012.02.004

Hashmi I, Paul C, Al-Dourobi A, Sandoz F, Deschamps P, Junier T, Junier P, Bindschedler S (2019) Comparison of the plant growth-promotion performance of a consortium of Bacilli inoculated as endospores or as vegetative cells. FEMS Microbiol Ecol 95:fiz147. https://doi.org/10.1093/femsec/fiz147

He D-c, Zhan J-s, Xie L-h (2016) Problems, challenges and future of plant disease management: from an ecological point of view. J Integr Agric 15:705–715. https://doi.org/10.1016/S2095-3119(15)61300-4

Hematy K, Cherk C, Somerville S (2009) Host-pathogen warfare at the plant cell wall. Curr Opin Plant Biol 12:406–413. https://doi.org/10.1016/j.pbi.2009.06.007

Hungria M, Nogueira MA, Araujo RS (2013) Co-inoculation of soybeans and common beans with rhizobia and azospirilla: strategies to improve sustainability. Biol Fertil Soils 49:791–801. https://doi.org/10.1007/s00374-012-0771-5

Ijaz M, Tahir M, Shahid M, Ul-Allah S, Sattar A, Sher A, Mahmood K, Hussain M (2019) Combined application of biochar and PGPR consortia for sustainable production of wheat under semiarid conditions with a reduced dose of synthetic fertilizer. Braz J Microbiol 50: 449–458. https://doi.org/10.1007/s42770-019-00043-z

Jain S, Varma A, Tuteja N, Choudhary DK (2016) Plant growth-promoting microbial-mediated induced systemic resistance in plants: induction, mechanism, and expression. In: Choudhary DK, Varma A (eds) Microbial-mediated induced systemic resistance in plants. Springer Singapore, Singapore

Janiak AM, Milewski S (2001) Mechanism of antifungal action of kanosamine. Med Mycol 39(5): 401–408

Jansson JK, Hofmockel KS (2020) Soil microbiomes and climate change. Nat Rev Microbiol 18: 35–46. https://doi.org/10.1038/s41579-019-0265-7

Jetiyanon K (2007) Defensive-related enzyme response in plants treated with a mixture of *Bacillus* strains (IN937a and IN937b) against different pathogens. Biol Control 42:178–185. https://doi.org/10.1016/j.biocontrol.2007.05.008

Jiang W, Fan W (2008) Bioremediation of heavy metal–contaminated soils by sulfate-reducing bacteria. Ann N Y Acad Sci 1140:446–454. https://doi.org/10.1196/annals.1454.050

Jiménez-Vázquez KR, García-Cárdenas E, Barrera-Ortiz S, Ortiz-Castro R, Ruiz-Herrera LF, Ramos-Acosta BP, Coria-Arellano JL, Sáenz-Mata J, López-Bucio J (2020) The plant beneficial rhizobacterium *Achromobacter* sp. 5B1 influences root development through auxin signaling and redistribution. Plant J 103:1639–1654. https://doi.org/10.1111/tpj.14853

Jukanti A (2017) Function(s)/role(s) of Polyphenol Oxidases. In: Polyphenol Oxidases (PPOs) in plants. Springer Singapore, Singapore

Kakar KU, Ren XL, Nawaz Z, Cui ZQ, Li B, Xie GL, Hassan MA, Ali E, Sun GC (2016) A consortium of rhizobacterial strains and biochemical growth elicitors improve cold and drought stress tolerance in rice (Oryza sativa L.). Plant Biol (Stuttg) 18:471–483. https://doi.org/10.1111/plb.12427

Kenawy A, Dailin DJ, Abo-Zaid GA, Malek RA, Ambehabati KK, Zakaria KHN, Sayyed RZ, El Enshasy HA (2019) Biosynthesis of antibiotics by PGPR and their roles in biocontrol of plant diseases. In: Sayyed RZ (ed) Plant growth promoting rhizobacteria for sustainable stress management, Rhizobacteria in biotic stress management, vol 2. Springer Singapore, Singapore

Khan MA, Asaf S, Khan AL, Jan R, Kang S-M, Kim K-M, Lee I-J (2020) Thermotolerance effect of plant growth-promoting *Bacillus cereus* SA1 on soybean during heat stress. BMC Microbiol 20: 175. https://doi.org/10.1186/s12866-020-01822-7

Kim IS, Yang SY, Park SK, Kim YC (2017) Quorum sensing is a key regulator for the antifungal and biocontrol activity of chitinase-producing *Chromobacterium* sp. C61. Mol Plant Pathol 18: 134–140. https://doi.org/10.1111/mpp.12379

Klessig DF, Choi HW, Dempsey DMA (2018) Systemic acquired resistance and salicylic acid: past, present, and future. Mol Plant Microbe Interact 31:871–888. https://doi.org/10.1094/mpmi-03-18-0067-cr

Kloepper JW, Leong J, Teintze M, Schroth MN (1980) *Pseudomonas* siderophores: a mechanism explaining disease-suppressive soils. Curr Microbiol 4:317–320. https://doi.org/10.1007/BF02602840

Köhl J, Kolnaar R, Ravensberg WJ (2019) Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. Front Plant Sci 10:845. https://doi.org/10.3389/fpls.2019.00845

Kohler J, Hernandez J, Caravaca F, Roldán A (2008) Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plants. Funct Plant Biol 35(2):141–151. https://doi.org/10.1071/FP07218

Kramer J, Özkaya Ö, Kümmerli R (2020) Bacterial siderophores in community and host interactions. Nat Rev Microbiol 18:152–163. https://doi.org/10.1038/s41579-019-0284-4

Kumar A, Verma JP (2018) Does plant–microbe interaction confer stress tolerance in plants: a review? Microbiol Res 207:41–52. https://doi.org/10.1016/j.micres.2017.11.004

Kumar S, Nayyar H, Bhanwara R, Upadhyaya H (2010) Chilling stress effects on reproductive biology of chickpea. SAT eJ 8:1–14

Kumar A, Maurya BR, Raghuwanshi R (2014) Isolation and characterization of PGPR and their effect on growth, yield and nutrient content in wheat (Triticum aestivum L.). Biocatal Agric Biotechnol 3:121–128. https://doi.org/10.1016/j.bcab.2014.08.003

Kumar P, Pandey P, Dubey RC, Maheshwari DK (2016) Bacteria consortium optimization improves nutrient uptake, nodulation, disease suppression and growth of the common bean (*Phaseolus vulgaris*) in both pot and field studies. Rhizosphere 2:13–23. https://doi.org/10.1016/j.rhisph.2016.09.002

Kumawat KC, Sharma P, Sirari A, Singh I, Gill BS, Singh U, Saharan K (2019) Synergism of *Pseudomonas aeruginosa* (LSE-2) nodule endophyte with *Bradyrhizobium* sp. (LSBR-3) for improving plant growth, nutrient acquisition and soil health in soybean. World J Microbiol Biotechnol 35:47. https://doi.org/10.1007/s11274-019-2622-0

Kyselkova M, Kopecky J, Frapolli M, Defago G, Sagova-Mareckova M, Grundmann GL, Moenne-Loccoz Y (2009) Comparison of rhizobacterial community composition in soil suppressive or conducive to tobacco black root rot disease. ISME J 3:1127–1138. https://doi.org/10.1038/ismej.2009.61

Link V, Sinha AK, Vashista P, Hofmann MG, Proels RK, Ehness R, Roitsch T (2002) A heat-activated MAP kinase in tomato: a possible regulator of the heat stress response. FEBS Lett 531: 179–183. https://doi.org/10.1016/S0014-5793(02)03498-1

Liu X, Huang B (2000) Heat stress injury in relation to membrane lipid peroxidation in creeping bentgrass. Crop Sci 40:503–510. https://doi.org/10.2135/cropsci2000.402503x

Liu H, Wang X, Wang D, Zou Z, Liang Z (2011) Effect of drought stress on growth and accumulation of active constituents in *Salvia miltiorrhiza* Bunge. Ind Crop Prod 33:84–88. https://doi.org/10.1016/j.indcrop.2010.09.006

Lucas JA, Ramos Solano B, Montes F, Ojeda J, Megias M, Gutierrez Mañero FJ (2009) Use of two PGPR strains in the integrated management of blast disease in rice (*Oryza sativa*) in Southern Spain. Field Crops Res 114:404–410. https://doi.org/10.1016/j.fcr.2009.09.013

Ma Q, Han L, Zhang J, Zhang Y, Lang Q, Li F, Han A, Bao Y, Li K, Alu S (2019) Environmental risk assessment of metals in the volcanic soil of Changbai mountain. Int J Environ Res Public Health 16:2047. https://doi.org/10.3390/ijerph16112047

Maathuis FJM (2009) Physiological functions of mineral macronutrients. Curr Opin Plant Biol 12: 250–258. https://doi.org/10.1016/j.pbi.2009.04.003

Mathur S, Jajoo A (2014) Effects of heat stress on growth and crop yield of wheat (*Triticum aestivum*). In: Physiological mechanisms and adaptation strategies in plants under changing environment. Springer Science+Business Media, New York, pp 163–191

Mathur S, Allakhverdiev SI, Jajoo A (2011) Analysis of high temperature stress on the dynamics of antenna size and reducing side heterogeneity of Photosystem II in wheat leaves (*Triticum aestivum*). BBA-Bioenergetics 1807:22–29. https://doi.org/10.1016/j.bbabio.2010.09.001

Mayak S, Tirosh T, Glick BR (2004) Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. Plant Sci 166:525–530. https://doi.org/10.1016/j.plantsci.2003.10.025

Mehla N, Sindhi V, Josula D, Bisht P, Wani SH (2017) An introduction to antioxidants and their roles in plant stress tolerance. In: Khan MIR, Khan NA (eds) Reactive oxygen species and antioxidant systems in plants: role and regulation under abiotic stress. Springer Singapore, Singapore

Mehta CM, Palni U, Franke-Whittle IH, Sharma AK (2014) Compost: its role, mechanism and impact on reducing soil-borne plant diseases. Waste Manag 34:607–622. https://doi.org/10.1016/j.wasman.2013.11.012

Mendes R, Kruijt M, de Bruijn I, Dekkers E, van der Voort M, Schneider JH, Piceno YM, DeSantis TZ, Andersen GL, Bakker PA, Raaijmakers JM (2011) Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science 332:1097–1100. https://doi.org/10.1126/science.1203980

Mishra PK, Bisht SC, Ruwari P, Selvakumar G, Joshi GK, Bisht JK, Bhatt JC, Gupta HS (2011) Alleviation of cold stress in inoculated wheat (*Triticum aestivum* L.) seedlings with psychrotolerant Pseudomonads from NW Himalayas. Arch Microbiol 193:497–513. https://doi.org/10.1007/s00203-011-0693-x

Miura K, Tada Y (2014) Regulation of water, salinity, and cold stress responses by salicylic acid. Front Plant Sci 5:4. https://doi.org/10.3389/fpls.2014.00004

Molina-Romero D, Baez A, Quintero-Hernández V, Castañeda-Lucio M, Fuentes-Ramírez LE, Bustillos-Cristales MR, Rodríguez-Andrade O, Morales-García YE, Munive A, Muñoz-Rojas J (2017) Compatible bacterial mixture, tolerant to desiccation, improves maize plant growth. PLoS One 12:e0187913. https://doi.org/10.1371/journal.pone.0187913

Morillo Pérez JA, García-Ribera R, Quesada T, Aguilera M, Ramos-Cormenzana A, Monteoliva-Sánchez M (2008) Biosorption of heavy metals by the exopolysaccharide produced by *Paenibacillus jamilae*. World J Microbiol Biotechnol 24:2699. https://doi.org/10.1007/s11274-008-9800-9

Mukhtar T, Rehman S, Smith D, Sultan T, Seleiman MF, Alsadon AA, Amna, Ali S, Chaudhary HJ, Solieman THI, Ibrahim AA, Saad MAO (2020) Mitigation of heat stress in *Solanum lycopersicum* L. by ACC-deaminase and exopolysaccharide producing *Bacillus cereus*: effects on biochemical profiling. Sustainability 12:2159

Nagajyoti PC, Lee KD, Sreekanth TVM (2010) Heavy metals, occurrence and toxicity for plants: a review. Environ Chem Lett 8:199–216. https://doi.org/10.1007/s10311-010-0297-8

Niu B, Paulson JN, Zheng X, Kolter R (2017) Simplified and representative bacterial community of maize roots. Proc Natl Acad Sci U S A 114:E2450–E2459. https://doi.org/10.1073/pnas.1616148114

Ojuederie OB, Babalola OO (2017) Microbial and plant-assisted bioremediation of heavy metal polluted environments: a review. Int J Environ Res Public Health 14:1504. https://doi.org/10.3390/ijerph14121504

Ortíz-Castro R, Martínez-Trujillo M, López-Bucio J (2008) N-acyl-L-homoserine lactones: a class of bacterial quorum-sensing signals alter post-embryonic root development in *Arabidopsis thaliana*. Plant Cell Environ 31:1497–1509. https://doi.org/10.1111/j.1365-3040.2008.01863.x

Palacio-Rodríguez R, Coria-Arellano JL, López-Bucio J, Sánchez-Salas J, Muro-Pérez G, Castañeda-Gaytán G, Sáenz-Mata J (2017) Halophilic rhizobacteria from *Distichlis spicata* promote growth and improve salt tolerance in heterologous plant hosts. Symbiosis 73:179–189. https://doi.org/10.1007/s13199-017-0481-8

Pandey P, Maheshwari DK (2007) Bioformulation of *Burkholderia* sp. MSSP with a multispecies consortium for growth promotion of *Cajanus cajan*. Can J Microbiol 53:213–222. https://doi.org/10.1139/w06-118

Parihar P, Singh S, Singh R, Singh VP, Prasad SM (2015) Effect of salinity stress on plants and its tolerance strategies: a review. Environ Sci Pollut Res 22:4056–4075. https://doi.org/10.1007/s11356-014-3739-1

Passardi F, Cosio C, Penel C, Dunand C (2005) Peroxidases have more functions than a Swiss army knife. Plant Cell Rep 24:255–265. https://doi.org/10.1007/s00299-005-0972-6

Perrot-Rechenmann C (2010) Cellular responses to auxin: division versus expansion. Cold Spring Harb Perspect Biol 2:a001446. https://doi.org/10.1101/cshperspect.a001446

Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH (2013) Going back to the roots: the microbial ecology of the rhizosphere. Nat Rev Microbiol 11:789–799. https://doi.org/10.1038/nrmicro3109

Pieterse CMJ, Zamioudis C, Berendsen RL, Weller DM, Wees SCMV, Bakker PAHM (2014) Induced systemic resistance by beneficial microbes. Annu Rev Phytopathol 52:347–375. https://doi.org/10.1146/annurev-phyto-082712-102340

Pliego C, Ramos C, de Vicente A, Cazorla FM (2011) Screening for candidate bacterial biocontrol agents against soilborne fungal plant pathogens. Plant Soil 340:505–520. https://doi.org/10.1007/s11104-010-0615-8

Popp J, Pető K, Nagy J (2013) Pesticide productivity and food security. A review. Agron Sustain Dev 33:243–255. https://doi.org/10.1007/s13593-012-0105-x

Raaijmakers JM, Paulitz TC, Steinberg C, Alabouvette C, Moënne-Loccoz Y (2009) The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. Plant Soil 321:341–361. https://doi.org/10.1007/s11104-008-9568-6

Rajput L, Imran A, Mubeen F, Hafeez F (2018) Wheat (*Triticum aestivum* L.) growth promotion by halo-tolerant PGPR-consortium. Soil Environ 37:178–189. https://doi.org/10.25252/SE/18/61522

Rana A, Saharan B, Nain L, Prasanna R, Shivay YS (2012) Enhancing micronutrient uptake and yield of wheat through bacterial PGPR consortia. Soil Sci Plant Nutr 58:573–582. https://doi.org/10.1080/00380768.2012.716750

Rymen B, Fiorani F, Kartal F, Vandepoele K, Inzé D, Beemster GTS (2007) Cold nights impair leaf growth and cell cycle progression in maize through transcriptional changes of cell cycle genes. J Plant Physiol 143:1429–1438. https://doi.org/10.1104/pp.106.093948%

Saikia J, Sarma RK, Dhandia R, Yadav A, Bharali R, Gupta VK, Saikia R (2018) Alleviation of drought stress in pulse crops with ACC deaminase producing rhizobacteria isolated from acidic soil of Northeast India. Sci Rep 8:3560. https://doi.org/10.1038/s41598-018-21921-w

Samarah N, Alqudah A (2011) Effects of late-terminal drought stress on seed germination and vigor of barley (*Hordeum vulgare* L.). Arch Agron Soil Sci 57:27–32. https://doi.org/10.1080/03650340903191663

Sanguin H, Sarniguet A, Gazengel K, Moenne-Loccoz Y, Grundmann GL (2009) Rhizosphere bacterial communities associated with disease suppressiveness stages of take-all decline in wheat monoculture. New Phytol 184:694–707. https://doi.org/10.1111/j.1469-8137.2009.03010.x

Santhanam R, Menezes RC, Grabe V, Li D, Baldwin IT, Groten K (2019) A suite of complementary biocontrol traits allows a native consortium of root-associated bacteria to protect their host plant from a fungal sudden-wilt disease. Mol Ecol 28:1154–1169. https://doi.org/10.1111/mec.15012

Sarkar J, Chakraborty B, Chakraborty U (2018) Plant growth promoting rhizobacteria protect wheat plants against temperature stress through antioxidant signalling and reducing chloroplast and membrane injury. J Plant Growth Regul 37:1396–1412. https://doi.org/10.1007/s00344-018-9789-8

Sarma BK, Yadav SK, Singh DP, Singh HB (2012) Rhizobacteria mediated induced systemic tolerance in plants: prospects for abiotic stress management. In: Maheshwari DK (ed) Bacteria in agrobiology: stress management. Springer Berlin Heidelberg, Berlin, Heidelberg

Sasse J, Martinoia E, Northen T (2018) Feed your friends: do plant exudates shape the root microbiome? Trends Plant Sci 23:25–41. https://doi.org/10.1016/j.tplants.2017.09.003

Savary S, Willocquet L, Pethybridge SJ, Esker P, McRoberts N, Nelson A (2019) The global burden of pathogens and pests on major food crops. Nat Ecol Evol 3:430–439. https://doi.org/10.1038/s41559-018-0793-y

Scavino AF, Pedraza RO (2013) The role of siderophores in plant growth-promoting bacteria. In: Maheshwari DK, Saraf M, Aeron A (eds) Bacteria in agrobiology: crop productivity. Springer Berlin Heidelberg, Berlin, Heidelberg

Schlatter D, Kinkel L, Thomashow L, Weller D, Paulitz T (2017) Disease suppressive soils: new insights from the soil microbiome. Phytopathology 107:1284–1297. https://doi.org/10.1094/phyto-03-17-0111-rvw

Selin C, Fernando WGD, de Kievit T (2012) The PhzI/PhzR quorum-sensing system is required for pyrrolnitrin and phenazine production, and exhibits cross-regulation with RpoS in *Pseudomonas chlororaphis* PA23. Microbiology 158:896–907. https://doi.org/10.1099/mic.0.054254-0

Shah N, Gislason AS, Becker M, Belmonte MF, Fernando WGD, de Kievit TR (2020) Investigation of the quorum-sensing regulon of the biocontrol bacterium *Pseudomonas chlororaphis* strain PA23. PLoS One 15:e0226232. https://doi.org/10.1371/journal.pone.0226232

Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot 2012:217037. https://doi.org/10.1155/2012/217037

Shi Y, Yang S (2014) ABA regulation of the cold stress response in plants. In: Zhang D-P (ed) Abscisic acid: metabolism, transport and signaling. Springer Netherlands, Dordrecht

Shi Y, Tian S, Hou L, Huang X, Zhang X, Guo H, Yang S (2012) Ethylene signaling negatively regulates freezing tolerance by repressing expression of CBF and Type-A ARR genes in *Arabidopsis*. Plant Cell 24:2578–2595. https://doi.org/10.1105/tpc.112.098640

Shilev S, Babrikova I, Babrikov T (2020) Consortium of plant growth-promoting bacteria improves spinach (*Spinacea oleracea* L.) growth under heavy metal stress conditions. J Chem Technol Biotechnol 95:932–939. https://doi.org/10.1002/jctb.6077

Silambarasan S, Logeswari P, Cornejo P, Kannan VR (2019) Role of plant growth–promoting rhizobacterial consortium in improving the *Vigna radiata* growth and alleviation of aluminum and drought stresses. Environ Sci Pollut Res 26:27647–27659. https://doi.org/10.1007/s11356-019-05939-9

Singh A, Mehta S, Singh HB, Nautiyal CS (2003) Biocontrol of collar rot disease of betelvine (Piper betle L.) caused by *Sclerotium rolfsii* by using rhizosphere-competent *Pseudomonas fluorescens* NBRI-N6 and *P. fluorescens* NBRI-N. Curr Microbiol 47:0153–0158. https://doi.org/10.1007/s00284-002-3938-8

Singh A, Sarma BK, Upadhyay RS, Singh HB (2013) Compatible rhizosphere microbes mediated alleviation of biotic stress in chickpea through enhanced antioxidant and phenylpropanoid activities. Microbiol Res 168:33–40. https://doi.org/10.1016/j.micres.2012.07.001

Singh R, Shelke G, Kumar A, Jha P (2015) Biochemistry and genetics of ACC deaminase: a weapon to “stress ethylene” produced in plants. Front Microbiol 6:937. https://doi.org/10.3389/fmicb.2015.00937

Stintzi A, Evans K, Meyer JM, Poole K (1998) Quorum-sensing and siderophore biosynthesis in *Pseudomonas aeruginosa*: lasR/lasI mutants exhibit reduced pyoverdine biosynthesis. FEMS Microbiol Lett 166:341–345. https://doi.org/10.1111/j.1574-6968.1998.tb13910.x

Tan Y, Cui Y, Li H, Kuang A, Li X, Wei Y, Ji X (2017) Diversity and composition of rhizospheric soil and root endogenous bacteria in *Panax notoginseng* during continuous cropping practices. J Basic Microbiol 57:337–344. https://doi.org/10.1002/jobm.201600464

Tombesi S, Nardini A, Frioni T, Soccolini M, Zadra C, Farinelli D, Poni S, Palliotti A (2015) Stomatal closure is induced by hydraulic signals and maintained by ABA in drought-stressed grapevine. Sci Rep 5:12449. https://doi.org/10.1038/srep12449

Torres MA, Jones JDG, Dangl JL (2006) Reactive oxygen species signaling in response to pathogens. J Plant Physiol 141:373–378. https://doi.org/10.1104/pp.106.079467

Troppens DM, Dmitriev RI, Papkovsky DB, O'Gara F, Morrissey JP (2013) Genome-wide investigation of cellular targets and mode of action of the antifungal bacterial metabolite 2,4-diacetylphloroglucinol in *Saccharomyces cerevisiae*. FEMS Yeast Res 13:322–334. https://doi.org/10.1111/1567-1364.12037

Vargas LK, Volpiano CG, Lisboa BB, Giongo A, Beneduzi A, Passaglia LMP (2017) Potential of rhizobia as plant growth-promoting rhizobacteria. In: Zaidi A, Khan MS, Musarrat J (eds) Microbes for legume improvement. Springer International Publishing, Cham

Vesuna AP, Nerurkar AS (2020) Biocontrol impact of AHL degrading actinobacteria on quorum sensing regulated virulence of phytopathogen *Pectobacterium carotovorum* subsp. carotovorum BR1. Plant Soil. https://doi.org/10.1007/s11104-020-04623-z

Wang C, Wang C, Gao Y-L, Wang Y-P, Guo J-H (2016) A consortium of three plant growth-promoting rhizobacterium strains acclimates *Lycopersicon esculentum* and confers a better tolerance to chilling stress. J Plant Growth Regul 35:54–64. https://doi.org/10.1007/s00344-015-9506-9

Wassie M, Zhang W, Zhang Q, Ji K, Chen L (2019) Effect of heat stress on growth and physiological traits of alfalfa (*Medicago sativa* L.) and a comprehensive evaluation for heat tolerance. Agronomy 9:597. https://doi.org/10.3390/agronomy9100597

Wei W, Ma R, Sun Z, Zhou A, Bu J, Long X, Liu Y (2018) Effects of mining activities on the release of heavy metals (HMs) in a typical mountain headwater region, the Qinghai-Tibet Plateau in China. Int J Environ Res Public Health 15:1987. https://doi.org/10.3390/ijerph15091987

Weller DM, Landa BB, Mavrodi OV, Schroeder KL, De La Fuente L, Blouin Bankhead S, Allende Molar R, Bonsall RF, Mavrodi DV, Thomashow LS (2007) Role of 2,4-diacetylphloroglucinol-producing fluorescent *Pseudomonas* spp. in the defense of plant roots. Plant Biol 9:4–20. https://doi.org/10.1055/s-2006-924473

Whiteley M, Lee KM, Greenberg EP (1999) Identification of genes controlled by quorum sensing in *Pseudomonas aeruginosa*. Proc Natl Acad Sci U S A 96:13904–13909. https://doi.org/10.1073/pnas.96.24.13904

Yadav SK (2010) Cold stress tolerance mechanisms in plants. A review. Agron Sustain Dev 30: 515–527. https://doi.org/10.1051/agro/2009050

Yu W, Wang L, Zhao R, Sheng J, Zhang S, Li R, Shen L (2019) Knockout of SlMAPK3 enhances tolerance to heat stress involving ROS homeostasis in tomato plants. BMC Plant Biol 19:354. https://doi.org/10.1186/s12870-019-1939-z

Yuan Z, Yi H, Wang T, Zhang Y, Zhu X, Yao J (2017) Application of phosphate solubilizing bacteria in immobilization of Pb and Cd in soil. Environ Sci Pollut Res 24:21877–21884. https://doi.org/10.1007/s11356-017-9832-5

Zhang L-N, Wang D-C, Hu Q, Dai X-Q, Xie Y-S, Li Q, Liu H-M, Guo J-H (2019) Consortium of plant growth-promoting rhizobacteria strains suppresses sweet pepper disease by altering the rhizosphere microbiota. Front Microbiol 10:1668. https://doi.org/10.3389/fmicb.2019.01668