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Beneficial features of plant growth-promoting rhizobacteria for improving plant growth and health in challenging conditions: a methodical review

Ewa Oleńska[1*], Wanda Małek[2], Małgorzata Wójcik[3], Izabela Swiecicka[1], Sofie Thijs[4], Jaco Vangronsveld[4]

Highlights

Bacteria facilitate plant growth under stressful environmental conditions.

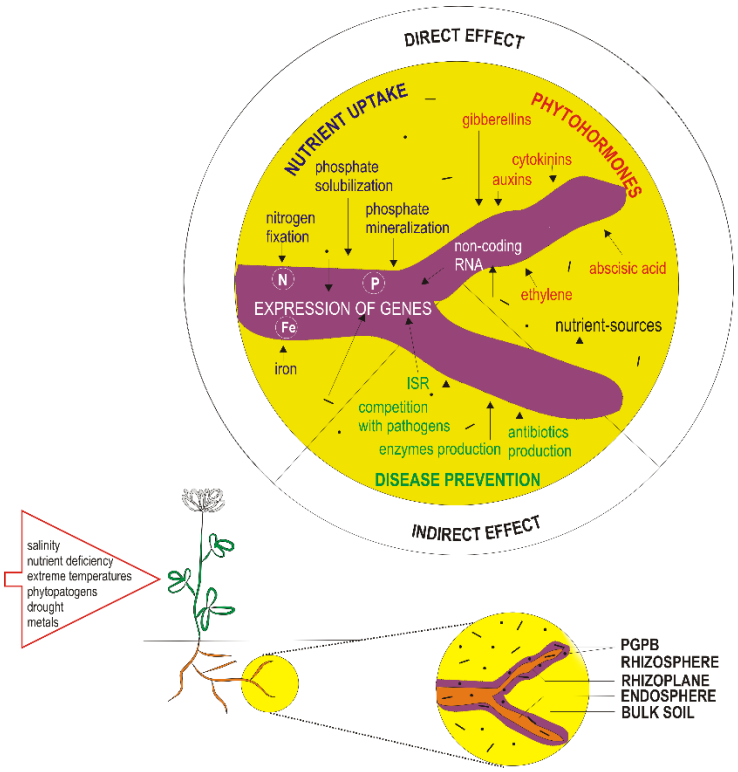
Direct and indirect mechanisms are involved in improvement of plant growth and development.

Plant-growth promoting rhizobacteria and host-plant interaction under stress.

Agriculture and phytoremediation efficiency may be significantly improved by using plant-growth promoting bacteria.

Abstract

New eco-friendly approaches are required to improve plant biomass production. Beneficial plant growth-promoting (PGP) bacteria may be exploited as excellent and efficient biotechnological tools to improve plant growth in various – including stressful – environments. We present an overview of bacterial mechanisms which contribute to plant health, growth, and development. Plant growth promoting rhizobacteria (PGPR) can interact with plants directly by increasing the availability of essential nutrients (*e.g.* nitrogen, phosphorus, iron), production and regulation of compounds involved in plant growth (*e.g.* phytohormones), and stress hormonal status (*e.g.* ethylene levels by ACC-deaminase). They can also indirectly affect plants by protecting them against diseases via competition with pathogens for highly limited nutrients, biocontrol of pathogens through production of aseptic-activity compounds, synthesis of fungal cell wall lysing enzymes, and induction of systemic responses in host plants. The potential of PGPR to facilitate plant growth is of fundamental importance, especially in case of abiotic stress, where bacteria can support plant fitness, stress tolerance, and/or even assist in remediation of pollutants. Providing additional evidence and better understanding of bacterial traits underlaying plant growth-promotion can inspire and stir up the development of innovative solutions exploiting PGPR in times of highly variable environmental and climatological conditions.



Key words: bacterial volatile compounds (BVCs), induced systemic resistance (ISR), nutrients, phytohormones, rhizobacteria, siderophores

1. Introduction

The supply of appropriate quantity and quality of food, as well as feed for animals, biomass as a feedstock for biofuel production and other industrial processes encounter various challenges of abiotic, biotic, and anthropogenic (*e.g.*, pollution and climate change) origin. The limited resources and non-renewable nature of soil services, makes soils the most vulnerable ecosystems that are under great pressure, especially in tropical, semiarid, and arid regions of our planet, resulting in extreme poverty and hunger in many developing countries. The Food and Agriculture Organization of the United Nations (FAO) reported that the number of undernourished people in the world is still growing; in 2017 it reached 21% of the African population (256 millions people) and 11.4% in Asia (515 millions people) (FAO, IFAD – International Fund for Agricultural Development, UNICEF – United Nations Children's Fund, WFP – World Food Programme, WHO – World Health Organization, 2018). Moreover, it was estimated that approximately 34% of the population in Ethiopia has to survive with less than US$1.90 per person per day (World Bank, 2017; Silva et al., 2019).

The main consequences of intensive anthropogenic activities and climate change are degraded soils and loss of ecosystem services (Dewulf et al., 2015). Drought, combined with enhanced water and air erosion, results in a systematical reduction of soil fertility and plant biomass production, and has become a highly substantial and urgent global problem (Karmakar et al., 2016). According to the European Environment Agency (EEA, 2003; 2009), about 16% of European Union

agricultural lands are threatened by water erosion, while another 4% is susceptible to wind erosion, which may intensify the dispersion of xenobiotics and potential eutrophying pollutants (Timmusk et al., 2017). Furthermore, long-lasting use of pesticides, artificial fertilizers, and growth stimulators as soil supplements lead to adverse effects on soil ecosystems. Thus high plant biomass production, reduction of the use of chemical fertilizers and chemical plant protection products, and reduction of pollution with xenobiotics are currently important objectives.

In order to mitigate these harmful factors and also enhance the plant biomass production, many different innovative and smart farming technologies, such as smart irrigation systems (*e.g.* controlled-release drip-irrigation), integrated fertilization, biocontrol techniques for plant diseases, and environmentally friendly microbial biotechnologies have been developed (Bargaz et al., 2018). In addition, different microbial-based approaches, in the form of biofertilizers, biostimulants, and/or biopesticides are currently proposed as alternatives for improving crop yield. A particular group of microorganisms, termed plant growth-promoting rhizobacteria (PGPR), positively influence plant growth, and represent promising sustainable solutions to increase plant biomass production (Thijs and Vangronsveld, 2015; Lindemann et al., 2016; Umesha et al., 2018; Liu et al., 2020). PGPR also have the ability to counteract most of the aforementioned problems and disadvantages of modern agriculture.

Bacteria are a dominant group in the soil microorganism community; approximately one gram of soil contains 10^8-10^9 bacteria, 10^6-10^8 archaea, 10^7-10^8 actinomycetes, 10^5-10^6 fungi, 10^3-10^6 algae, 10^3-10^5 protozoa, and 10 nematodes (Rughöft et al., 2016). Their diverse metabolism and capacity to use a wide range of different substances as nutrient and energy sources, makes bacteria important partners in interaction with plants. Bacteria that positively affect plant growth are categorized as plant growth-promoting bacteria (PGPB), often interchangeably called plant health-promoting bacteria (PHPB). They are represented by both (i) endophytes localized inside plant cells (iPGP – intracellular PGP), vascular tissues (Weyens et al., 2009a), or seeds (Truyens et al., 2015; Sánchez-López et al., 2018), and (ii) bacteria localized outside cells (ePGP – extracellular PGP), including endophytes living between cells of plant tissues (Mastretta et al., 2009; Truyens et al., 2015), rhizoplane (on the root surface), rhizosphere soil (thin soil layer around the roots) (Backer et al., 2018), or phyllosphere (leaves and stems) (Weyens et al., 2009b).

The bacterial mechanisms of plant growth promotion and communication are still being studied (Bharti et al., 2016). There is a diverse number of PGPR-induced changes in plants, and the promotion of growth is most likely a result of a complex combination of a plethora of pathways, which affect both plant development and nutrition (Bharti et al., 2016). PGPB exert positive effects on plant growth both in direct and indirect ways (Weyens et al., 2009b; Asad et al., 2019). Plant growth under the rhizobacteria influence is a multigene process, which is specific to the individually participating bacteria and plants. This “additive hypothesis” is a complex phenomenon that involves a cumulative effect of changes in expression of various genes, which ultimately influences the global plant multifactor metabolic system (Bharti et al.,

2016; Meena et al., 2017). Direct mechanisms of plant growth stimulation by bacteria rely on facilitating the uptake of nutrients, and synthesizing or regulating the hormonal status of plants (Kong and Glick, 2017; Backer et al., 2018). Indirect mechanisms of PGPB influence plant growth and comprise a whole range of mechanisms that prevent or suppress plant diseases (Goswami et al., 2016; Asad et al., 2019). As an example, the phosphorus solubilizing, nitrogen fixing and auxins producing PGP *Providencia rettgeri* strain P2, *Advenella incenata* strain P4, *Acinetobacter calcoaceticus* strain P19, and *Serratia plymuthica* strain P35 as inoculants significantly increased (i) growth parameters, *e.g.* dry weight, plant height, root length, root average diameter, root surface area, root volume, and chlorophyll content of oat (*Avena sativa*), alfalfa (*Medicago sativa*), and cucumber (*Cucumis sativus*), and (ii) the activity of antioxidative enzymes, *e.g.* peroxidase, catalase, superoxide dismutase, as well as (iii) soil conditions, *e.g.* soil urease, invertase, alkaline phosphatase, catalase activity, available nitrogen, phosphorus, potassium, and organic carbon (Li, H. et al., 2020).

The above mentioned positive PGPB pathways occur as the bacterial reply to plant carbon-rich exudates, constituting the investment of almost 20% of the photosynthetically fixed carbon-sources in the maintenance of the rhizosphere microbiota (Philippot et al., 2013; Stringlis et al., 2018a). Using *Arabidopsis thaliana* – PGP *Pseudomonas fluorescens* strain WCS417 as a model system, it was revealed that the WCS417-induced early root response ISR is not an effect of plant defense costs, but is a defense priming phenomenon that does not rule out the WCS417 by local root immune responses (Martinez-Medina et al., 2016; Moreau et al., 2019; Zhang, S. et al., 2019). PGPB are recognized by plants because of molecules with a specific and conserved chemical structure/pattern termed microbe-associated molecular patterns (MAMPs), which are detected by members of a large family of plant pattern recognition receptors (PRRs). These PRRs activate the signaling cascades to induce the first line of plant defense, called MAMP-triggered immunity (MTI) (Choi and Klessing, 2016; Offor et al., 2020). Among the best characterized MAMPs are flagellin (flg22), a bacterial flagella component recognized by the PRR flagellin-sensitive2 receptor FLS2, and chitin, a fungal carbohydrate cell wall component that is recognized by the PRR chitin elicitor receptor kinase1 (CERK1) (Jelenska et al., 2017; Lawrence II et al., 2020). It is worth to mention that flagellins, specifically $flg22^{417}$ isolated from PGP *P. fluorescens* WCS417, $flg22^{Pa}$ from the pathogen *P. aeruginosa*, and the living WCS417 strain reflected similar patterns of gene expression in *Arabidopsis* upon their influence (Stringlis et al., 2018a). Upon MAMPs the genes involved in immunity, such as those responding to bacteria, fungi, chitin, wounding, hypoxia, salicylic acid, ethylene, or abscisic acid were found to be upregulated. Genes related to growth and development, like those having to do with amino acid export, ion transport, glucosinolate biosynthetic process, metabolism of terpenoids, and secondary metabolic processes were downregulated. It is notable that MAMP-repressed genes which were not affected by the elicitors have a strong auxin signature. In this system, the auxins were found as trade-off involved molecules, playing a dual role in the balance of promoting root growth while simultaneously leading the systemic immunity-eliciting defense response to PGPR (Stringlis et al., 2018a). Mwita

et al. (2016) reported that the expression of plant growth promoting bacteria genes, which are involved in root colonization is under the host-plant root exudates control. Upon *Bacillus atrophaeus* strain UCMB-5137 the maize (*Zea mays*) colonization is under control of the repressors, *e.g.* CcpA (mediated carbon catabolite repressor), CodY (pleiotropic repressor), AbrB (transition to stationary phase), and probably a DegU transcription factor regulation. It was also reported that the non-coding RNA is involved in regulation of genes involved in early stages of rhizosphere colonization. The gene expression regulation during maize rhizosphere UCMB-5137 colonization was positively correlated with some ncRNAs like ncr628, ncr818, ncr2198, ncr3198, ncr3519, and ncr3877 (Mwita et al., 2016). Moreover, Morcillo et al. (2020a) found that an exposure of *Arabidopsis thaliana* to *Bacillus amyloliquefaciens* strain GB03 can exert either beneficial or deleterious effects to plants. The shift from beneficial to deleterious effect depends on the P-availability to plants and is mediated by diacetyl, a bacterial volatile organic compound (VOC). Under phosphate-defcient conditions, diacetyl suppresses plant production of reactive oxygen species (ROS) and enhances symbiont colonization without compromising disease resistance via enhancing phytohormone-mediated immunity followed by plant hyper-sensitivity to phosphate deficiency (Morcillo et al., 2020a).

Millions of years of evolution in variable, selective environmental conditions brought about adaptations of all organisms in response to a wide range of stresses. Bacteria, as well plants, have evolved a plethora of ways to deal with both abiotic and biotic stressors, namely by enhancing the action of specific plant growth promoting traits or/and resistance mechanisms (Oleńska and Małek, 2013; Singh, S. et al., 2015; Numan et al., 2018; Chen et al., 2019) as well as preventing diseases (Ilangumaran and Smith, 2017; Leinweber et al., 2018; Pereira, 2019). In this review, we focus on rhizobacteria (from rhizosphere, rhizoplane, and root endosphere) and their involvement in plant health and development (Fig. 1).

2. Alleviation of plant abiotic stress by plant growth promoting rhizobacteria

2.1. PGPR that enhance the availability of nutrients essential to plant growth

Drought, extreme temperature events, salinity, flooding, ultraviolet irradiation, and heavy metal pollution are abiotic stress factors of high concern mainly because of their unfavorable effects on plant growth, which ultimately lead to serious reductions in yield. Bacterial involvement in increasing abiotic stress tolerance and enhancing defense responses in plants exposed to different stressors has been widely studied (Table 1) (Rajkumar et al., 2012; Salomon et al., 2014; Zhao and Zhang, 2015; Ma et al., 2016; Hashem et al., 2016; Egamberdieva et al., 2017; Kudoyarova et al., 2019; Jatan et al., 2019; Safdarian et al., 2019; Bruno et al., 2020; Shreya et al., 2020; Ramirez et al., 2020; Javed et al., 2020). Numerous studies have investigated plant-microbe interactions under heavy metal stress conditions (Glick, 2014; Wu et al., 2016; Ma et al., 2016; Kong and Glick, 2017; Paredes-Páliz et al., 2018; Sánchez-López et al., 2018; Raklami et al., 2019; Bellabarba et al., 2019; Bruno et al., 2020; Manoj et al., 2020). Heavy metals exert noxious effects on all biota, including

139 microorganisms by blocking essential functional groups of organic molecules and modifying their active conformations
140 (Li et al., 2017), hence disturbing metabolism and inducing oxidative damage or genotoxicity (Epelde et al., 2015). These
141 disruptions lead to a decrease in the total amount of soil microbial biomass (Ayangbenro and Babalola, 2017) and a
142 reduction in genetic polymorphism in populations (Oleńska and Małek, 2015; Zhang et al., 2018; Oleńska and Małek,
143 2019). For example, under severe metal exposure where toxic ions compete with essential nutrients like iron, magnesium,
144 phosphorus, calcium, or zinc during root uptake, plant associated bacteria can improve nutrient acquisition by enhancing
145 the nutrient's availability, and as a result increase plant biomass.

146 *2.1.1. Nitrogen*

147 Feeding plants under challenging conditions is of crucial importance, especially in soils deficient in biogenic nutrients
148 like nitrogen (N). Nitrogen is an essential constituent of many biomolecules, namely enzymes, structural proteins, nucleic
149 acids, porphyrins, alkaloids, and N-glycosides, and it plays a crucial role in various physiological processes in plants
150 (Leghari et al., 2016). Estimations show that the total amount of nitrogen in the geosphere reaches about 1.6×10^{17} t. Most
151 of it is found in the atmosphere (3.86×10^{15} t), the lithosphere (1.64×10^{15} t), and the biosphere (2.8×10^{11} t) (Stevens, 2019).
152 Despite such high abundance, most of the nitrogen in the geosphere is not available to organisms, and it is the main
153 nutrient limiting plant growth in terrestrial ecosystems. It is assumed that only approximately 2% of the total pool of
154 nitrogen in the geosphere may be assimilated by plants, typically after biotransformation by soil microorganisms.
155 Different forms of nitrogen are present in the atmosphere (N_2, N_2O, NO, NO_2), soil (NO_3^-, NO_2^-, NH_4^+, humic acids)
156 (circa 3×10^{11} t), and detritus (10^{11} t). Plants mainly use nitrate (NO_3^-) and ammonium (NH_4^+) and, to a lesser extent a few
157 organic forms, including amino acids, oligopeptides, nucleotides, or urea, as sources of nitrogen. Normally, the non-plant-
158 available or hardly available forms may be converted into more available forms by microbial activities through
159 mineralization, nitrification, and fixation (Subba et al., 2017; Moreau et al., 2019; Zhang, S. et al., 2019; Mahmud et al.,
160 2020).

161 Mineralization involves a cascade of microbial and enzymatic activities which leads to conversion of soil organic N to
162 inorganic forms (Zhang et al., 2019). The soil organic matter decomposition is accomplished through aminization (from
163 macromolecules of organic N compounds to simple organic N compounds such as amino acids, amino sugars, and nucleic
164 acids) and further through ammonification (from simple organic N compounds to ammonium) (Kemmit et al. 2008). The
165 resulting NH_4^+ can be readily taken up by plants.

166 The ammonia pool in soils may undergo a nitrification process. Nitrification consists of the oxidation of ammonia to
167 nitrite (NO_2^-) and subsequently to nitrate (NO_3^-). Nitrification is a dominant pathway of nitrogen input in agricultural
168 systems, since nitrates account for more than 95% of the total nitrogen uptake by plants (Subba et al., 2017). The two-
169 step reaction is performed by consortia of aerobic chemoautotrophic bacteria catabolizing ammonia to nitrite (*e.g.*

Nitrosomonas spp., *Nitrosococcus* spp., *Nitrosospira* spp., *Nitrosolobus* spp., and *Nitrosovibrio* spp.), and then transforming nitrite into nitrate (*e.g. Nitrobacter* spp., *Nitrococcus* spp., *Nitrospira* spp., and *Nitrospina* spp.) (Hagopian and Riley, 1998).

Atmospheric nitrogen (N_2), comprising almost 78% of the atmosphere, can be transformed into ammonia due to natural events (*e.g.* lightning, fires) but most of what is transferred to the biota is biologically fixed by diazotrophs (Mus et al., 2016; Smercina et al., 2019). Diazotrophic microorganisms transform the diatomic trivalent N_2 molecule into ammonia (NH_3), that is useful and available to most organisms, using a nitrogenase enzyme complex consisting of two components, nitrogenase and nitrogenase reductase (Mahmud et al., 2020).

Biological nitrogen fixation (BNF) is accomplished by free-living microorganisms, *e.g. Acetobacter* spp., *Arthrobacter* spp., *Azospirillum* spp., *Azotobacter* spp., *Bacillus* spp., *Burkholderia* spp., *Citrobacter* spp., *Clostridium* spp., *Enterobacter* spp., *Erwinia* spp., *Klebsiella* spp., *Kluyvera* spp., *Phyllobacterium* spp., *Pseudomonas* spp., *Serratia* spp., *Streptomyces* spp., and symbiotic microorganisms, *e.g. Frankia* spp. associated with certain dicotyledonous species (acrinorhizal plants); certain species of *Azospirillum* spp., *Azoarcus* spp., and *Herbaspirillum* spp. associated with cereal grasses, or rhizobia associated with leguminous plants (Mahmud et al., 2020).

Rhizobia are Gram-negative bacteria of the family *Rhizobiaceae* (class α- and β-*Proteobacteria*, order *Rhizobiales*), which mainly colonize roots of legumes (Andrews and Andrews, 2017) and improve the growth of their host plant in nitrogen limited conditions. Rhizobia are taxonomically highly diverse; they include about 98 species belonging to 13 different genera and can be subdivided into two groups: (1) common "true" rhizobia covering *Azorhizobium* spp., *Bradyrhizobium* spp., *Ensifer* spp. (syn. *Sinorhizobium*), *Mesorhizobium* spp., and *Rhizobium* spp. ~~(Hayat et al., 2010)~~, and (2) "new rhizobia" represented by *Burkholderia* spp. (*B. caribensis*, *B. cepacia*, *B. mimosarum*, *B. nodosa*, *B. phymatum*, *B. sabiae*, *B. tuberum*), *Cupriavidus* spp. (*C. taiwanensis*), *Devosia* spp. (*D. neptuniae*), *Methylobacterium* spp. (*M. nodulans*), *Microvirga* spp. (*M. lupini*, *M. lotononidis*, *M. zambiensis*), *Ochrobactrum* spp. (*O. cytisi*, *O. lupini*), *Phyllobacterium* spp. (*P. trifolii*, *P. leguminum*, *P. ifriqiyense*), and *Shinella* spp. (*S. kummerowiae*), which achieved legume nodulation capabilities as a result of horizontal gene transfer (Gnat et al., 2015; Andrews and Andrews, 2017). The rhizobia-plant cooperation is one of the best known examples of symbiosis in nature. Whereas rhizobia provide plants with nitrogen by fixing N_2 solely in a symbiotic association with leguminous host plants, visible as nodules, the host plant supplies the microorganisms with nutrients and offers favorable conditions for their development. In fact, almost 70% of biologically fixed N_2 derives from symbiosis of rhizobia with leguminous plants, and rhizobia provide up to 90% of the nitrogen required by these plants (Mus et al., 2016).

PGPR enhance nitrogen bioavailability indirectly by increasing the root surface area and root morphology to effectuate a higher nitrogen uptake. Other PGPR types affect nitrogen bioavailability directly, *i.e.* converting nitrogen forms to easily

available ones or affecting the root nutrient transport systems (Calvo et al., 2019). It was documented that PGP *Bacillus* spp. mixtures, composed of different *Bacilli* species, trigger the expression of genes determining nitrate (NO_3^-) and ammonium (NH_4^+) uptake and transport and enhance host-plant growth and development in *Arabidopsis thaliana*. *Bacilli*-inoculated *A. thaliana* showed significantly higher transcript levels of nitrate transporters NRT1 (AtNRT1), NRT2 (AtNRT2), and ammonium transporter AMT1 (AtAMT1), which were accompanied with enhanced nutrient uptake and plant growth. Liu et al. (2017) received similar results in *Arabidopsis* when inoculating *B. subtilis* strain GB03. Jang et al. (2018) suggested that improved growth of plants induced by associated PGPR may be partially achieved by improved accessibility and acquisition of nitrogen. Improved nitrogen accessibility, P-solubilization and auxins synthesis were documented in peanut *Arachis hypogaea* inoculated with a consortium of diazotrophic root-origin bacteria isolated from the halophyte *Arthrocnemum indicum*. Inoculation of *Klebsiella* spp., *Pseudomonas* spp., *Agrobacterium* spp., and *Ochrobacterium* spp., lead to enhanced salt-tolerance in peanut plants, which was accompanied with low level of reactive oxygen species (ROS) that are considered beneficial under stress conditions (Sharma et al., 2016).

Typically, heavy metals adversely affect legume growth, nodulation, dinitrogenase activity, and N fixation effectiveness (Haddad et al., 2015; Fagorzi et al., 2018), and can act as agents that select the heavy metal tolerant genotypes. For example, under a gradient of pH and metals Cr(II), Cd(II), Zn(II), Cu(II), Ni(II), *Rhizobium* spp. strain UFSM-B74, *Bradyrhizobium* spp. strains UFSM-B53 and UFSM-B54, and *Burkholderia* spp. strain UFSM-B33/UFSM-B34 isolated from *Macroptilium atropurpureum* and *Vicia sativa* were tolerant to alkaline (pH=9.0), acidic (pH=4.0), and extremely acidic pH levels (3.0) (*Bradyrhizobium* sp. strain UFSM-B21, *Burkholderia* spp. strain UFSM-B33/UFSM-B34), as well as to high metal concentrations in the following order of tolerance Cr > Cd > Zn > Ni > Cu (Ferreira et al., 2018). *M. atropurpureum* strains significantly influenced the growth of their host-plant, the nodule number, and the efficiency of the nitrogen fixation. The combined inoculation of *Phaseolus vulgaris* grown under Cd(II) stress with PGP rhizobia, *i.e. Rhizobium tropici* strain CIAT899 and *Rhizobium etli* strain ISP42 together with *Azospirillum brasiliense* promoted seedlings root branching and proper legume-rhizobia molecular dialogue resulting in effective nodule organogenesis (Dardanelli et al., 2008). Moreover, the nitrogen-fixing *Bacillus subtilis* strain OSU-142 as well as the P-solubilizing *Bacillus megaterium* together with *Rhizobium leguminosarum* bv. *phaseoli* used as co-inoculants of *Phaseolus vulgaris* L. *cv.'elkoca-05'* increased N and P solubilization, nodulation, and improved plant growth (Elkoca et al., 2010). Co-inoculation of *Lens culinaris* with PGPR *Pseudomonas* spp. and *Rhizobium leguminosarum* increased the total N content in the plant (Mishra et al., 2011; Gómez-Sagasti and Marino, 2015). It was found that excessive amounts of heavy metals like Cu(II) and Zn(II) decreased dinitrogenase activity and nodule formation in *Medicago lupulina*, while co-inoculation of host-plant with *Ensifer meliloti* and PGPR *Rhizobium radiobacter* (formerly *Agrobacterium tumefaciens*) alleviated heavy metal stress and significantly enhanced dinitrogenase activity and plant biomass (Jian et al., 2019).

An alleviation of heavy metal and heat stress was reported for *Medicago sativa* inoculated with a consortium of PGPRs, composed of *Proteus* spp. strain DSP1, *Pseudomonas* spp. strain DSP17, *Ensifer melilotistrain* strain RhOL6, and *E. meliloti* strain RhOL8 (Raklami et al., 2019). These strains possessed several plant growth promoting traits, more specifically nitrogen fixation, phosphorus solubilization, and IAA production. PGPR-inoculated host plants showed an increases growth and reductions of the levels of glutathione reductase and phytochelatin synthase (PCS) that are involved in celluar defense against metal toxicity. Raklami et al. (2019) also suggested an important role for the metal transporter *NRAMP1* (natural resistance-associated macrophage protein) in the management of *M. sativa* inoculated with PGPR the metal stress.

The novel non-coding RNA (ncRNA), which plays a role at the post-transcriptional level by regulating a number of physiological processes such as stress responses (Fan et al., 2015), was identified in *Pseudomonas stutzeri* strain A1501 and may shed a light on the regulation pathways of the dinitrogenase enzyme in conditions of environmental stress and nutrient deficiency (Zhan et al., 2016). The *P. stutzeri* ncRNA present in the core genome, called NfiS, is involved in oxidative and osmotic stress responses and regulates the expression of genes located in the genomic island containing nitrogen-fixing genes (*nif*). NfiS optimizes nitrogen fixation by posttranscriptional regulation of dinitrogenase *nifK* mRNA and through the induction of the RpoN/NtrC/NifA (transcriptional activator of all *nif* operons) regulatory cascade via unidentified mechanisms (Zhan et al., 2016). NfiS upregulates regulators, *e.g.* RpoN (global nitrogen activator), NtrC (nif-specific activator), GlnK (PII family protein), RpoS (RNA polymerase sigma factor of the general stress response) are involved in stress response control and nitrogen fixation. Yet, under drought stress in *Medicago truncatula* dehydrin MtCAS31 (*Medicago truncatula* cold-acclimation-specific 31) was found as a leghemoglobin MtLb120-1 protector from denaturation under thermal stress *in vivo*. Its gene *MtCAS31* is expressed in nodules, and a *cas31* mutant demonstrates a lower dinitrogenase activity, a lower ATP/ADP ratio, as well as a higher expression of nodule senescence genes in comparison to wilde type *M. truncatula* (Li et al., 2018). It should be pointed out that the rhizobial stress response genes *otsA* (trehalose-6-phosphate synthase), *groEL* (heat shock protein), *clpB* (chaperone), and *rpoH* (transcriptional regulator) play a substantial role in tolerance of saprophytic rhizobia to different environmental conditions, and some of these genes are involved in symbiosis (da Silva et al., 2017), *e.g.* mainly genes encoding heat shock proteins such as ClpB and GroESL which were detected in *Bradyrhizobium japonicum* and *Sinorhizobium meliloti* nodules in accordance to their transcriptomic up-regulation.

2.1.2. Phosphorus

Phosphorus (P) is an important element of many macromolecules in the cell such as DNA, RNA, ATP, or phospholipids. It is essential for normal plant growth and development, and positively influences flowering, and the formation and ripening of seeds. Moreover, it improves disease resistance, increases shoot stiffness, and stimulates root system

development (Razaq et al., 2017). However, at the same time, the concentration of P in the soil solution, which is available for plant uptake is very limited. The mean total concentration of phosphorus in the Earth's crust is about 1200 mg P kg^{-1} (0.01-0.2% P_2O_5) (Tiessen, 2008; Tang et al., 2018). Over 99% of the naturally occurring phosphorus exists in an inorganic form (Pi), deposited as insoluble phosphate rocks such as sedimentary rocks (about 39% P_2O_5), igneous rocks (about 2.0% P_2O_5), and metamorphic rocks (about 1.3% P_2O_5). The remainder of naturally occurring phosphorus exists in its organic form (Po). However, only about 4% of the total phosphorus in soil is available to plants in its orthophosphate form (Alori et al., 2017). Inorganic forms of phosphorus account for 35-70% of total phosphorus in soil (Guignard et al., 2017), and the solubilization of phosphates, *e.g.* dicalcium phosphate, tricalcium phosphate, or hydroxyl apatite, is performed mainly by bacterial strains belonging to the genera *Achromobacter* spp., *Aerobacter* spp., *Agrobacterium* spp., *Azotobacter* spp., *Bacillus* spp., *Burkholderia* spp., *Cladosporium* spp., *Enterobacter* spp., *Erwinia* spp., *Flavobacterium* spp., *Micrococcus* spp., *Pseudomonas* spp., *Bradyrhizobium* spp., *Rhizobium* spp. (De Boer et al., 2019). Inorganic phosphate solubilizing bacteria (iPSB) are of great interest due to their promising effect as bio-fertilizers on plant growth and yield, as well as soil fertility (Suleman et al., 2018; Emami et al., 2020). Peix et al. (2015) reported the significant influence of *Mesorhizobium mediterraneum* bacteria present in soil on the growth and phosphorus content in chickpea and barley plants. Likewise, *Rhizobium* spp. and *Bradyrhizobium* spp. promote the growth of legumes, even when rhizobia remain in non-symbiotic conditions.

An increase in biomass production and phosphorus uptake was reported, among others, in *Triticum aestivum* inoculated with *Pseudomonas* spp., *Arachis hypogaea* inoculated with *Pantoea* spp. strain J49, or *Ricinus communis* and *Helianthus annuus* inoculated with *Psychrobacter* spp. strain SRS8 (Ma et al., 2011), as a consequence of dissolving phosphorus from inorganic forms by decreasing the pH in the rhizosphere. Zheng et al. (2019) demonstrated the major role of soil pH in shaping the phosphorus solubilization communities; the abundance of the iPSB bacteria increased with pH. The phosphate solubilizing activity as well as the production of pyruvic acid by the PSB *Burkholderia multivorans* strain WS-FJ9 lowered with increasing concentrations of soluble phosphate. Transcriptome profiling of PSB *Burkholderia multivorans* strain WS-FJ9 at three levels of exogenous phosphate revealed 446 differentially expressed genes involved in cell growth and P-solubilization; when the soluble phosphate concentration was increased; 44 genes were continuously up-regulated while 81 genes were downregulated (Zeng et al., 2017). Phosphate deficiency may increase the expression of some genes, like *e.g.* genes encoding for glycerate kinase and 2-oxoglutarate dehydrogenase, both involved in glucose metabolism and the production of organic acids were upregulated, as well as a gene encoding histidine protein kinase *PhoR*, whose expression product acts as a sensor in a signaling process responding to soluble phosphate deficiency (Zeng et al., 2017).

Bacteria can solubilize inorganic phosphates in several ways (Alori et al., 2017). The phosphate solubilization may be achieved by an acid-independent mechanism through the release of H^+ to the outer surface of bacteria cells in exchange for cation uptake (Rodríguez and Fraga, 1999), but phosphates are predominantly released as a result of soil acidification from organic acid discharge. Organic acids of bacterial origin are the product of the direct oxidation in the periplasmic space (Zhao et al., 2015). The carboxyl and hydroxyl residues of organic acid chelate cations bind to phosphate, resulting in a reduction of pH and release of phosphate anions after H^+ substitution. Among many diverse organic acid excretes, *e.g.*, lactic, isovaleric, isobutyric, acetic (*Bacillus amyloliquefaciens*, *B. licheniformis*), glycolic, oxalic, malonic, succinic, citric, and propionic acids, the most frequently synthesized by PSB is gluconic acid, followed by 2-ketogluconic acid (*Bacillus firmus*, *Burkholderia cepacia*, *Erwinia herbicola*, *Pseudomonas cepacia*, *Rhizobium leguminosarum*, *R. meliloti*) (Naraian and Kumari, 2017). Gluconic acid is a product of the direct oxidation pathway of glucose (DOPG, non-phosphorylating oxidation). In the periplasmic space glucose dehydrogenase (GCD/GDH) and gluconate dehydrogenase (GAD) enzymes oxidize the substrate, which leads to organic acids that diffuse freely outside the cell, releasing high quantities of soluble phosphate from mineral phosphates, by supplying both protons and metal complexing organic acid anions (Chhabra et al., 2013). Gluconic acid is a product of a reaction catalyzed by glucose dehydrogenase, which requires a pyrroloquinoline quinone (PQQ) cofactor (Ge et al., 2015; Chen et al., 2016). PQQ is a small, redox active molecule encoded by the *pqq* operon, which involves six core genes *pqqABCDEF*, of which *pqqA*, *pqqC*, *pqqD*, and *pqqE* are essential for the phosphate solubilizing capacity of many iPSB strains. The mutation of any gene of the *pqq* cluster may lead to a decrease in phosphate release (Li et al., 2014; Oteino et al., 2015; An and Moe, 2016; Suleman et al., 2018). The PqqA, a 22-24 amino acid long peptide serves as the substrate for PqqE, which is a functional radical S-adenosyl-L-methionine (SAM) enzyme that transforms SAM into methionine and 5'-deoxyadenosyl radical. The role of PqqD is not fully recognized, but it is known that this peptide interacts with PqqE. PqqC is an oxygen-activating enzyme, which catalyzes the final step of PQQ synthesis (Oteino et al., 2015).

In salt-affected soils, inoculation with phosphate solubilizing halotolerant bacteria, improves plant growth, and suppresses the adverse effects of salt (Etesami and Beattie, 2018). *Avicennia marina*, a halotolerant mangrove, and rhizosphere-associated bacteria such as *Arthrobacter* spp., *Bacillus* spp., *Azospirillum* spp., *Vibrio* spp., *Phyllobacterium* spp., *Oceanobacillus picturae*, were shown to solubilize $Ca_3(PO_4)_2$, $AlPO_4$, and $FePO_4$. Thant et al. (2018) revealed that the growth and phosphate solubilizing abilities of *Bacillus megaterium* were substantially higher due to their adaptation to sodium chloride stress, while *B. aquimaris* inoculated wheat showed a higher P content under salinity stress in the field (Upadhyay and Singh, 2015). Srivastava and Srivastava (2020) showed good growth of *Arabidopsis thaliana* inoculated with the PSB *Pseudomonas putida* strain MTCC 5279 under salt stress and P-deficiency conditions. Besides the significantly higher biomass of *A. thaliana* inoculated with *P. putida* MTCC 5279 higher acidic and alkaline phosphatases

activity, high IAA and ABA levels as well as upregulation or/and over-expression of several genes were detected like for inststance: *At5g39610* encoding *NAC*-domain transcription factor that positively regulates ageing-induced apoptosis and senescence in leaves, the gene encoding for calcium-dependent protein kinase (*CPK32*, *At3g57530*) which is of high importance in the signal transduction Ca^{2+} dependent pathway and in regulating the expression of ABA responsive genes potentially helping in stress adaptation, the jasmonate responsive gene (*JAR1*, *At2g46370*), the putative DNA repair protein gene (*AT3g32920*), and the gene expression of different P transporters (*PT1*, *PT2*, *PHO2*) playing a role under stress conditions. Barra et al. (2018) showed that phosphobacteria, *i.e. Klebsiella* spp. strains RC3 and RCJ4, *Stenotrophomonas* spp. strain RC5, *Serratia* spp. RCJ6, and *Enterobacter* spp. RJAL6 exhibited high acid and alkaline phosphatase activity under P-deficiency and aluminum toxicity. Moreover, under heavy metal stress conditions, *Ensifer adhaerens* strain OS3 was proven to be an effective phosphate solubilizer and chromium reducer (Oves et al., 2017).

About 30-65% of the total phosphorus in soil is present in organic form (Po), which is released from organophosphates by bacteria due to mineralization processes (Alori et al., 2017). For example, strains *Arthrobacter* spp., *Bacillus* spp., *Citrobacter* spp., *Delftia* spp., *Enterobacter* spp., *Klebsiella* spp., *Phyllobacterium* spp., *Proteus* spp., *Pseudomonas* spp., *Rhizobium* spp., *Rhodococcus* spp., *Serratia* spp. are able to enzymatically hydrolyze the P-organic substrates into inorganic forms. Three types of enzymes are involved in this process, (i) non-specific acid phosphatases (NSAPs), represented predominantly by acid and alkaline phosphomonoesterases (phosphatases), which dephosphorylate phosphoester and phosphoanhydride bonds of organic matter, (ii) phytases able to degrade phytate, and (iii) phosphonatases and C-P lyases, that cleave C-P bond of organophosphonates (Sharma et al., 2013; Jain et al., 2016; Alori et al., 2017). Phytases (myo-inositol hexakisphosphate phosphohydrolases) catalyze the conversion of organic phosphorus from phytate (inositol hexakisphosphate) to inorganic phosphorus, which can be easily taken up by plants (Azeem et al., 2014). It was found that phytases are produced by *Enterobacter* spp., *Serratia* spp., *Citrobacter brakii*, *Rhizobium* spp., *Pseudomonas* spp., *Proteus* spp., and *Klebsiella* spp. (Kumar et al., 2016). The activity of bacterial phytases is pH-dependent. Specifically for *Bacillus* spp. the optimum activity of phytase is at a pH between 6.0 and 8.0. Functional metagenomics of red rice crop residues led to the identification of the PhyRC001 sodium phytate hydrolyzing enzyme, which has an optimal activity at pH 7.0 and 35°C (Farias et al., 2018). An *Arabidopsis thaliana* mutant over-expressing bacterial phytase PHY-US417 showed a significantly higher osmotolerance to sodium chloride in comparison to the reference and knock out mutant (Belgaroui et al., 2018; Valeeva et al., 2018). A significant reduction of the phytase activity of *Enterobacter sakazakii*, *Enterococcus hirae*, or *Bacillus subtilis* strain B.S.46 was detected due to exposure to metal ions (Mn^{2+}, Zn^{2+}, Fe^{2+}, Co^{2+}, Cu^{2+}, Hg^{2+}, Cd^{2+}) (Kumar et al., 2016; Rocky-Salimi et al., 2016).

Triticum aestivum inoculated with P-solubilizing PGP *Arthrobacter nitroguajacolicus* exposed to a salt stress gradient showed an increase in biomass. Using comparative transcriptome analysis revealed, the significant influence of bacteria

on plant genes expression; 152 genes were up-regulated, and down-regulation was found for five genes (Safdarian et al., 2019). It concerned the genes involved in phenylpropanoid biosynthesis, porphyrin metabolism, cysteine and methionine metabolism, flavonoids biosynthesis, and pathways of biosynthesis of secondary metabolites. *A. nitroguajacolicus* increases the tolerance of wheat to sodium chloride stress due to up-regulation of antioxidative enzymes genes cytochrome P450, ascorbate peroxidase (APX), and also genes encoding for nicotianamine (NAS), and ABC transporters (Safdarian et al., 2019).

2.1.3. Iron

Under stress conditions, siderophores synthesis is one of the major bacterial mechanisms of supplying plants with available forms of iron (Fe) (Jian et al., 2019). Iron plays a role in chlorophyll synthesis and in the maintenance of chloroplast structure and function, it has key roles in DNA synthesis and respiration, and acts as a prosthetic group constituent of many enzymes, including those involved in redox reactions (Rout and Sahoo, 2015). Despite its huge abundance in the lithosphere (it is the fourth most common element in Earth's crust by weight), the plant availability of Fe is very limited due to its low solubility (Hider and Kong, 2010; Zhang, X. et al., 2019). In aerobic conditions, iron exists as ferric Fe(III) ions which accumulate in mineral phases as highly stable hydroxide [$Fe(OH)_3$] and oxyhydroxide [FeO(OH)] complexes, leading to free Fe(III) concentrations in soils of 10^{-9}-10^{-18} M, which are not sufficient to meet the needs of plants (Rout and Sahoo, 2015).

To cope with this situation, plants have evolved two different strategies for iron acquisition from the soil (Tripathi et al., 2018; Zhang, X. et al., 2019). In the first strategy (reduction-based strategy), which is characteristic for non-graminaceous plants, protons and phenolic compounds are released by plant roots into the rhizosphere to increase its acidification and promote Fe(III) solubility. Subsequently, Fe(III) ions are reduced to the more soluble Fe(II) ions by ferric reduction oxidases (FRO) at the apoplast and in this form the iron is imported into root cells by the iron-regulated transporter (IRT1). The second strategy (chelation-based strategy) is used by graminaceous plants only. In response to Fe deficiency, these plants release into the rhizosphere phytosiderophores (PS) with a high affinity for binding Fe(III). The resulting Fe(III)-PS complexes are readily transported into the root epidermis through the yellow stripe (YS) or yellow stripe-like (YSL) transporters. The most common phytosiderophores are synthesized from three S-adenosyl-methionine molecules and belong to the family of mugineic acid (MAs), with the best known member mugineic acid (MA), 2'-deoxymugineic acid (DMA), 3-epihydroxymugineic acid (epi-HMA), and 3-epihydroxy 2'-deoxymugineic acid (epi-HDMA) (Masuda et al., 2019). The production of siderophores to increase the availability of iron in the soil is also a common mechanism adopted by bacteria and resulting Fe(III)-siderophores can be an excellent source of iron for plants too (Kramer et al., 2020). Phytosiderophores consist of carboxyl, amine, and hydroxyl groups as the ligand functional groups, while most microbial siderophores have hydroxamate or phenolate groups as Fe(III)-coordination donors (Ahmed and Holmström, 2014). There

are three possible mechanisms of iron uptake by plant roots using the siderophore-metal complexes: (i) chelate degradation and iron release, (ii) uptake of the siderophore-Fe(III) complexes, or (iii) a ligand exchange reaction (Zhang, X et al., 2019).

Siderophores, formerly mycobactins, are low molecular mass (400-1500 Da) chelators of a high affinity for ferric Fe(III) (formation constant $K_f > 10^{30}$), synthesized under iron-limited conditions, which can form stable complexes with other metals, such as aluminum, cadmium, copper, gallium, indium, lead and zinc (Yu et al., 2017). Siderophores are generally synthesized by non-ribosomal peptide synthetases (NRPSs) or polyketide synthase (PKS) that cooperates with NRPS modules (Carrol and Moore, 2018). The secretion of siderophores is an energy-dependent process, mediated by efflux-pumps (Lamb, 2015). Siderophores are a group of 500 different compounds, diverse in their structure, with about 270 structurally characterized so far (Kramer et al., 2020). According to the chemical character of the metal binding site, three main categories of siderophores are distinguished: catecholates, hydroxamates, and (α-hydroxy)-carboxylates (Hider and Kong, 2010). The biochemical structures of chosen important members of these compounds are shown in Fig. 2.

Within the catecholates, the catecholate [$C_6H_4(OH)_2$ – 1,2-dihydroxybenzene] or phenolate [C_6H_5OH – hydroxybenzene] groups are connected with a backbone of polyamine, peptide, or macrocyclic lactone. Each catecholate group provides two oxygen atoms for chelation with Fe(III), forming a hexadentate octahedral complex. The main catecholate members are enterobactin (produced by *Escherichia coli*), pyoverdine (*Pseudomonas aeruginosa*), salmochelin (*Salmonella enterica*), bacillibactin (*Bacillus anthracis*, *B. subtilis*, *B. thuringiensis*), agrobactin (*Agrobacterium tumefaciens*), parabactin (*Paracoccus denitrificans*), and azotobactin (*Azotobacter vinelandii*) (Pahari et al., 2017). Siderophores of hydroxamate nature contain C(=O)N(-OH) groups connected to the backbone of the amino acid or its derivatives. Each of the hydroxamate groups, serving as chelating agents, provide two molecules of oxygen and form a bidentate ligand with iron. As a result, the complex hydroxamate with Fe(III) possesses a hexadentate octahedral structure. Among the hydroxamates, ferribactin is synthesized by *Pseudomonas fluorescens*, whereas desferrioxamine is produced by *Streptomyces coelicolor* (Ali and Vidhale, 2013; Pahari et al., 2017). Siderophores classified as (α-hydroxy)-carboxylates (complexones) are produced mainly by *Rhizobium* spp. and *Staphylococcus* spp., as well as fungi (*Mucorales*), and bind to Fe(III) through hydroxy- and carboxylate groups. For example, rhizobactin synthesized by *Rhizobium meliloti* strain DM4 is an amino polycarboxylic acid with ethylenediaminedicarboxyl and hydroxycarboxyl moieties as Fe(III) chelating groups, while staphylloferrin A, produced by *Staphylococcus hyicus* and *S. auricus*, consists of one D-ornithine and two citric acid residues linked by two amide bonds (Ali and Vidhale, 2013; Pahari et al., 2017).

Siderophores of bacterial origin influence host-plant iron homeostasis, immune function, and growth (Yu et al., 2017; Hesse et al., 2018). For example, the *Pseudomonas fluorescens* strain C7R12 siderophore pyoverdine analog (apo-pyoverdine) modulates the expression of approximately 2,000 genes in *Arabidopsis thaliana*, including up-regulation of

the expression of genes related to development and iron acquisition, and down-regulation of the expression of defense-related genes such as transcription factors ERF, WRKY, MYB, salicylic acid (SA)-related gene (such as *AT5G24210*, which encodes protein belonging to the lipase class 3 protein family), and an abscisic acid (ABA)-related gene (encoding the lipid transfer protein LTP3) (Trapet et al., 2016). Apo-pyoverdine was impaired in iron-regulated transporter1 (IRT1) and ferric reduction oxidase2 (FRO2) knockout mutants and was prioritized over immunity, reflecting the increased susceptibility to *Botrytis cinerea*. Due to this, an overexpression of the transcription factor HBI1, a key node for the cross talk between growth and immunity, was detected. In *P. fluorescens* strain WCS417 colonized *A. thaliana* many genes were positively regulated, including *FIT*, *FRO2*, *IRT1*, and MYB72 transcription factor that regulates the biosynthesis of iron-mobilizing phenolic compounds. In addition, the *BGLU42* and *PDR9* genes, whose products are involved in the secretion of iron-mobilizing phenolic compounds under iron-limited conditions, were also upregulated (Verbon et al., 2017). Similar iron-binding phenolic compounds are produced in *A. thaliana* in response to inoculation with *Paenibacillus polymyxa* strain BFKC01 (Zhou et al., 2016).

Bacterial strains that produce large amounts of siderophores showed lower growth inhibition by toxic copper concentrations, and the proportion of siderophore-synthesizing strains increased along with the ion gradient increase (Hesse et al., 2018). Furthermore, Cd(II) and Zn(II) stimulated the total siderophore synthesis, *e.g.* pyoverdine synthesis of *Pseudomonas aeruginosa* strain ZGKD3 (Shi et al., 2017). *Streptomyces* spp. isolated from *Betula pendula* and *Alnus glutinosa* rhizosphere containing Cd(II) and from the root endosphere produced hydroxamates, catecholates and phenolates, particularly ferrioxamine B (Złoch et al., 2016). *Bacillus* spp. PZ-1 under Pb(II) abundance synthesized siderophores of hydroxamate structure, which enhanced assimilation of Pb from the soil, translocated lead to the aerial tissues, and was assumed to be a bioaugmentation facilitator in *B. juncea* (Yu et al., 2017; Jinal et al., 2019). Inoculation of *Bacillus* spp. strain SC2b improved the *Sedum plumbizincicola* growth parameters, and enhanced Zn(II) and Cd(II) accumulation in roots and shoots (Ma et al., 2015), while the siderophore-producing *Bacillus thuringiensis* strain GDB-1 removed heavy metals from mine tailings and supported *Alnus firma* growth (Babu et al., 2013).

2.2. Rhizobacteria synthesizing phytohormones or influencing the hormone balance of the host plant

Another way of a direct improvement of plant growth by both free-living and symbiotic bacteria is the formation of compounds that are similar in structure and function to phytohormones synthesized by the plant. A subsequent option is influencing the biosynthesis of hormones by the host plant itself. Some compounds that are important in the regulation of cellular processes crucial for plant growth and development are auxins, cytokinins, gibberellins, abscisic acid, and ethylene (Shah and Daverey, 2020).

2.2.1. Auxins

Beneficial effects of phytohormone-synthesizing PGP rhizobacteria on the reduction of abiotic stress in plants has been widely reported (Ngumbi and Kloepper, 2014; Hashem et al., 2016). Numerous studies have demonstrated the significant role of auxins, most notably indolyl-3-acetic acid (IAA). Auxins are powerful molecules produced naturally by plants and involved in almost every aspect of plant physiology, controlling, amongst others, cell division, expansion, differentiation, and alleviation of abiotic stress (Paque and Weijers, 2016). While auxins are key regulators of plant development, indolyl-3-acetic acid (IAA) and its biosynthesis determining genes are also found in a wide range of different bacteria or fungi (Matsuda et al., 2018). Although IAA can impact gene expression in some bacteria, it does not seem to function as a factor in bacterial growth, but rather acts as a signal to communicate with plants in an ecological context to obtain profits from improved plant growth. Moreover, IAA biosynthesis is used by some pathogenic bacteria to hijack plant development. For example, it is involved in the formation of the crown galls induced by *R. radiobacter* in a range of plant species.

Auxins are produced and excreted by over 80% of the rhizosphere bacteria, *e.g*. *Azospirillum* spp., *Azotobacter* spp., *Enterobacter* spp., *Pseudomonas* spp., or *Staphylococcus* spp. (Patten and Glick, 1996; Rajkumar et al., 2012; Park, S-H. et al., 2017). The amounts of produced auxins vary between bacterial strains. For example, *Herbaspirillum seropedicae*, synthesizes an average of 8 µg mL^{-1} of IAA while *P. fluorescens* produces 28 µg mL^{-1} (Rajkumar et al., 2009). In bacteria, auxin synthesis was detected from only one precursor, tryptophan (Spaepen and Vanderleyden, 2011). It was revealed that beneficial rhizospheric bacteria predominantly use the indole-3-pyruvate (IPyA) pathway for the production of auxins, whereas the pathogenic plant-associated bacteria most often use the indole-3-acetamide (IAM) pathway (Ma et al., 2011) (Fig. 3). In the presence of *Azospirillum* spp., a positive correlation was reported between a stimulation of plant root cell membrane activity and the increases of IAA and indole-3-butyric acid (IBA) levels. Bacteria also supply other plant growth regulation compounds to their host plant, *e.g.* indole-3-acetaldehyde, indole-3-lactic acid (ILA), indole-3-ethanol (tryptophol, TOL), indole-3-acetamide (IAM) (Spaepen and Vanderleyden, 2011; Patten et al., 2013). IAA synthesis sometimes proceeds due to modified pathways. The indole-3-pyruvic acid (IPyA) pathway is mediated by the key protein indole-3-pyruvate decarboxylase, encoded by the pyruvate decarboxylase (*ipdC*) gene, and catalyzes the decarboxylation of IPyA to the indole-3-acetalaldehyde (IAAld) intermediate that is further oxidized to IAA. For instance, genome searching of the PGP *Gluconacetobacter diazotrophicus* strain PAL5, that is using the IPyA pathway for IAA synthesis, showed the lack of the pyruvate decarboxylase gene (*ipdC*). Rodrigues et al. (2016) provided evidence when *G. diazotrophicus* synthesizes IAA via the IPyA pathway; it does not use IPyA as a substrate, but rather uses the L-amino acid oxidase gene cluster, constituted of *lao*, *ccc*A, and *rid*A genes, which are encoding for L-amino acid oxidase LAAO, a putative cytochrome C, and reactive intermediate deaminase A protein RidA respectively. While LAAO catalyzes the production of IPyA from L-tryptophan, cytochrome C likely plays a redox role in *G. diazotrophicus*, and RidA hydrolyzes

intermediates produced by L-amino acid oxidases to α-ketoacids (Gao et al., 2016). The cucumber-*Bacillus amyloliquefaciens* strain SQR9 system, used as a model for the verification of the plant-microbe communication contributing to auxin synthesis by PGPR and plant growth promotion, showed that upon inoculation with *B. amyloliquefaciens* strain SQR9, the roots secreted high amounts of tryptophan and in turn the bacteria synthesized more IAA in the rhizosphere, which was promoting plant growth (Liu et al., 2016). In accordance with the increased tryptophan secretion by the cucumber roots, an increased expression of the plant specific tryptophan transport gene (*Csa024547*) was detected in the cucumber roots. An increase in the anthranilate synthesis gene (*Csa013682*), which product is involved in the synthesis of tryptophan, was not detected (Liu et al., 2016). The ability to improve the growth of the host-plant by *B. amyloliquefaciens* was confirmed in a gnotobiotic system. Significant increases of both, the expression of the IAA biosynthesis indole-3-acetonitrilase gene (*yhcX*) as well as of plant growth were observed (Liu et al., 2016).

It was reported that *Paenibacillus polymyxa* and *Azospirillum* spp. release both tryptophan, and auxin-type compounds like TOL to the rhizosphere, which can indirectly improve plant growth (Lebuhn et al., 1997; El-Khawas and Adachi, 1999). At low concentrations, bacterial auxins stimulate elongation of primary plant roots, but at higher doses auxins promote the formation of lateral and adventitious roots, which can enhance uptake of minerals, and increase the production of root exudates that increase bacterial proliferation (Patten et al., 2013; Verbon and Liberman, 2016). Patten and Glick (2002) found enhanced roots formation in canola (*Brassica napus*) developed from seeds inoculated with *Pseudomonas putida* strain GR12-2 in comparison to plants inoculated with an IAA-deficient *P. putida* mutant. Moreover, bacteria-derived auxins may prevent the deleterious effects of various environmental stresses, like drought, salinity, or soil pollution (Kudoyarova et al., 2019). For example, Defez et al. (2019) reported that salt tolerance of *Medicago truncatula* inoculated with IAA-overexpressing *Ensifer meliloti* strain DR-64 was enhanced in comparison with the plants inoculated with the *E. meliloti* IAA-deficient mutant. Also, switchgrass inoculated with *Pseudomonas grimontii* strain Bc09, *Pantoea vagans* strain So23, *Pseudomonas veronii* strain E03, and *Pseudomonas fluorescens* strain Oj24 under Cd stress demonstrated increased biomass and IAA synthesis, as well as reduced Cd accumulation compared to reference plants (Begum et al., 2019). An enhanced IAA production was observed in *Leifsonia xyli* strain SE134 under Cu exposure (Kang et al., 2017). The halophilic *Leclercia adecarboxylata* strain MO1, which overproduces IAA, improves the growth and salinity resistance of *Solanum lycopersicum* (Kang et al., 2019b). The IAA-overproducing *Rhizobium* strain RD64 protects *Medicago sativa* against drought, predominantly by the production of low molecular weight osmolites, such as proline and pinitol (Defez et al., 2017). An increased IAA synthesis was observed in *Bacillus cereus* strain So3II and *B. subtilis* strain Mt3b in a temperature gradient (Wagi and Ahmed, 2019). *B. licheniformis* strain HSW-16 mitigated salt stress and stimulated the growth of *T. aestivum* in correlation with elevated IAA concentrations (Singh and Jha, 2016). Similarly, *Enterobacter* spp. strain NIASMVII produced significant amounts of IAA that correlated with enhanced seed

germination of *T. aestivum* (Sorty et al., 2016). Some IAA-synthesizing rhizobacteria are efficient stimulators of plant growth in drought conditions. For example, positive correlations were found between increased biomass of *T. repens* developed from seeds inoculated with *P. putida* and *B. megaterium* and increased IAA levels under water deficiency (Marulanda et al., 2009). Zaheer et al. (2016) reported a correlation between enhanced IAA synthesis of chickpea-origin *Serratia* spp. and increased chickpea grain yield in a nutrient-poor soil. IAA-synthesizing bacteria are also able to improve plant growth in heavy metal polluted soils. For instance, the IAA-producing *B. megaterium* strain MCR-8 alleviated nickel (Ni) stress in *Vinca rosea* in comparison with non-inoculated plants which led to increases in root and shoot growth, as well as higher amounts of phenols, flavonoids, and antioxidative enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) (Khan et al., 2017). Cadmium-resistant and IAA-producing *Leifsonia* spp. and *Bacillus* spp. significantly increased the growth of *Zea mays* in metal polluted soils compared to nonpolluted soils (Ahmad et al., 2016). Exposure of the halotolerant plant *Spartina densiflora* to metals enhanced the levels of antioxidative enzymes, *e.g.* superoxide dismutase and catalase. Inoculation with the metal-tolerant *P. agglomerans* strains RSO6 and RSO7 and *B. aryabhattai* strain RSO25 lowered the levels of these antioxidative enzymes. The alleviation of the metal exposure enhanced expression of the PAL gene, encoding for phenyloalanine ammonia lyase involved in the secondary metabolism of lignin synthesis after inoculation with the above mentioned strains indicates that the lignin metabolism pathway might be involved in metal stress management (Paredes-Páliz et al., 2018).

2.2.2. Cytokinins

Alleviation of abiotic stress in plants can also result from the activity of cytokinins. Naz et al. (2009) revealed that under salt stress conditions, cytokinin-producing bacteria such as *Arthrobacter* spp., *Bacillus* spp., *Azospirillum* spp., or *Pseudomonas* spp. increased *Glycine max* root and shoot biomass as well as the proline content in its tissues. *Bacillus aryabhattai* strain SRB02 synthesizes cytokinins and improves soybean growth under an oxidative, nitrosative, and temperature gradient (Park, Y-G., et al., 2017). Cytokinins play crucial roles in many aspects of plant growth and development, including embryogenesis, maintenance of root and shoot meristems activity, vascular development, root elongation, lateral root and nodule formation, and apical dominance in response to environmental stimuli (Osugi and Sakakibara, 2015). It was found that, in *in vitro* conditions, an average 90% of rhizobacteria synthesize and release cytokinin-like growth stimulators. *Coleus forskohlii* associated rhizobacteria, *e.g. Pseudomonas stutzeri* MTP40, *Stenotrophomonas maltophilia* MTP42 and *Pseudomonas putida* MTP50 synthesize plant growth enhancing cytokinins (Patel and Saraf, 2017). In *Bacteria*, the cytokinin synthesis pathway is initiated by a transfer of the isopentenyl moiety from DMAPP (dimethylallyl diphosphate) to the adenine compound adenosine monophosphate (AMP), a reaction catalyzed by isopentenyltransferase, the *ipt* gene product. As an alternative, bacteria are able to initiate the cytokinin

production by transferring the isopentenyl moiety from HMBDP (1-hydroxy-2-methyl-2(E)-butenyl 4-diposphate) to AMP (Wong et al., 2015).

Recently, the dual role of bacterial cytokinins include optimizing nutrient supply and modulating host immunity in plants infected with pathogens was reported (Akhtar et al., 2020). Bacterial-origin cytokinins induced resistance against bacterial pathogens in *Arabidopsis* (Grosskinsky et al., 2016). In the *Arabidopsis-Bacillus megaterium* system, plant cytokinin recognition was responsible for *B. megaterium* properties that were beneficial to plants. As biocontrol agents, cytokinins regulated the *P. fluorescens* strain G20-18 against *P. syringae* infection in *Arabidopsis* (Grosskinsky et al., 2016). The exact mechanisms of cytokinin biosynthesis in bacteria is not yet fully elucidated. The proposed role of *miaA* is to encode a tRNA Δ(2)-isopentenylpyrophosphate transferase similar to tRNAIPTs, which are responsible for cytokinin biosynthesis (Stringlis et al., 2018b).

2.2.3. Gibberellins

Gibberellins (GAs) can alleviate abiotic stress and influence other physiological processes (Halo et al., 2015; Kang et al., 2019a). This class of compounds is involved in a plethora of developmental processes in plants, including regulation of seed dormancy, quiescence, germination, flowering, ripening of fruits, promotion of root growth, and root hair abundance (Binebaun et al., 2018). Similarly to auxins and cytokinins, production of GAs is not restricted to plants, but is also a common phenomenon in fungi and bacteria. However, there is no known function for GAs in these organisms; most probably they play a role as signaling factors towards the host plants, *e.g.* in *Rhizobiaceae* symbiotic associations with legumes (Nett et al., 2017a, b). Indeed, the first report on gibberellin characterization in bacteria concerned gnotobiotic cultures of *Rhizobium meliloti* where the presence of GA1, GA4, GA9, and GA20 was demonstrated (Atzorn et al., 1988). Since then, GA synthesis was confirmed in numerous rhizospheric bacteria, including *Acetobacter diazotrophicus*, *Herbaspirillum seropedicae, Bacillus* spp., or *Azospirillum* spp. (Nett et al., 2017b; Nagel et al., 2018). To date, 136 different chemical structures have been characterized as naturally occurring gibberellins, of which GA3 (gibberellic acid) is most often produced by bacteria. In *Bacteria* the gibberellins biosynthetic pathway starts from geranyl-geranyl diphosphate (GGPP) transformation by *ent*-copalyl diphosphate synthase (CPS) to produce *ent*-copalyl diphosphate, which is subsequently transformed by *ent*-kaurene synthase into *ent*-kaurene (Fig. 4). The oxidation of *ent*-kaurene at position C-19 via *ent*-kaurenol and *ent*-kaurenal generates *ent*-kaurenoic acid, which is oxidized to *ent*-7α-hydroxykaurenoic acid. Finally, oxidation of *ent*-7α-hydroxykaurenoic acid at C-6β yields GA12-aldehyde. GA12-aldehyde is subsequently converted in several steps to GA1 and GA3 (Tudzynski, 2005; Morrone et al., 2009; Hedden and Thomas, 2012; Hershey et al., 2014; Nett et al., 2017a; b; Salazar-Cerezo et al., 2018).

Numerous reports have confirmed that gibberellins produced by bacteria stimulate plant growth and yield. For instance, inoculation of maize roots with different *Azospirillum* strains increased the levels of GA3 in the roots and promoted their

growth (Revolti et al., 2018). *Enterococcus faecium* strain LKE12 was shown to enhance the length and biomass of rice grains and oriental melon through the secretion of an array of gibberellins (GA1, GA3, GA7, GA8, GA9, GA12, GA19, GA20, GA24, and GA53) along with IAA (Lee et al., 2015). GAs produced by *Leifsonia xyli* strain SE134 are involved in maintaining the growth of *Solanum lycopersicum* and most likely provide the plant host tolerance to Cu(II) (Kang et al., 2017). Enhanced bacterial gibberellin production was accompanied by enhanced production of glutamic acid, threonine, phenylalanine, glycine, proline, and arginine which potentially had substantial influence on the biomass production of inoculated plant (Kang et al., 2017). The total polyphenol and flavonoid contents positively correlated with reduced superoxide dismutase activity, which was most likely the mechanism involved in Cu(II) stress alleviation (Kang et al., 2017). Moreover, the role of gibberellin's in plant thermotolerance was recognized (Kang et al., 2019a). Soybean-assisted *Bacillus tequilensis* strain SSB07 produced GA1, GA3, GA5, GA8, GA19, GA24, and GA53, which increased the shoot length and biomass of the host plant under the high-temperature stress (Kang et al., 2019a). The tolerance to heat stress provided by *B. tequilensis* strain SSB07 was possibly related to a phytohormone regulation mechanism. The levels of jasmonic acid and salicylic acid were upregulated in soybean plants inoculated with this strain SSB07 and exposed to supraoptimal temperatures (Kang et al., 2019a). GA4 synthesizing PGP *Sphingomonas* spp. LK11 improved the growth of *Solanum lycopersicum* and increased its salinity stress tolerance (Halo et al., 2015). The promotion of tomato growth during NaCl stress correlated with a decrease in lipid peroxidation, as well as a higher glutathione content accompanied with lower peroxidase, catalase, and polyphenol oxidase activities in relation to non-inoculated plants (Halo et al., 2015).

2.2.4. Abscisic acid

Abscisic acid (ABA) is a hormone that mainly functions as an inhibitor of growth and metabolic activities in plants. This sesquiterpenoid fulfils many important roles in seed development and maturation, induction of seed and bud dormancy, senescence processes, synthesis of proteins and compatible osmolytes, and regulation of the ability of plants to survive in harsh and changing environments due to abiotic and biotic stress factors (Belimov et al., 2014; Shu et al., 2018). Under a sodium chlorite gradient, the wheat-associated rhizobacterium *Dietzia natronolimnaea* strain STR1 provided protection against salt stress to host-plant by modifying the transcriptional machinery, including the ABA-signaling cascade. In comparison to non-inoculated plants, PGPR-inoculated wheat plants showed up-regulation of the ABA-responsive genes *TaABARE* and *TaOPR1*, which led to an induction of the gene expression of the transcription factors *TaMYB* and *TaWRKY*. As a result, multiple stress related genes were activated, including salt stress-induced genes (*TaST – T. aestivum* Salt-Tolerant) involved in salinity tolerance, as well as SOS (Salt Overly Sensitive) pathway related genes (*SOS1* and *SOS4*). Moreover, in *D. natronolimnaea* strain STR1-inoculated plants, the high transcript levels of genes participating in ion transport and tissue specific responses of ion transporters, *e.g.* TaNHX1, TaHAK, and TaHKT1, were observed,

along with higher proline content and enhanced gene expression of several antioxidative enzymes, particularly ascorbate peroxidase, Mn superoxide dismutase (*MnSOD*), catalase, peroxidase, glutathione peroxidase, and glutathione reductase (*GR*) (Bharti et al., 2016).

The presence of ABA in the rhizosphere was found to mitigate drought stress in plants and to support plant growth under water-logged conditions (Cohen et al., 2015; Tsukanova et al., 2017). For instance, ABA was detected as a product of PGPB activity by *Azospirillium brasiliense* strains Cd and Az39, *Achromobacter xylosoxidans*, *Bacillus lycheniformis*, *B. pumilus*, *Brevibacterium halotolerans*, *Lysinibacillus fusiformis*, and *Rhizobium* spp. (Egamberdieva et al., 2017). It was also found that inoculation of maize with the ABA-producing *Azospirillum lipoferum* strain USA59b increased plant biomass in water-deficient conditions (Cohen et al., 2015). Abscisic acid-producing *Bacillus aryabhattai* strain SRB02, isolated from soybean rhizosphere, significantly promotes the host-plant biomass and nodule formation under drought stress conditions (Park, Y-G. et al., 2017).

The ABA-synthesising *Pseudomonas putida* strain MTCC5279 associated with *Cicer arietinum* (chickpea) provided salt and drought tolerance to their host-plants by altering morpho-physiological and biochemical properties and modulating the expression of stress-responsive genes (Tiwari et al., 2016). The variable expression levels of miRNAs and their target genes under both types of abiotic stress at different experimental time points suggest various mechanisms of miRNA responses to various stresses (Jatan et al., 2019). MicroRNAs (miRNAs), non-coding regulator elements that modulate transcriptional and post-transcriptional genes expression, are involved in resistance to biotic and abiotic stresses, including drought and salinity (Li and Zang, 2016; Shriram et al., 2016). Significant alterations in the gene expression patterns of *C. arietinum* inoculated with strain MTCC5279 in NaCl and drought stresses connected with miR159, miR160, miR166, miR167, miR169, miR171, miR172, miR393, and miR396 suggest that miRNAs play a crucial role in chickpea stress alleviation (Jatan et al., 2019).

In psychrophilic *Bacillus* spp. strains (CJCL2, RJGP41), the genes involved in cold stress tolerance, specifically genes related to signal transduction pathways, antioxidative activity, and sugar-ABC transporters were identified and their enhanced expression under cold stress conditions was documented. It was also shown that psychrophilic PGP *Bacillus* spp. bacteria regulated cold stress response parameters in wheat and decreased the expression levels of ABA. They are also involved in the expression of lipid peroxidation encoding genes and can increase expression of proline synthesis genes. Psychrophilic *Bacillus* spp. strains are also able to upregulate the expression of genes encoding important plant growth hormones such as auxin, cytokinin, alpha expansin, and ethylene under cold stress conditions (Zubair et al., 2019).

Bacteria can potentially influence plant growth through the usage of ABA as nutrients. Belimov et al. (2014) reported that *Rhodococcus* spp. strain P1Y and *Novosphingobium* spp. strain P6W in association with plant roots may utilize ABA as a carbon and energy source, decrease ABA concentrations of inoculated plants, and potentially alter plant growth.

Nevertheless, the exact mechanisms of decrease amounts of ABA *in planta* and its effects on plant growth is still unclear. Although it was reported that plants such as *Gossypium hirsutum* inoculated with *Raoultella planticola* strain Rs-2, or *Solanum tuberosum* inoculated with *Promicromonospora* spp. strain SE188 showed decreased ABA concentrations, more data are required to better understand the mechanisms of how bacterial ABA-utilizers influence plant biomass (Kang et al., 2012; Wu et al., 2012). ABA-catabolizing *Rhodococcus quingshengii* associated with *Arabidopsis* under heavy metal stress significantly increased the expression of Cd, Zn, and Ni-related transporters, and increased the accumulation of metal ions possibly via ABA-mediated mechanisms (Lu et al., 2020).

2.2.5. Ethylene

Indole-3-acetic acid (IAA) accumulation in plants induces the transcription of 1-aminocyclopropane-1-carboxylate (ACC) synthase genes, leading to increased ACC and ethylene levels (Gamelaro and Glick, 2015; Abts et al., 2017). Ethylene (ET) is a plant growth regulator that plays a role in different stages of plant ontogenesis, including germination, growth, development, flowering and senescence. Moreover, ethylene promotes formation of adventitious roots, stimulates seed germination, and breaks seed dormancy. Ethylene is also involved in stress signaling pathways. Its overproduction can be induced by biotic and abiotic stresses such as pathogen interaction, temperature gradients, flooding, drought, salinity, and metals (Han et al., 2015; Vacheron et al., 2016). High levels can lead to inhibition of root elongation, inhibition of nodule formation and nitrogen fixation by symbionts of leguminous plants, ultimately inducing hypertrophy, and accelerate senescence and abscission (Singh, S. et al., 2015). Yet, PGPB may play an important role in plant ethylene homeostasis by reducing its levels in the plant tissues because of their rhizobitoxine synthesis and/or 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme (ACCD) production (Singh, R.P. et al., 2015).

Ethylene is synthesized from the amino acid precursor of L-methionine (L-aspartic acid), which is subsequently converted to S-adenosyl-L-methionine (SAM) by SAM synthetases, and further transformed to 1-aminocyclopropane-1-carboxylic acid (ACC) by ACC synthases (Fig. 5). Next, ACC is transformed to ethylene by ethylene oxidases. Bacteria may disturb the synthesis of ethylene through the production of rhizobitoxine, a competitive inhibitor of ACC synthetase (Yasuta et al., 1999; Sugawara et al., 2006). Rhizobitoxine is an enol-ether amino acid (2-amino-4-[2-amino-3-hydroxypropoxy]-trans-3-butenoic acid). It was reported that the biochemical functions of rhizobitoxine relay on the inhibition of both β-cystathionase in the methionine biosynthesis pathway (Sugawara, 2006) and ACC-synthase in the ethylene biosynthesis pathway (Yasuta et al., 1999).

Decrease of ethylene biosynthesis due to the activity of an ACCD enzyme, involves the hydrolysis of the ethylene precursor ACC into ammonia and α-ketobutyrate. It was reported that plants inoculated with bacteria producing ACCD possess longer roots and exhibit higher resistance levels to fungal (*e.g. Pythium* spp., *Fusarium* spp.) and bacterial (*e.g. Erwinia* spp.) pathogens, as well as to flooding (Ravanbakhsh et al., 2017; Ghosh et al., 2018; Saikia et al., 2018; Gupta

and Pandey, 2019). The ACCD was found as crucial enzyme in improving rice growth under salt and heavy metals stress in the presence of the *Pseudomonas stutzeri* strain A1501 (Han et al., 2015). A *P. stutzeri* mutant in the ACCD encoding gene (*acdS*) showed lack of ACCD activity and lower resistance to NaCl as well as to metal salts like $NiCl_2$ in comparison with the wild type bacteria. Moreover, a mutation of *acdS* correlated with a lower dinitrogenase activity under NaCl stress, as well as a lack of ability to promote host-plant growth in salt and metal stress conditions (Han et al., 2015). Jaemsaeng et al. (2018) reported that inoculation of the ACCD producing endophyte *Streptomyces* spp. strain GMKU 336 significantly improved salt tolerance of rice plants by decreasing ethylene and reactive oxygen species, and balancing ion content and osmotic pressure. The strain GMKU 336 significantly influenced stress response involved genes, *e.g. ACO1* and *EREBP1* encoding enzymes involved in the ethylene pathway, which were down-regulated, whereas genes involved in osmotic balance (*BADH1*), Na^+ transporters (*NHX1*, *SOS1*), calmodulin (*Cam1-1*), antioxidant enzymes (*Cu/ZnSOD1*, *CATb*), and *acdS* in *Streptomyces* spp. GMKU 336 were up-regulated (Jaemsaeng et al., 2018). Enhanced SOD activity and growth parameters were detected in *Parastrephia quadrangularis* exposed to salt stress and inoculated with ACCD-producing *Klebsiella* spp strains 8LJA and 27IJA (Acuña et al., 2019). Yet, ACCD-producing rhizobacteria associated with *Panicum maximum* reduced salt and drought stress (Tiwari et al., 2018), similarly to ACCD-producing *Lactobacillus* spp., *P. putida*, and *Azotobacter chroococcum* in respect to *Lactuca sativa* and *Raphanus sativus* (Hussein and Joo, 2018).

3. Increasing tolerance to biotic stresses

Under biotic stress conditions, bacteria assist plants by (i) competing with pathogens for limited nutrient resources, mainly iron; (ii) biocontrol of pathogen activity, including production of antibiotic compounds; (iii) synthesis of fungal cell wall lytic enzymes, and (iv) induction of systemic response in host plants (Glick, 2014; Ma et al., 2016). An improvement of plant resistance against pathogens may be attributed to competition of beneficial microorganisms with pathogenic ones for nutrients with limited availability. PGPB, which produce siderophores, may reduce the pool of iron ions accessible to their competitors (Verbon et al., 2017). Kramer et al. (2020) indicated that bacteria that usually live in consortia with interacting strains produce different siderophores, each requiring a specific cognate receptor for iron uptake (Kümmerli et al., 2014). In addition, siderophores can function as competitive agents against other bacteria (Niehus et al., 2017). For example, *Pseudomonas aeruginosa* strain 7NSK2 competes with the pathogenic *Colletotrichum lindemuthianum* in the rhizosphere of bean (Bigirimana and Höfte, 2002), and with a *Pyricularia grisea*, which is ultimately deleterious to rice (De Vleesschauwer et al., 2006). The beneficial *Pseudomonas fluorescens* strain CHA0 competes with *Peronospora parasitica*, a pathogen of *Arabidopsis* sp. (Iavicoli et al., 2003) while *Pseudomonas putida* strain WCS358 competes with *Pseudomonas syringae* pv. *tomato* in the rhizosphere of *Arabidopsis* sp. (Meziane et al., 2005), and *Serratia marcescens* strain 90-166 with *Colletotrichum orbiculare* in the rhizosphere of cucumber (Press et al., 2001; Wei et al., 2015; Compant

et al., 2019; Gu et al., 2020). Bacteria can use at least 15 different iron-uptake pathways, more specifically the one ferrous Fe(II)-uptake pathway, three heme-acquisition pathways, one ferric Fe(III)-uptake pathway by siderophores, pyoverdine and pyochelin, and (iv) ten different "siderophore piracy" strategies to take up Fe(III) (Cornelis and Dingemans, 2013; Perraud et al., 2020). Using proteomic and RT-qPCR approaches and *Pseudomonas aeruginosa* as a model, the catechol-type siderophores, which were efficient in inducing expression of their transporters, were evidenced as the most common pathway to bind the iron, while expression of pyochelin and pyoverdine pathways were repressed (Perraud et al., 2020). *P. aeruginosa* upregulated siderophore production in competition with *Staphylococcus aureus*, while with *Burkholderia cenocepacia*, *P. aeruginosa* increased not only the total synthesis of pyoverdine but also the rate of the early growth phase (Leinweber et al., 2018).

Furthermore, plant beneficial bacteria maintain control over the pathogens due to synthesis of antifungal and antibacterial metabolites. Members of *Bacillus* spp. produce a wide variety of antibiotics both of ribosomal origin like *e.g.* subtilin, subtilosin A, TasA (spore associated antibacterial protein), and sublancin, as well as synthesized through non-ribosomal peptide synthases (NRPSs) or polyketide synthases (PKS), such as bacilysin, chlorotetain, mycobacillin, rhizocticin, bacillaene, difficidin, and lipopeptides belonging to the surfactin, iturin, and fengycin families (Goswami et al., 2016; Li, Z. et al., 2020). Moreover, *Pseudomonas fluorescens* and *P. aeruginosa* are efficient in the synthesis of antiseptic compounds, *e.g.* 2,4 diacetyl phloroglucinol (DAPG), phenazine-1-carboxylic acid (PCA), phenazine-1-carboxamide (PCN), pyoluteorin (Plt), pyrrolnitrin (Prn), oomycinA, viscosinamide, butyrolactones, kanosamine, zwittermycin-A, aerugine, rhamnolipids, cepaciamide A, ecomycins, pseudomonic acid, azomycin, antitumor antibiotic FR901463, cepafungins, and karalicins (Goswami et al., 2016).

Fungistatic activity of beneficial bacteria may also be due to the synthesis of fungal cell-wall degrading enzymes, like chitinase, β-1,3-glucanase, protease, or cellulase resulting in a direct inhibitory effect on the hyphal growth. For example, β-1,3-glucanase produced by strains of *Paenibacillus* spp. and *Streptomyces* spp. suppressed the growth of *Fusarium oxysporum*, while *Bacillus cepacia* destroyed soil borne fungi *Rhizoctonia solani* and *Sclerotium rolfsii* (Compant et al., 2019). Moreover, non-pathogenic *Rhizobium* spp., *Azospirillum* spp., *Klebsiella pneumoniae*, *Yersinia* spp., and *Frankia* spp. demonstrate pectinolytic capability.

Induced systemic resistance (ISR) is another major mechanism through which PGPB support plants for a better defense against pathogens commonly occurring in soils (Persello-Cartieaux et al., 2003; Van Loon, 2007; Arora and Jha, 2019). Rhizobacteria-induced resistance in hosts (R-ISR) relies on pathways regulated by jasmonic acid (JA) and ethylene, and leads to a response in distant plant tissues without involvement of pathogen-related (PR) proteins like antifungal chitinases, glucanases, thaumatins, oxidative enzymes (peroxidases, polyphenol oxidases, lipoxygenases), and low-molecular weight phytoalexins (Pieterse et al., 2014). Rhizobacterial-ISR provides plants a long-lasting resistance to

pathogens that are sensitive to JA- and ET-dependent defense mechanisms. For example, *Bacillus amyloliquefaciens* strain IN 937a bacteria present in the rhizosphere of *Arabidopsis* sp. induces ISR against the pathogenic *Erwinia carotovora* (Ryu et al., 2004), *B. pumilus* strain SE34 protects against infectious *Pseudomonas syringae* (Ryu et al., 2003a, b), and *Pseudomonas fluorescens* strain CHA0 shields against *Meloidogyne javanica* (Siddiqui and Saukat, 2004; Annapurna et al., 2013). Important bacterial resistance-inducing elicitors are lipopolysaccharides, siderophores (*e.g.* pseudobactins, pyochelin), antibiotics (*e.g.* pyocyanin, 2,4-diacetylphloroglucinol), N-acylhomoserine lactones or volatile compounds (*e.g.* 2,3-butanediol) (Van Loon and Baker, 2005; Sharifi and Ryu, 2018a; Tyagi et al., 2018; Villena et al., 2018; Romera et al., 2019). Inoculation of blackberries (*Rubus* sp.) with a plant growth promoting rhizobacterium *Pseudomonas fluorescens* strain N21.4 triggered phenylopropanoids and flavonoid biosynthesis as a part of an ISR defense pathway. Most likely, in the interaction of *P. fluorescens* strain N21.4 with blackberries the gibberellins pathway is involved (Garcia-Seco et al., 2015). Inoculation of *Rubus* sp. with *P. fluorescens* strain N21.4 modulated plant gene expression and affected biosynthesis of secondary metabolites. Under the N21.4 influence the plant genes encoding enzymes involved in the conversion of phenyloalanine to flavonols, anthocyanins, and catechins, and the regulatory genes involved in controlling those enzyme activities, were identified. Furthermore, genes coordinating the expression of flavonoid biosynthetic genes with the accumulation of anthocyanins, catechins, and flavanols in blackberry fruits were determined (Garcia-Seco et al., 2015). In fruits of PGPR-associated blackberries, the PR proteins RuPR1, RuPR2 (β-1,3-glucanase), RuPR3 (chitinase), and RuPR4 (unknown function) demonstrated significant differences in expression. Increasing tolerance to pathogens is a common phenomenon related to the improvement of plant growth and health through inoculation of beneficial microbes (Algar et al., 2014).

2,3-butanediol (2,3-BD) and its precursor acetoin (3-hydroxy-2-butanone, AC) (Fig. 6) were found as significant inducers of ISR and helped improve plant growth (Ji et al., 2011; Sharifi and Ryu, 2018b). Both compounds are members of a numerous group of volatile organic compounds (VOCs) that gather gas-phase low molecular weight hydrocarbons (<300 Da) of low boiling points and vapour pressure (0.01 kPa), which are emitted in a gaseous phase or secreted into liquids (Ali et al., 2015; Audrain et al., 2015). Bacterial volatile compounds (BVCs) may play important roles in the bacterial life cycle (*e.g.* regulation of bacterial motility, antibiotic resistance, biofilm formation), and their associations with host-plants (*e.g.* increase biomass, fruit yield, seed production, lateral root and root hair formation, nutrient uptake, and photosynthetic activity (Sharifi and Ryu, 2018a; b; Morcillo et al., 2020a; b). 2,3-BD and AC are involved in ISR in tobacco (Wang et al., 2009). 2,3-BD significantly reduced symptoms caused by fungal and bacterial pathogens, which was positively correlated with enhanced expression of basic PR genes in the JA pathway (Cortes-Barco et al., 2010 a; b). 2,3-BD was also reported to be implicated in ISR also in *Arabidopsis* sp. and pepper (Choi et al., 2014). Furthermore, acetoin synthesized by *Bacillus subtilis* strain FB17 as inoculum of *Arabidopsis thaliana*, was found to be an ISR inducer,

which protects plants from infection in an ethylene-dependent manner against the pathogenic *Pseudomonas syringae* pv. tomato strain DC3000 (Ali et al., 2015). It is noteworthy that, the ISR plant response to PGPR may be induced also in the absence of any physical contact with plants via VOCs emissions. In P-deficient conditions, *Arabidopsis thaliana* enhanced salicylic acid and jasmonic acid mediated immunity and hyper-sensitivity to phosphate deficiency, under the influence of a VOC-type diacetyl, synthesized by *B. amyloloquefaciens* strain GB03 (Morcillo et al., 2020b).

4. Conclusions and prospects

Under changing environmental conditions, the need to produce appropriate amounts of plant biomass is a serious challenge. Numerous microorganisms that inhabit the root/rhizoplane interface as well as the soil surrounding the roots are capable of beneficially influencing plant growth and enhancing plant biomass production. The potential of rhizobacteria to promote health, growth, and development of plants, which predominantly occurs as a result of bacterial activities to enhance the availability of nutrients, synthesis of phytohormones, and decrease pathogenic infections, is of significant importance, especially under abiotic stress conditions. The potential of microorganisms to support and improve plant growth under unfavorable environmental conditions is still underestimated. Therefore, more studies are needed to better understand the mechanisms of plant-microbe interactions, and the pathways of their bilateral "molecular dialogue" under both abiotic and biotic stress conditions. Based on that knowledge, new biotechnological products may be developed and innovative solutions may be introduced that exploit plant-beneficial bacteria for biological control of plant diseases (biopesticides) and for plant growth promotion (biofertilizers) for sustainable agricultural practices and phytoremediation (Mesa-Marín et al., 2020).

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6. Acknowledgments

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Author contributions

Ewa Oleńska, Sofie Thijs, Jaco Vangronsveld, Wanda Małek: Conceptualization, Ewa Oleńska, Wanda Małek, Małgorzata Wójcik: Original draft preparation, Ewa Oleńska, Izabela Swiecicka: Visualization, Jaco Vangronsveld: Supervision, Ewa Oleńska, Wanda Małek, Małgorzata Wójcik, Izabela Swiecicka, Sofie Thijs, Jaco Vangronsveld: Reviewing and Editing

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

List of Tables and Figures

Table 1. Examples of plant growth promoting rhizobacteria and features alleviating abiotic stress in plants

Plant	Bacterium	Abiotic stressor	Feature of plant growth promotion[#]
Alyssum bertolonii	*Staphylococcus* spp., *Microbacterium* spp., *Pseudomonas* spp.	nickel pollution	siderophores
Acacia gerrardii	*Bacillus subtilis*	sodium chlorite excess	IAA
Brassica juncea	*Azotobacter chroococcum* strain HKN-5	chromium pollution	nitrogen fixation
	Pseudomonas spp.	chromium pollution	siderophores, IAA
	Achromobacter xylosoxidans	copper pollution	P-solubilisation, IAA
Brassica napus	*Mycobacterium* spp. strain ACC14	cadmium, nickel, and copper pollution	siderophores, IAA
	Pseudomonas chlororaphis strain SZY6	copper pollution	ACC deaminase, P-solubilisation, siderophores, IAA
Brassica oxyrrhina	*Pseudomonas* spp. strain SR12	nickel pollution	ACC deaminase, P-solubilisation, siderophores, IAA
Cicer arietinum	*Pseudomonas* spp.	nickel pollution	siderophores
	Serratia spp.	nutrient deficience	IAA
Cucumis sativus	*Trichoderma asperellum*	sodium chlorite pollution	IAA, GA, ABA
Helianthus annuus	*Bacillus weihenstephanensis* strain SM3	copper, zinc, and nickel pollution	P-solubilisation, IAA
Oryza sativa	*Methylobacterium oryzae* strain CBMB20	nickel, and cadmium pollution	ACC deaminase,
Pisum sativum	*Pseudomonas marginalis* strain Dp1	cadmium pollution	nutrient uptake, ACC deaminase
Ricinus communis	*Pseudomonas* spp.	nickel, zinc, and copper pollution	ACC deaminase, siderophores, IAA
Salix caprea	*Serratia marcescens*	cadmium, zinc, and lead pollution	siderophores, IAA
Solanum nigrum	*Bacillus* spp. strain SLS18	cadmium pollution	siderophores, IAA, ACC deaminase
Sorghum vulgare var. *sudanense*	*Bacillus* spp. strain J119	cadmium pollution	siderophores, IAA, ACC deaminase
Thlaspi goesingense	*Methylobacterium* spp.	nickel pollution	siderophores, IAA
Trifolium repens	*Bacillus cereus*	iron, manganese, zinc, and cadmium pollution	IAA, nutrient uptake
Trifolium pratense	*Brevibacillus* spp.	lead pollution	IAA
Triticum aestivum	*Bacillus lycheniformis*	sodium chlorite excess	IAA
Vigna radiata	*Pseudomonas putida* strain KNP9	cadmium, and lead pollution	siderphores
Vinca rosea	*Bacillus megaterium*	ickel pollution	IAA
Vitis vinifera	*Bacillus lycheniformis*, *Pseudomonas fluorescens*	flooding	ABA
Zea mays	*Burkholderia* spp. strain J62, *Leifsonia* spp., *Bacillus* spp.	cadmium, and lead pollution	IAA, siderophores, ACC deaminase

Based on References: ~~Braud et al. 2009~~, Rajkumar et al., 2009;~~,~~ Glick, 2014~~0~~;~~,~~ ~~Rajkumar et al. 2010~~, Ma et al., 2011;~~,~~ Rajkumar et al., 2012;~~,~~ Salomon et al., 2014;~~,~~ Zhao and Zhang, 2015;~~,~~ Hashem et al., 2016;~~,~~ Zaheer et al., 2016;~~,~~ Ahmad et al., 2016;~~,~~ Egamberdieva et al., 2017;~~,~~ Khan et al., 2017;~~,~~ Singh and Jha, 2019;~~,~~ Kudoyarova et al., 2019

Figure 1. Distribution of rhizobacteria and their mechanisms of improvement plant growth and development

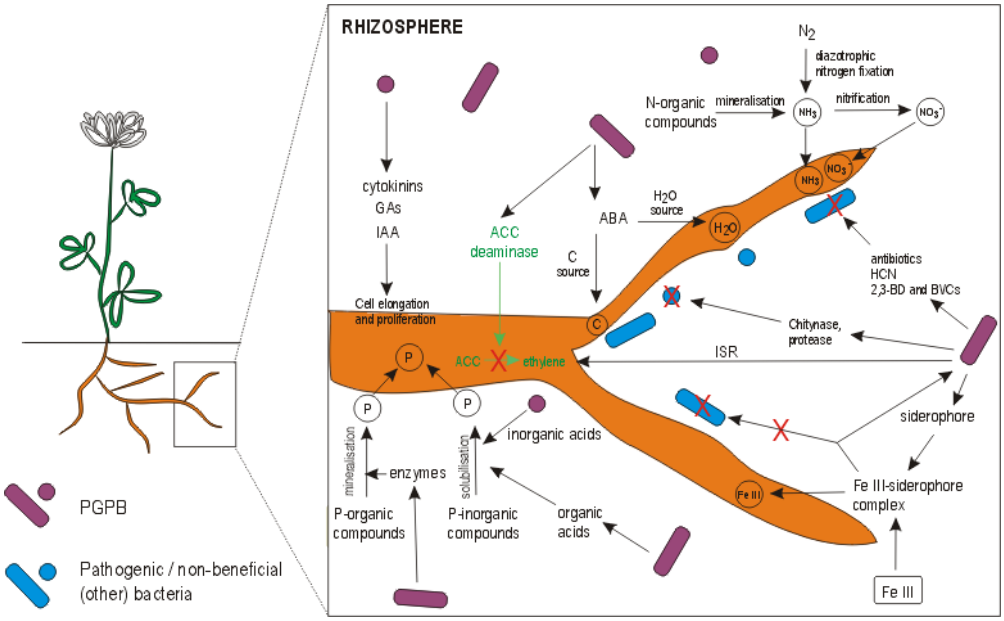

Figure 2. Examples of main categories of siderophores: (A) enterobactin as catecholate, (B) desferrioxamine B as hydroxamate, and (C) staphylloferrin A as (α-hydroxy)-carboxylate

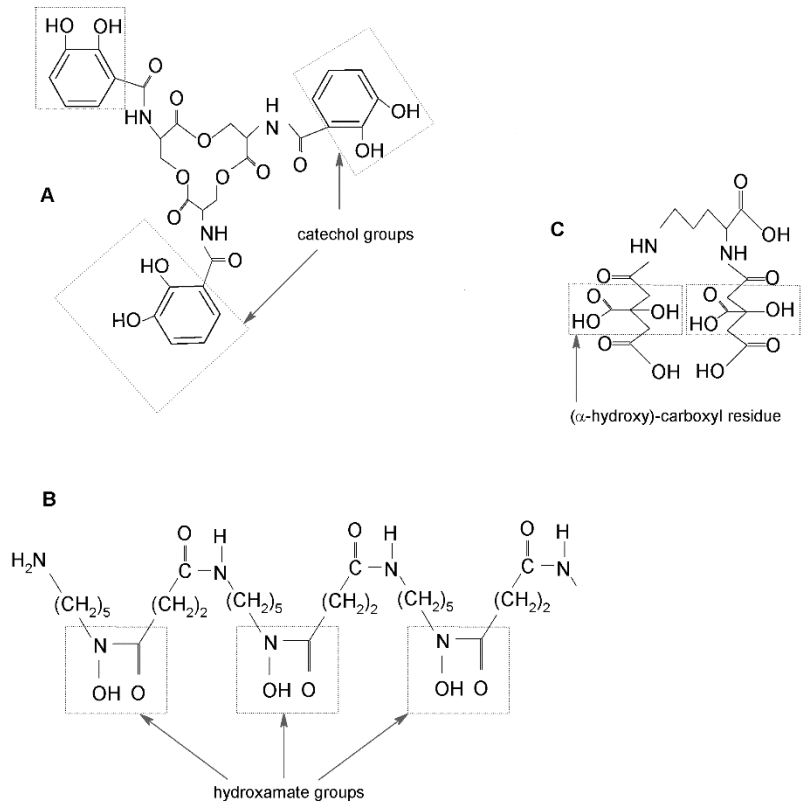

Figure 3. Scheme of tryptophan-dependent pathways of IAA biosynthesis in bacteria. Numbers in circles correspond to: 1 – nitrile hydratase, 2 – tryptophan monooxygenase, 3 – tryptophan decarboxylase, 4 – nitrilase, 5 – indole-3-acetamide (IAM) hydrolase, 6 – amine oxidase, 7 – aminotransferase, 8 – IPDC, indole-3-pyruvate decarboxylase, 9 – indole-3-acetaldehyde (IAAld) dehydrogenase. Based on Patten and Glick, 1996; Spaepen and Vanderleyden, 2011; Lin et al., 2015; Goswami et al., 2016

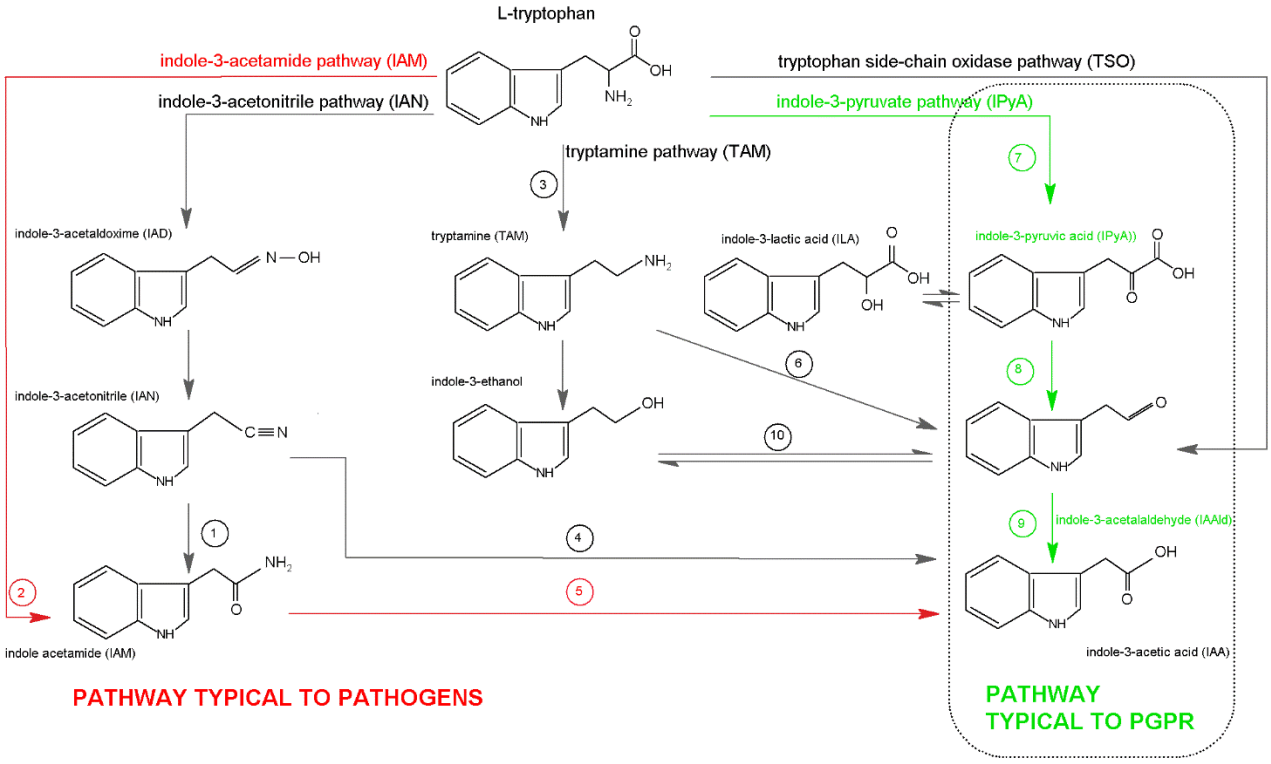

Figure 4. Pathway of gibberellins synthesis in bacteria. Numbers in circles correspond to: 1 – *ent*-copalyl diphosphate synthase, 2 – *ent*-kaurene synthase, 3 – *ent*-kaurene oxidase, 4 – *ent*-kaurenoic acid oxidase, 5 – 20-oxoglutarate-dependent dioxygenase, 6 – 3-oxidase, 7 – cytochrome 450 monooxygenase 1, 8 – cytochrome 450 monooxygenase 2. Abbreviations correspond to: GGPP – geranyl-geranyl diphosphate, CPP – *ent*-copalyl diphosphate. Based on Hayashi et al., 2014; Salazar-Cerezo et al., 2018

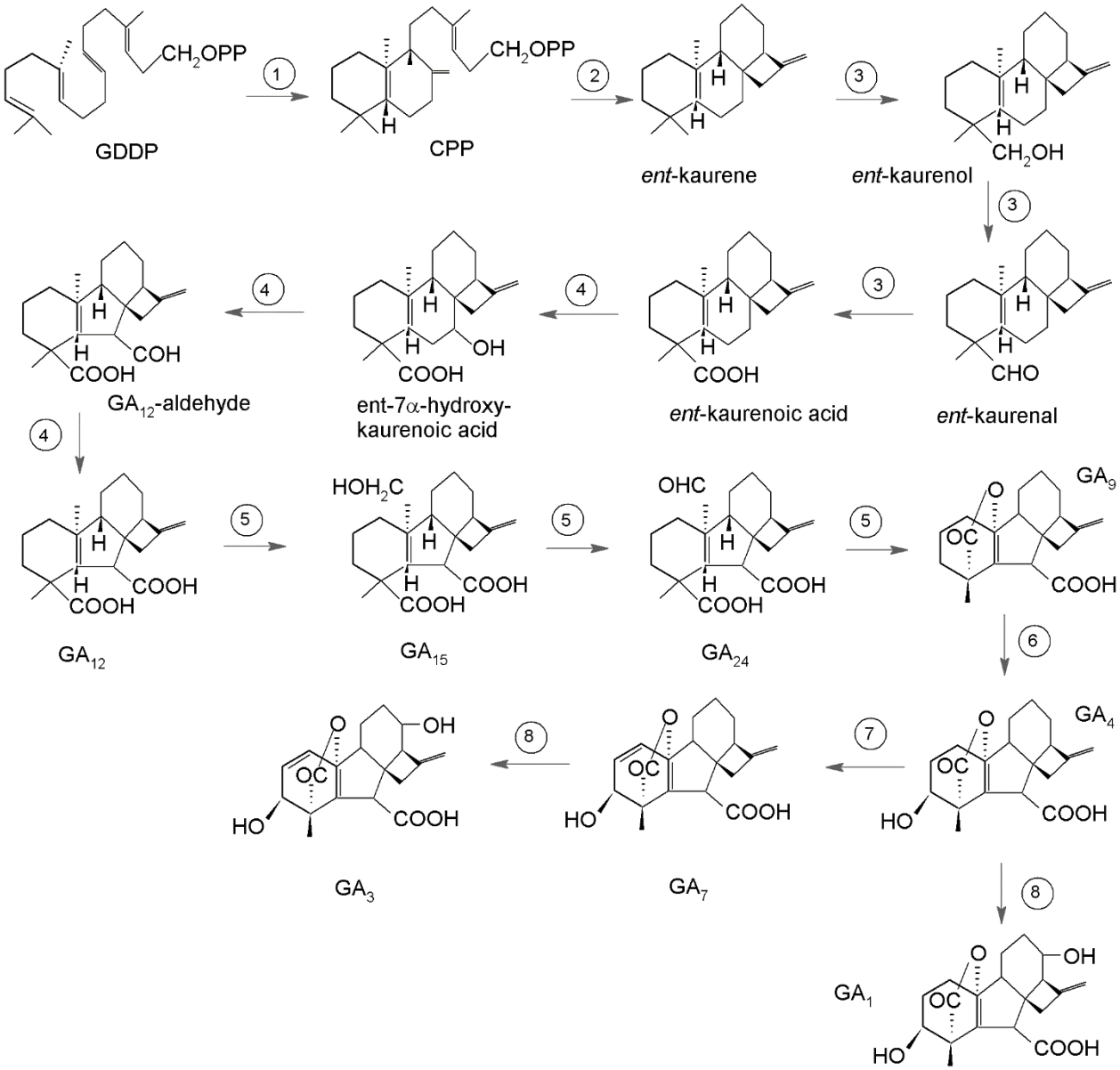

Figure 5. Ethylene biosynthesis in plants and the mechanisms of affecting this pathway by bacteria: 1 – suppression of a ACC synthetase by a rhizobitoxine, and 2 – degradation of ethylene intermediate ACC with ACC deaminase. Numbers in circles correspond to: 1 – aspartokinase (AspK), 2 – aspartate semildehyde dehydrogenase (AspSD), 3 – homoserine dehydrogenase (HSD), 4 – cystathionine β-synthase, 5 – β-cystathionase, 6 – methionine synthetase, 7 – S-adenosylmethionine (SAM) synthase, 8 – 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, 9 – ACC oxidase. Based on Yashuta et al., 1999; Sugawara, 2006; Ong et al., 2015

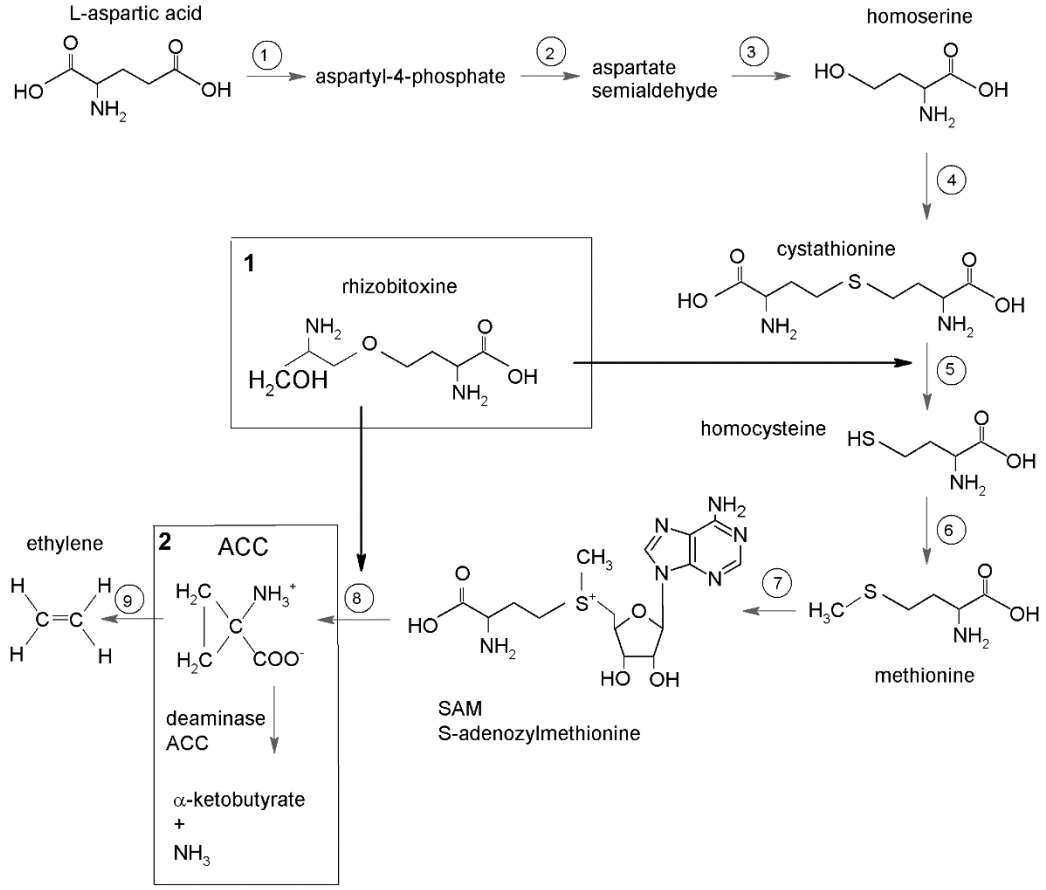

Figure 6. Simplified diagram of 2,3-butanediol biosynthesis in bacteria. Numbers in circles correspond to: 1 – α-acetolactate synthase (ALS), 2 - α-acetolactate decarboxylase (ALDC), 3 – 2,3-butanediol dihydrogenase (acetoin reductase). Based on Ji et al., 2011; Kandasamy et al., 2016; Ji et al., 2018