

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

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

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7 **Highlights**

8 Bacteria facilitate plant growth under stressful environmental conditions.

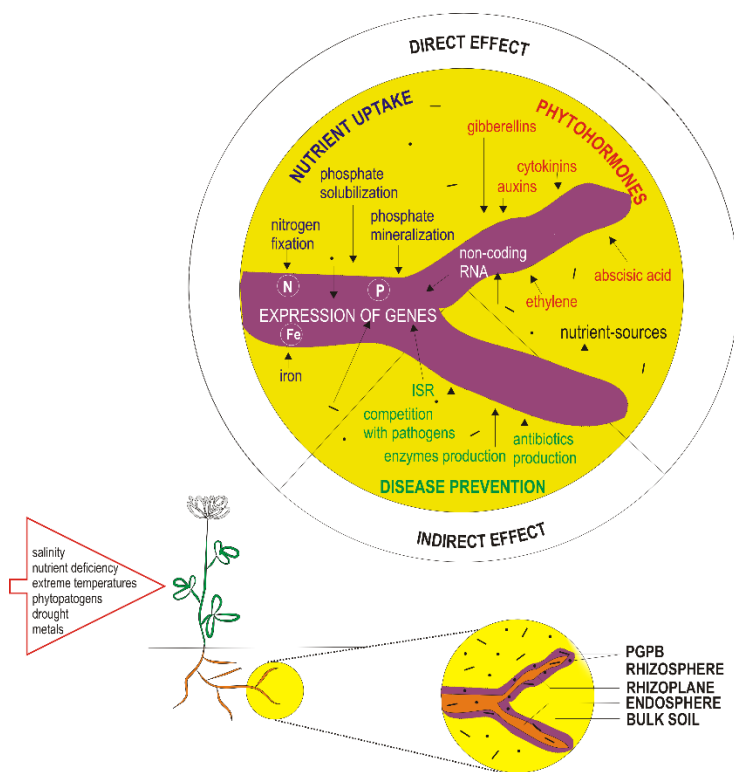
9 Direct and indirect mechanisms are involved in improvement of plant growth and development.

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

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

12
13 **Abstract**

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



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

31 **1. Introduction**

32 The supply of appropriate quantity and quality of food, as well as feed for animals, biomass as a feedstock for biofuel
 33 production and other industrial processes encounter various challenges of abiotic, biotic, and anthropogenic (*e.g.*,
 34 pollution and climate change) origin. The limited resources and non-renewable nature of soil services, makes soils the
 35 most vulnerable ecosystems that are under great pressure, especially in tropical, semiarid, and arid regions of our planet,
 36 resulting in extreme poverty and hunger in many developing countries. The Food and Agriculture Organization of the
 37 United Nations (FAO) reported that the number of undernourished people in the world is still growing; in 2017 it reached
 38 21% of the African population (256 millions people) and 11.4% in Asia (515 millions people) (FAO, IFAD – International
 39 Fund for Agricultural Development, UNICEF – United Nations Children’s Fund, WFP – World Food Programme, WHO
 40 – World Health Organization, 2018). Moreover, it was estimated that approximately 34% of the population in Ethiopia
 41 has to survive with less than US\$1.90 per person per day (World Bank, 2017; Silva et al., 2019).

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

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

51 In order to mitigate these harmful factors and also enhance the plant biomass production, many different innovative and
52 smart farming technologies, such as smart irrigation systems (*e.g.* controlled-release drip-irrigation), integrated
53 fertilization, biocontrol techniques for plant diseases, and environmentally friendly microbial biotechnologies have been
54 developed (Bargaz et al., 2018). In addition, different microbial-based approaches, in the form of biofertilizers,
55 biostimulants, and/or biopesticides are currently proposed as alternatives for improving crop yield. A particular group of
56 microorganisms, termed plant growth-promoting rhizobacteria (PGPR), positively influence plant growth, and represent
57 promising sustainable solutions to increase plant biomass production (Thijs and Vangronsveld, 2015; Lindemann et al.,
58 2016; Umesha et al., 2018; Liu et al., 2020). PGPR also have the ability to counteract most of the aforementioned problems
59 and disadvantages of modern agriculture.

60 Bacteria are a dominant group in the soil microorganism community; approximately one gram of soil contains 10^8 - 10^9
61 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
62 (Rughöft et al., 2016). Their diverse metabolism and capacity to use a wide range of different substances as nutrient and
63 energy sources, makes bacteria important partners in interaction with plants. Bacteria that positively affect plant growth
64 are categorized as plant growth-promoting bacteria (PGPB), often interchangeably called plant health-promoting bacteria
65 (PHPB). They are represented by both (i) endophytes localized inside plant cells (iPGP – intracellular PGP), vascular
66 tissues (Weyens et al., 2009a), or seeds (Truyens et al., 2015; Sánchez-López et al., 2018), and (ii) bacteria localized
67 outside cells (ePGP – extracellular PGP), including endophytes living between cells of plant tissues (Mastretta et al.,
68 2009; Tuyens et al., 2015), rhizoplane (on the root surface), rhizosphere soil (thin soil layer around the roots) (Backer et
69 al., 2018), or phyllosphere (leaves and stems) (Weyens et al., 2009b).

70 The bacterial mechanisms of plant growth promotion and communication are still being studied (Bharti et al., 2016).
71 There is a diverse number of PGPR-induced changes in plants, and the promotion of growth is most likely a result of a
72 complex combination of a plethora of pathways, which affect both plant development and nutrition (Bharti et al., 2016).
73 PGPB exert positive effects on plant growth both in direct and indirect ways (Weyens et al., 2009b; Asad et al., 2019).
74 Plant growth under the rhizobacteria influence is a multigene process, which is specific to the individually participating
75 bacteria and plants. This “additive hypothesis” is a complex phenomenon that involves a cumulative effect of changes in
76 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 flg22⁴¹⁷ 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

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

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

127

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

129 *2.1. PGPR that enhance the availability of nutrients essential to plant growth*

130 Drought, extreme temperature events, salinity, flooding, ultraviolet irradiation, and heavy metal pollution are abiotic
131 stress factors of high concern mainly because of their unfavorable effects on plant growth, which ultimately lead to serious
132 reductions in yield. Bacterial involvement in increasing abiotic stress tolerance and enhancing defense responses in plants
133 exposed to different stressors has been widely studied (Table 1) (Rajkumar et al., 2012; Salomon et al., 2014; Zhao and
134 Zhang, 2015; Ma et al., 2016; Hashem et al., 2016; Egamberdieva et al., 2017; Kudoyarova et al., 2019; Jatan et al., 2019;
135 Safdarian et al., 2019; Bruno et al., 2020; Shreya et al., 2020; Ramirez et al., 2020; Javed et al., 2020). Numerous studies
136 have investigated plant-microbe interactions under heavy metal stress conditions (Glick, 2014; Wu et al., 2016; Ma et al.,
137 2016; Kong and Glick, 2017; Paredes-Páliz et al., 2018; Sánchez-López et al., 2018; Raklami et al., 2019; Bellabarba et
138 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.*

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

173 Atmospheric nitrogen (N₂), comprising almost 78% of the atmosphere, can be transformed into ammonia due to natural
174 events (e.g. lightning, fires) but most of what is transferred to the biota is biologically fixed by diazotrophs (Mus et al.,
175 2016; Smercina et al., 2019). Diazotrophic microorganisms transform the diatomic trivalent N₂ molecule into ammonia
176 (NH₃), that is useful and available to most organisms, using a nitrogenase enzyme complex consisting of two components,
177 nitrogenase and nitrogenase reductase (Mahmud et al., 2020).

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

184 Rhizobia are Gram-negative bacteria of the family *Rhizobiaceae* (class α - and β -*Proteobacteria*, order *Rhizobiales*),
185 which mainly colonize roots of legumes (Andrews and Andrews, 2017) and improve the growth of their host plant in
186 nitrogen limited conditions. Rhizobia are taxonomically highly diverse; they include about 98 species belonging to 13
187 different genera and can be subdivided into two groups: (1) common “true” rhizobia covering *Azorhizobium* spp.,
188 *Bradyrhizobium* spp., *Ensifer* spp. (syn. *Sinorhizobium*), *Mesorhizobium* spp., and *Rhizobium* spp. (Hayat et al., 2010),
189 and (2) “new rhizobia” represented by *Burkholderia* spp. (*B. caribensis*, *B. cepacia*, *B. mimosarum*, *B. nodosa*, *B.*
190 *phymatum*, *B. sabiae*, *B. tuberum*), *Cupriavidus* spp. (*C. taiwanensis*), *Devosia* spp. (*D. neptuniae*), *Methylobacterium*
191 spp. (*M. nodulans*), *Microvirga* spp. (*M. lupini*, *M. lotononidis*, *M. zambiensis*), *Ochrobactrum* spp. (*O. cytisi*, *O. lupini*),
192 *Phyllobacterium* spp. (*P. trifolii*, *P. leguminum*, *P. ifriqiyense*), and *Shinella* spp. (*S. kummerowiae*), which achieved
193 legume nodulation capabilities as a result of horizontal gene transfer (Gnat et al., 2015; Andrews and Andrews, 2017).
194 The rhizobia-plant cooperation is one of the best known examples of symbiosis in nature. Whereas rhizobia provide plants
195 with nitrogen by fixing N₂ solely in a symbiotic association with leguminous host plants, visible as nodules, the host plant
196 supplies the microorganisms with nutrients and offers favorable conditions for their development. In fact, almost 70% of
197 biologically fixed N₂ derives from symbiosis of rhizobia with leguminous plants, and rhizobia provide up to 90% of the
198 nitrogen required by these plants (Mus et al., 2016).

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

201 available ones or affecting the root nutrient transport systems (Calvo et al., 2019). It was documented that PGP *Bacillus*
202 spp. mixtures, composed of different *Bacilli* species, trigger the expression of genes determining nitrate (NO₃⁻) and
203 ammonium (NH₄⁺) uptake and transport and enhance host-plant growth and development in *Arabidopsis thaliana*. *Bacilli*-
204 inoculated *A. thaliana* showed significantly higher transcript levels of nitrate transporters NRT1 (AtNRT1), NRT2
205 (AtNRT2), and ammonium transporter AMT1 (AtAMT1), which were accompanied with enhanced nutrient uptake and
206 plant growth. Liu et al. (2017) received similar results in *Arabidopsis* when inoculating *B. subtilis* strain GB03. Jang et
207 al. (2018) suggested that improved growth of plants induced by associated PGPR may be partially achieved by improved
208 accessibility and acquisition of nitrogen. Improved nitrogen accessibility, P-solubilization and auxins synthesis were
209 documented in peanut *Arachis hypogaea* inoculated with a consortium of diazotrophic root-origin bacteria isolated from
210 the halophyte *Arthrocnemum indicum*. Inoculation of *Klebsiella* spp., *Pseudomonas* spp., *Agrobacterium* spp., and
211 *Ochrobacterium* spp., lead to enhanced salt-tolerance in peanut plants, which was accompanied with low level of reactive
212 oxygen species (ROS) that are considered beneficial under stress conditions (Sharma et al., 2016).

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

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

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

259 2.1.2. Phosphorus

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

263 development (Razaq et al., 2017). However, at the same time, the concentration of P in the soil solution, which is available
264 for plant uptake is very limited. The mean total concentration of phosphorus in the Earth's crust is about 1200 mg P kg⁻¹
265 (0.01-0.2% P₂O₅) (Tiessen, 2008; Tang et al., 2018). Over 99% of the naturally occurring phosphorus exists in an
266 inorganic form (Pi), deposited as insoluble phosphate rocks such as sedimentary rocks (about 39% P₂O₅), igneous rocks
267 (about 2.0% P₂O₅), and metamorphic rocks (about 1.3% P₂O₅). The remainder of naturally occurring phosphorus exists
268 in its organic form (Po). However, only about 4% of the total phosphorus in soil is available to plants in its orthophosphate
269 form (Alori et al., 2017). Inorganic forms of phosphorus account for 35-70% of total phosphorus in soil (Guignard et al.,
270 2017), and the solubilization of phosphates, e.g. dicalcium phosphate, tricalcium phosphate, or hydroxyl apatite, is
271 performed mainly by bacterial strains belonging to the genera *Achromobacter* spp., *Aerobacter* spp., *Agrobacterium* spp.,
272 *Azotobacter* spp., *Bacillus* spp., *Burkholderia* spp., *Cladosporium* spp., *Enterobacter* spp., *Erwinia* spp., *Flavobacterium*
273 spp., *Micrococcus* spp., *Pseudomonas* spp., *Bradyrhizobium* spp., *Rhizobium* spp. (De Boer et al., 2019). Inorganic
274 phosphate solubilizing bacteria (iPSB) are of great interest due to their promising effect as bio-fertilizers on plant growth
275 and yield, as well as soil fertility (Suleman et al., 2018; Emami et al., 2020). Peix et al. (2015) reported the significant
276 influence of *Mesorhizobium mediterraneum* bacteria present in soil on the growth and phosphorus content in chickpea
277 and barley plants. Likewise, *Rhizobium* spp. and *Bradyrhizobium* spp. promote the growth of legumes, even when rhizobia
278 remain in non-symbiotic conditions.

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

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

315 In salt-affected soils, inoculation with phosphate solubilizing halotolerant bacteria, improves plant growth, and suppresses
316 the adverse effects of salt (Etesami and Beattie, 2018). *Avicennia marina*, a halotolerant mangrove, and rhizosphere-
317 associated bacteria such as *Arthrobacter* spp., *Bacillus* spp., *Azospirillum* spp., *Vibrio* spp., *Phyllobacterium* spp.,
318 *Oceanobacillus picturae*, were shown to solubilize Ca₃(PO₄)₂, AlPO₄, and FePO₄. Thant et al. (2018) revealed that the
319 growth and phosphate solubilizing abilities of *Bacillus megaterium* were substantially higher due to their adaptation to
320 sodium chloride stress, while *B. aquimaris* inoculated wheat showed a higher P content under salinity stress in the field
321 (Upadhyay and Singh, 2015). Srivastava and Srivastava (2020) showed good growth of *Arabidopsis thaliana* inoculated
322 with the PSB *Pseudomonas putida* strain MTCC 5279 under salt stress and P-deficiency conditions. Besides the
323 significantly higher biomass of *A. thaliana* inoculated with *P. putida* MTCC 5279 higher acidic and alkaline phosphatases

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

334 About 30-65% of the total phosphorus in soil is present in organic form (Po), which is released from organophosphates
335 by bacteria due to mineralization processes (Alori et al., 2017). For example, strains *Arthrobacter* spp., *Bacillus* spp.,
336 *Citrobacter* spp., *Delftia* spp., *Enterobacter* spp., *Klebsiella* spp., *Phyllobacterium* spp., *Proteus* spp., *Pseudomonas* spp.,
337 *Rhizobium* spp., *Rhodococcus* spp., *Serratia* spp. are able to enzymatically hydrolyze the P-organic substrates into
338 inorganic forms. Three types of enzymes are involved in this process, (i) non-specific acid phosphatases (NSAPs),
339 represented predominantly by acid and alkaline phosphomonoesterases (phosphatases), which dephosphorylate
340 phosphoester and phosphoanhydride bonds of organic matter, (ii) phytases able to degrade phytate, and (iii)
341 phosphonates and C-P lyases, that cleave C-P bond of organophosphonates (Sharma et al., 2013; Jain et al., 2016; Alori
342 et al., 2017). Phytases (myo-inositol hexakisphosphate phosphohydrolases) catalyze the conversion of organic phosphorus
343 from phytate (inositol hexakisphosphate) to inorganic phosphorus, which can be easily taken up by plants (Azeem et al.,
344 2014). It was found that phytases are produced by *Enterobacter* spp., *Serratia* spp., *Citrobacter braunii*, *Rhizobium* spp.,
345 *Pseudomonas* spp., *Proteus* spp., and *Klebsiella* spp. (Kumar et al., 2016). The activity of bacterial phytases is pH-
346 dependent. Specifically for *Bacillus* spp. the optimum activity of phytase is at a pH between 6.0 and 8.0. Functional
347 metagenomics of red rice crop residues led to the identification of the PhyRC001 sodium phytate hydrolyzing enzyme,
348 which has an optimal activity at pH 7.0 and 35°C (Farias et al., 2018). An *Arabidopsis thaliana* mutant over-expressing
349 bacterial phytase PHY-US417 showed a significantly higher osmotolerance to sodium chloride in comparison to the
350 reference and knock out mutant (Belgaroui et al., 2018; Valeeva et al., 2018). A significant reduction of the phytase
351 activity of *Enterobacter sakazakii*, *Enterococcus hirae*, or *Bacillus subtilis* strain B.S.46 was detected due to exposure to
352 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).

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

355 on plant genes expression; 152 genes were up-regulated, and down-regulation was found for five genes (Safdarian et al.,
356 2019). It concerned the genes involved in phenylpropanoid biosynthesis, porphyrin metabolism, cysteine and methionine
357 metabolism, flavonoids biosynthesis, and pathways of biosynthesis of secondary metabolites. *A. nitroguajacolicus*
358 increases the tolerance of wheat to sodium chloride stress due to up-regulation of antioxidative enzymes genes cytochrome
359 P450, ascorbate peroxidase (APX), and also genes encoding for nicotianamine (NAS), and ABC transporters (Safdarian
360 et al., 2019).

361 2.1.3. Iron

362 Under stress conditions, siderophores synthesis is one of the major bacterial mechanisms of supplying plants with
363 available forms of iron (Fe) (Jian et al., 2019). Iron plays a role in chlorophyll synthesis and in the maintenance of
364 chloroplast structure and function, it has key roles in DNA synthesis and respiration, and acts as a prosthetic group
365 constituent of many enzymes, including those involved in redox reactions (Rout and Sahoo, 2015). Despite its huge
366 abundance in the lithosphere (it is the fourth most common element in Earth's crust by weight), the plant availability of
367 Fe is very limited due to its low solubility (Hider and Kong, 2010; Zhang, X. et al., 2019). In aerobic conditions, iron
368 exists as ferric Fe(III) ions which accumulate in mineral phases as highly stable hydroxide [Fe(OH)₃] and oxyhydroxide
369 [FeO(OH)] complexes, leading to free Fe(III) concentrations in soils of 10⁻⁹-10⁻¹⁸ M, which are not sufficient to meet the
370 needs of plants (Rout and Sahoo, 2015).

371 To cope with this situation, plants have evolved two different strategies for iron acquisition from the soil (Tripathi et al.,
372 2018; Zhang, X. et al., 2019). In the first strategy (reduction-based strategy), which is characteristic for non-graminaceous
373 plants, protons and phenolic compounds are released by plant roots into the rhizosphere to increase its acidification and
374 promote Fe(III) solubility. Subsequently, Fe(III) ions are reduced to the more soluble Fe(II) ions by ferric reduction
375 oxidases (FRO) at the apoplast and in this form the iron is imported into root cells by the iron-regulated transporter (IRT1).
376 The second strategy (chelation-based strategy) is used by graminaceous plants only. In response to Fe deficiency, these
377 plants release into the rhizosphere phytosiderophores (PS) with a high affinity for binding Fe(III). The resulting Fe(III)-
378 PS complexes are readily transported into the root epidermis through the yellow stripe (YS) or yellow stripe-like (YSL)
379 transporters. The most common phytosiderophores are synthesized from three S-adenosyl-methionine molecules and
380 belong to the family of mugineic acid (MAs), with the best known member mugineic acid (MA), 2'-deoxymugineic acid
381 (DMA), 3-epihydroxymugineic acid (epi-HMA), and 3-epihydroxy 2'-deoxymugineic acid (epi-HDMA) (Masuda et al.,
382 2019). The production of siderophores to increase the availability of iron in the soil is also a common mechanism adopted
383 by bacteria and resulting Fe(III)-siderophores can be an excellent source of iron for plants too (Kramer et al., 2020).
384 Phytosiderophores consist of carboxyl, amine, and hydroxyl groups as the ligand functional groups, while most microbial
385 siderophores have hydroxamate or phenolate groups as Fe(III)-coordination donors (Ahmed and Holmström, 2014). There

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

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

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

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

417 the expression of genes related to development and iron acquisition, and down-regulation of the expression of defense-
418 related genes such as transcription factors ERF, WRKY, MYB, salicylic acid (SA)-related gene (such as *AT5G24210*,
419 which encodes protein belonging to the lipase class 3 protein family), and an abscisic acid (ABA)-related gene (encoding
420 the lipid transfer protein LTP3) (Trapet et al., 2016). Apo-pyoverdine was impaired in iron-regulated transporter1 (IRT1)
421 and ferric reduction oxidase2 (FRO2) knockout mutants and was prioritized over immunity, reflecting the increased
422 susceptibility to *Botrytis cinerea*. Due to this, an overexpression of the transcription factor HB11, a key node for the cross
423 talk between growth and immunity, was detected. In *P. fluorescens* strain WCS417 colonized *A. thaliana* many genes
424 were positively regulated, including *FIT*, *FRO2*, *IRT1*, and MYB72 transcription factor that regulates the biosynthesis of
425 iron-mobilizing phenolic compounds. In addition, the *BGLU42* and *PDR9* genes, whose products are involved in the
426 secretion of iron-mobilizing phenolic compounds under iron-limited conditions, were also upregulated (Verbon et al.,
427 2017). Similar iron-binding phenolic compounds are produced in *A. thaliana* in response to inoculation with *Paenibacillus*
428 *polymyxa* strain BFKC01 (Zhou et al., 2016).

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

440

441 **2.2. Rhizobacteria synthesizing phytohormones or influencing the hormone balance of the host plant**

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

447 *2.2.1. Auxins*

448 Beneficial effects of phytohormone-synthesizing PGP rhizobacteria on the reduction of abiotic stress in plants has been
449 widely reported (Ngumbi and Kloepper, 2014; Hashem et al., 2016). Numerous studies have demonstrated the significant
450 role of auxins, most notably indolyl-3-acetic acid (IAA). Auxins are powerful molecules produced naturally by plants and
451 involved in almost every aspect of plant physiology, controlling, amongst others, cell division, expansion, differentiation,
452 and alleviation of abiotic stress (Paque and Weijers, 2016). While auxins are key regulators of plant development, indolyl-
453 3-acetic acid (IAA) and its biosynthesis determining genes are also found in a wide range of different bacteria or fungi
454 (Matsuda et al., 2018). Although IAA can impact gene expression in some bacteria, it does not seem to function as a
455 factor in bacterial growth, but rather acts as a signal to communicate with plants in an ecological context to obtain profits
456 from improved plant growth. Moreover, IAA biosynthesis is used by some pathogenic bacteria to hijack plant
457 development. For example, it is involved in the formation of the crown galls induced by *R. radiobacter* in a range of plant
458 species.

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

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

489 It was reported that *Paenibacillus polymyxa* and *Azospirillum* spp. release both tryptophan, and auxin-type compounds
490 like TOL to the rhizosphere, which can indirectly improve plant growth (Lebuhn et al., 1997; El-Khawas and Adachi,
491 1999). At low concentrations, bacterial auxins stimulate elongation of primary plant roots, but at higher doses auxins
492 promote the formation of lateral and adventitious roots, which can enhance uptake of minerals, and increase the production
493 of root exudates that increase bacterial proliferation (Patten et al., 2013; Verbon and Liberman, 2016). Patten and Glick
494 (2002) found enhanced roots formation in canola (*Brassica napus*) developed from seeds inoculated with *Pseudomonas*
495 *putida* strain GR12-2 in comparison to plants inoculated with an IAA-deficient *P. putida* mutant. Moreover, bacteria-
496 derived auxins may prevent the deleterious effects of various environmental stresses, like drought, salinity, or soil
497 pollution (Kudoyarova et al., 2019). For example, Defez et al. (2019) reported that salt tolerance of *Medicago truncatula*
498 inoculated with IAA-overexpressing *Ensifer meliloti* strain DR-64 was enhanced in comparison with the plants inoculated
499 with the *E. meliloti* IAA-deficient mutant. Also, switchgrass inoculated with *Pseudomonas grimontii* strain Bc09, *Pantoea*
500 *vagans* strain So23, *Pseudomonas veronii* strain E03, and *Pseudomonas fluorescens* strain Oj24 under Cd stress
501 demonstrated increased biomass and IAA synthesis, as well as reduced Cd accumulation compared to reference plants
502 (Begum et al., 2019). An enhanced IAA production was observed in *Leifsonia xyli* strain SE134 under Cu exposure (Kang
503 et al., 2017). The halophilic *Leclercia adecarboxylata* strain MO1, which overproduces IAA, improves the growth and
504 salinity resistance of *Solanum lycopersicum* (Kang et al., 2019b). The IAA-overproducing *Rhizobium* strain RD64
505 protects *Medicago sativa* against drought, predominantly by the production of low molecular weight osmolites, such as
506 proline and pinitol (Defez et al., 2017). An increased IAA synthesis was observed in *Bacillus cereus* strain So3II and *B.*
507 *subtilis* strain Mt3b in a temperature gradient (Wagi and Ahmed, 2019). *B. licheniformis* strain HSW-16 mitigated salt
508 stress and stimulated the growth of *T. aestivum* in correlation with elevated IAA concentrations (Singh and Jha, 2016).
509 Similarly, *Enterobacter* spp. strain NIASMVII produced significant amounts of IAA that correlated with enhanced seed

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

526 2.2.2. Cytokinins

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

540 production by transferring the isopentenyl moiety from HMBDP (1-hydroxy-2-methyl-2(E)-butenyl 4-diphosphate) to
541 AMP (Wong et al., 2015).
542 Recently, the dual role of bacterial cytokinins include optimizing nutrient supply and modulating host immunity in plants
543 infected with pathogens was reported (Akhtar et al., 2020). Bacterial-origin cytokinins induced resistance against bacterial
544 pathogens in *Arabidopsis* (Grosskinsky et al., 2016). In the *Arabidopsis-Bacillus megaterium* system, plant cytokinin
545 recognition was responsible for *B. megaterium* properties that were beneficial to plants. As biocontrol agents, cytokinins
546 regulated the *P. fluorescens* strain G20-18 against *P. syringae* infection in *Arabidopsis* (Grosskinsky et al., 2016). The
547 exact mechanisms of cytokinin biosynthesis in bacteria is not yet fully elucidated. The proposed role of *miaA* is to encode
548 a tRNA $\Delta(2)$ -isopentenylpyrophosphate transferase similar to tRNAIPTs, which are responsible for cytokinin
549 biosynthesis (Stringlis et al., 2018b).

550 2.2.3. Gibberellins

551 Gibberellins (GAs) can alleviate abiotic stress and influence other physiological processes (Halo et al., 2015; Kang et al.,
552 2019a). This class of compounds is involved in a plethora of developmental processes in plants, including regulation of
553 seed dormancy, quiescence, germination, flowering, ripening of fruits, promotion of root growth, and root hair abundance
554 (Binebaun et al., 2018). Similarly to auxins and cytokinins, production of GAs is not restricted to plants, but is also a
555 common phenomenon in fungi and bacteria. However, there is no known function for GAs in these organisms; most
556 probably they play a role as signaling factors towards the host plants, *e.g.* in *Rhizobiaceae* symbiotic associations with
557 legumes (Nett et al., 2017a, b). Indeed, the first report on gibberellin characterization in bacteria concerned gnotobiotic
558 cultures of *Rhizobium meliloti* where the presence of GA1, GA4, GA9, and GA20 was demonstrated (Atzorn et al., 1988).
559 Since then, GA synthesis was confirmed in numerous rhizospheric bacteria, including *Acetobacter diazotrophicus*,
560 *Herbaspirillum seropedicae*, *Bacillus* spp., or *Azospirillum* spp. (Nett et al., 2017b; Nagel et al., 2018). To date, 136
561 different chemical structures have been characterized as naturally occurring gibberellins, of which GA3 (gibberellic acid)
562 is most often produced by bacteria. In *Bacteria* the gibberellins biosynthetic pathway starts from geranyl-geranyl
563 diphosphate (GGPP) transformation by *ent*-copalyl diphosphate synthase (CPS) to produce *ent*-copalyl diphosphate,
564 which is subsequently transformed by *ent*-kaurene synthase into *ent*-kaurene (Fig. 4). The oxidation of *ent*-kaurene at
565 position C-19 via *ent*-kaurenol and *ent*-kaurenal generates *ent*-kaurenoic acid, which is oxidized to *ent*-7 α -
566 hydroxykaurenoic acid. Finally, oxidation of *ent*-7 α -hydroxykaurenoic acid at C-6 β yields GA12-aldehyde. GA12-
567 aldehyde is subsequently converted in several steps to GA1 and GA3 (Tudzynski, 2005; Morrone et al., 2009; Hedden
568 and Thomas, 2012; Hershey et al., 2014; Nett et al., 2017a; b; Salazar-Cerezo et al., 2018).

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

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

589 2.2.4. Abscisic acid

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

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

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

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

623 In psychrophilic *Bacillus* spp. strains (CJCL2, RJGP41), the genes involved in cold stress tolerance, specifically genes
624 related to signal transduction pathways, antioxidative activity, and sugar-ABC transporters were identified and their
625 enhanced expression under cold stress conditions was documented. It was also shown that psychrophilic PGP *Bacillus*
626 spp. bacteria regulated cold stress response parameters in wheat and decreased the expression levels of ABA. They are
627 also involved in the expression of lipid peroxidation encoding genes and can increase expression of proline synthesis
628 genes. Psychrophilic *Bacillus* spp. strains are also able to upregulate the expression of genes encoding important plant
629 growth hormones such as auxin, cytokinin, alpha expansin, and ethylene under cold stress conditions (Zubair et al., 2019).
630 Bacteria can potentially influence plant growth through the usage of ABA as nutrients. Belimov et al. (2014) reported
631 that *Rhodococcus* spp. strain P1Y and *Novosphingobium* spp. strain P6W in association with plant roots may utilize ABA
632 as a carbon and energy source, decrease ABA concentrations of inoculated plants, and potentially alter plant growth.

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

640 2.2.5. Ethylene

641 Indole-3-acetic acid (IAA) accumulation in plants induces the transcription of 1-aminocyclopropane-1-carboxylate
642 (ACC) synthase genes, leading to increased ACC and ethylene levels (Gamelaro and Glick, 2015; Abts et al., 2017).

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

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

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

664 and Pandey, 2019). The ACCD was found as crucial enzyme in improving rice growth under salt and heavy metals stress
665 in the presence of the *Pseudomonas stutzeri* strain A1501 (Han et al., 2015). A *P. stutzeri* mutant in the ACCD encoding
666 gene (*acdS*) showed lack of ACCD activity and lower resistance to NaCl as well as to metal salts like NiCl₂ in comparison
667 with the wild type bacteria. Moreover, a mutation of *acdS* correlated with a lower dinitrogenase activity under NaCl stress,
668 as well as a lack of ability to promote host-plant growth in salt and metal stress conditions (Han et al., 2015). Jaemsaeng
669 et al. (2018) reported that inoculation of the ACCD producing endophyte *Streptomyces* spp. strain GMKU 336
670 significantly improved salt tolerance of rice plants by decreasing ethylene and reactive oxygen species, and balancing ion
671 content and osmotic pressure. The strain GMKU 336 significantly influenced stress response involved genes, e.g. *ACO1*
672 and *EREBP1* encoding enzymes involved in the ethylene pathway, which were down-regulated, whereas genes involved
673 in osmotic balance (*BADH1*), Na⁺ transporters (*NHX1*, *SOS1*), calmodulin (*Cam1-1*), antioxidant enzymes (*Cu/ZnSOD1*,
674 *CATb*), and *acdS* in *Streptomyces* spp. GMKU 336 were up-regulated (Jaemsaeng et al., 2018). Enhanced SOD activity
675 and growth parameters were detected in *Parastrephia quadrangularis* exposed to salt stress and inoculated with ACCD-
676 producing *Klebsiella* spp strains 8LJA and 27IJA (Acuña et al., 2019). Yet, ACCD-producing rhizobacteria associated
677 with *Panicum maximum* reduced salt and drought stress (Tiwari et al., 2018), similarly to ACCD-producing *Lactobacillus*
678 spp., *P. putida*, and *Azotobacter chroococcum* in respect to *Lactuca sativa* and *Raphanus sativus* (Hussein and Joo, 2018).

679

680 3. Increasing tolerance to biotic stresses

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

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

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

714 Fungistatic activity of beneficial bacteria may also be due to the synthesis of fungal cell-wall degrading enzymes, like
715 chitinase, β -1,3-glucanase, protease, or cellulase resulting in a direct inhibitory effect on the hyphal growth. For example,
716 β -1,3-glucanase produced by strains of *Paenibacillus* spp. and *Streptomyces* spp. suppressed the growth of *Fusarium*
717 *oxysporum*, while *Bacillus cepacia* destroyed soil borne fungi *Rhizoctonia solani* and *Sclerotium rolfsii* (Compant et al.,
718 2019). Moreover, non-pathogenic *Rhizobium* spp., *Azospirillum* spp., *Klebsiella pneumoniae*, *Yersinia* spp., and *Frankia*
719 spp. demonstrate pectinolytic capability.

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

726 pathogens that are sensitive to JA- and ET-dependent defense mechanisms. For example, *Bacillus amyloliquefaciens*
727 strain IN 937a bacteria present in the rhizosphere of *Arabidopsis* sp. induces ISR against the pathogenic *Erwinia*
728 *carotovora* (Ryu et al., 2004), *B. pumilus* strain SE34 protects against infectious *Pseudomonas syringae* (Ryu et al.,
729 2003a, b), and *Pseudomonas fluorescens* strain CHA0 shields against *Meloidogyne javanica* (Siddiqui and Saukat, 2004;
730 Annapurna et al., 2013). Important bacterial resistance-inducing elicitors are lipopolysaccharides, siderophores (*e.g.*
731 pseudobactins, pyochelin), antibiotics (*e.g.* pyocyanin, 2,4-diacetylphloroglucinol), N-acylhomoserine lactones or
732 volatile compounds (*e.g.* 2,3-butanediol) (Van Loon and Baker, 2005; Sharifi and Ryu, 2018a; Tyagi et al., 2018; Villena
733 et al., 2018; Romera et al., 2019). Inoculation of blackberries (*Rubus* sp.) with a plant growth promoting rhizobacterium
734 *Pseudomonas fluorescens* strain N21.4 triggered phenylpropanoids and flavonoid biosynthesis as a part of an ISR
735 defense pathway. Most likely, in the interaction of *P. fluorescens* strain N21.4 with blackberries the gibberellins pathway
736 is involved (Garcia-Seco et al., 2015). Inoculation of *Rubus* sp. with *P. fluorescens* strain N21.4 modulated plant gene
737 expression and affected biosynthesis of secondary metabolites. Under the N21.4 influence the plant genes encoding
738 enzymes involved in the conversion of phenylalanine to flavonols, anthocyanins, and catechins, and the regulatory genes
739 involved in controlling those enzyme activities, were identified. Furthermore, genes coordinating the expression of
740 flavonoid biosynthetic genes with the accumulation of anthocyanins, catechins, and flavanols in blackberry fruits were
741 determined (Garcia-Seco et al., 2015). In fruits of PGPR-associated blackberries, the PR proteins RuPR1, RuPR2 (β -1,3-
742 glucanase), RuPR3 (chitinase), and RuPR4 (unknown function) demonstrated significant differences in expression.
743 Increasing tolerance to pathogens is a common phenomenon related to the improvement of plant growth and health
744 through inoculation of beneficial microbes (Algar et al., 2014).

745 2,3-butanediol (2,3-BD) and its precursor acetoin (3-hydroxy-2-butanone, AC) (Fig. 6) were found as significant inducers
746 of ISR and helped improve plant growth (Ji et al., 2011; Sharifi and Ryu, 2018b). Both compounds are members of a
747 numerous group of volatile organic compounds (VOCs) that gather gas-phase low molecular weight hydrocarbons (<300
748 Da) of low boiling points and vapour pressure (0.01 kPa), which are emitted in a gaseous phase or secreted into liquids
749 (Ali et al., 2015; Audrain et al., 2015). Bacterial volatile compounds (BVCs) may play important roles in the bacterial
750 life cycle (*e.g.* regulation of bacterial motility, antibiotic resistance, biofilm formation), and their associations with host-
751 plants (*e.g.* increase biomass, fruit yield, seed production, lateral root and root hair formation, nutrient uptake, and
752 photosynthetic activity (Sharifi and Ryu, 2018a; b; Morcillo et al., 2020a; b). 2,3-BD and AC are involved in ISR in
753 tobacco (Wang et al., 2009). 2,3-BD significantly reduced symptoms caused by fungal and bacterial pathogens, which
754 was positively correlated with enhanced expression of basic PR genes in the JA pathway (Cortes-Barco et al., 2010 a; b).
755 2,3-BD was also reported to be implicated in ISR also in *Arabidopsis* sp. and pepper (Choi et al., 2014). Furthermore,
756 acetoin synthesized by *Bacillus subtilis* strain FB17 as inoculum of *Arabidopsis thaliana*, was found to be an ISR inducer,

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

762 4. Conclusions and prospects

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

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1495

1496 **Author contributions**

1497 Ewa Oleńska, Sofie Thijs, Jaco Vangronsveld, Wanda Małek: Conceptualization, Ewa Oleńska, Wanda Małek,
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1502 **Declaration of interests**

1503 The authors declare that they have no known competing financial interests or personal relationships that could have
1504 appeared to influence the work reported in this paper.

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1516 **List of Tables and Figures**1517 **Table 1.** Examples of plant growth promoting rhizobacteria and features alleviating abiotic stress in plants

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

1518 # Based on References: Braud et al., 2009; Rajkumar et al., 2009; Glick, 2014; Rajkumar et al., 2010; Ma et al., 2011;
1519 Rajkumar et al., 2012; Salomon et al., 2014; Zhao and Zhang, 2015; Hashem et al., 2016; Zaheer et al., 2016; Ahmad
1520 et al., 2016; Egamberdieva et al., 2017; Khan et al., 2017; Singh and Jha, 2019; Kudoyarova et al., 2019

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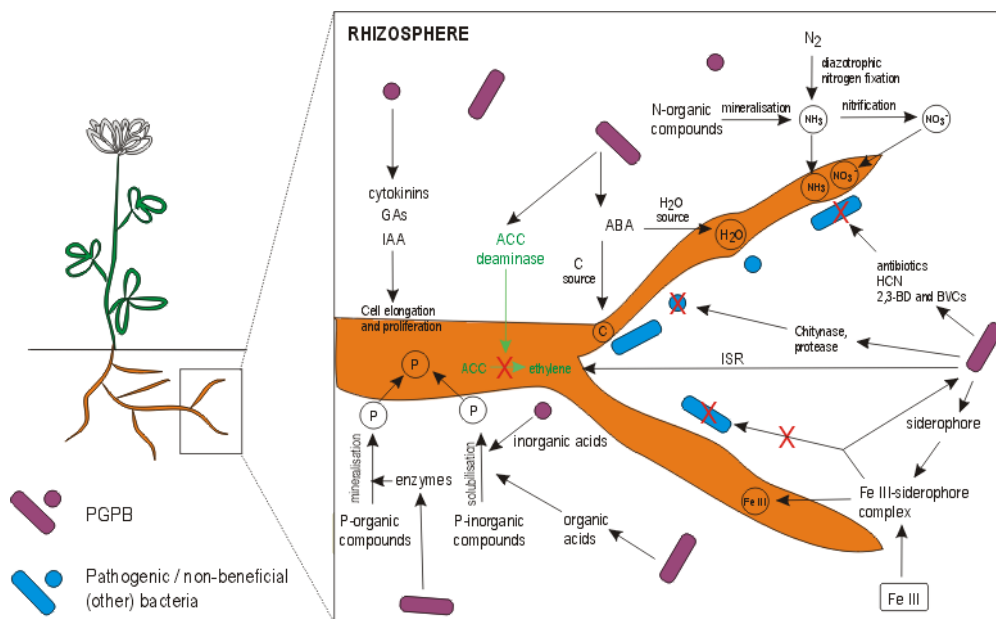
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1526 **Figure 1.** Distribution of rhizobacteria and their mechanisms of improvement plant growth and development

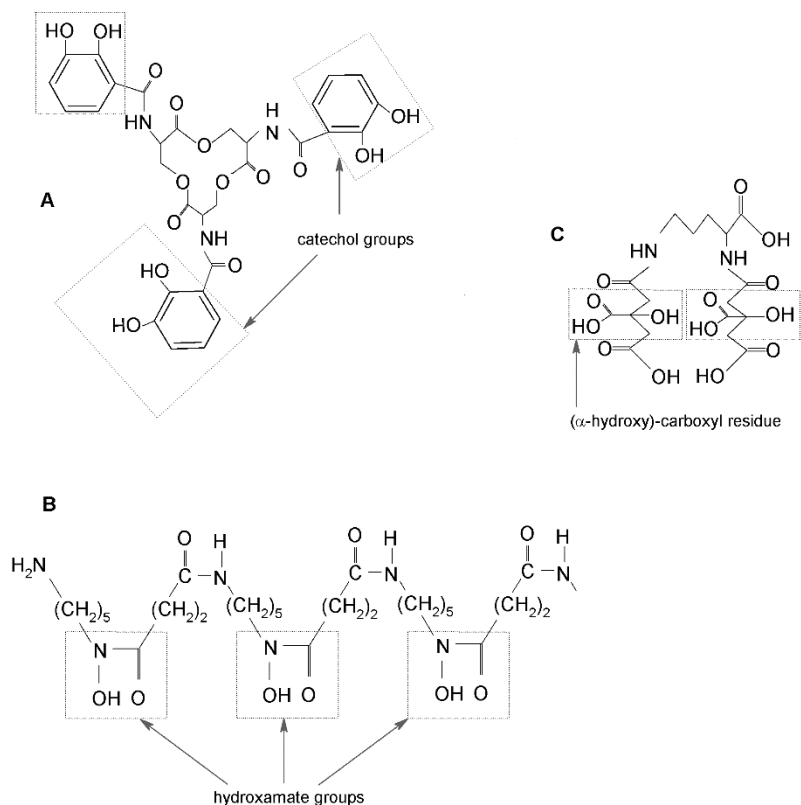


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1529 **Figure 2.** Examples of main categories of siderophores: (A) enterobactin as catecholate, (B) desferrioxamine B as

1530 hydroxamate, and (C) staphyloferrin A as (α -hydroxy)-carboxylate



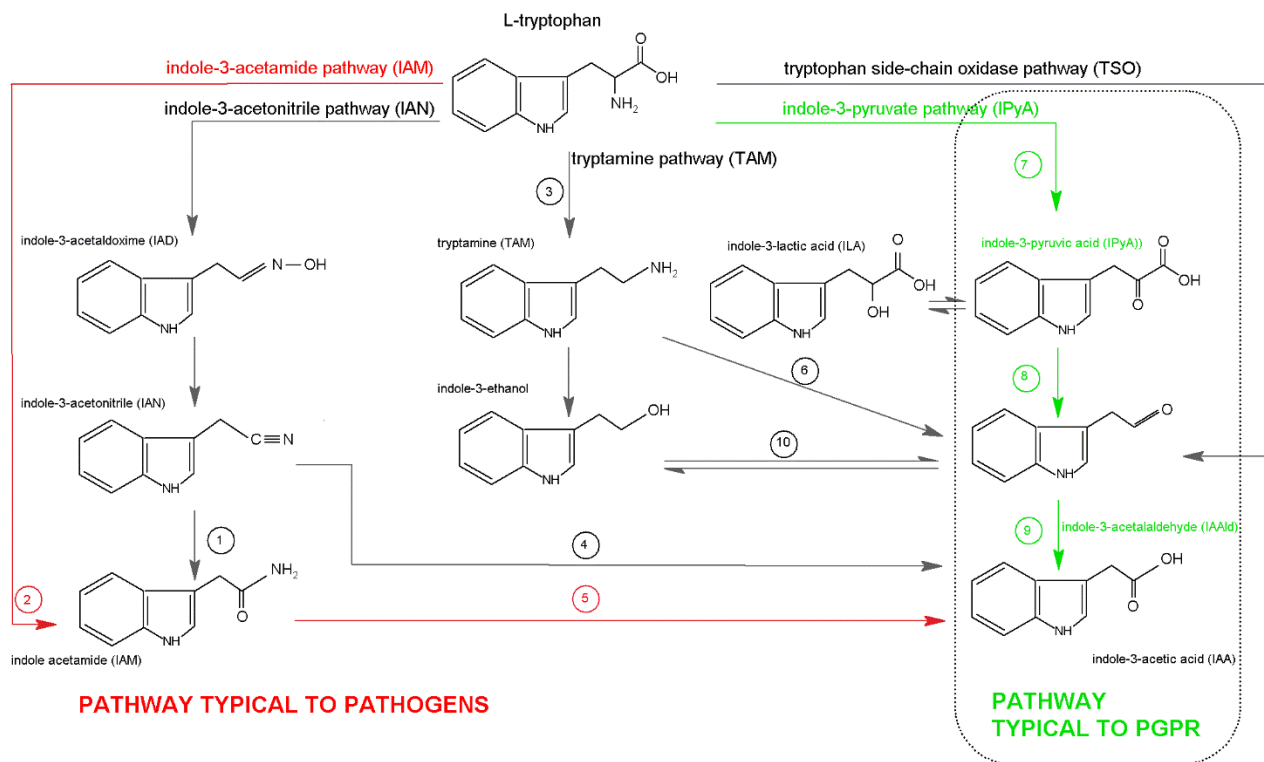
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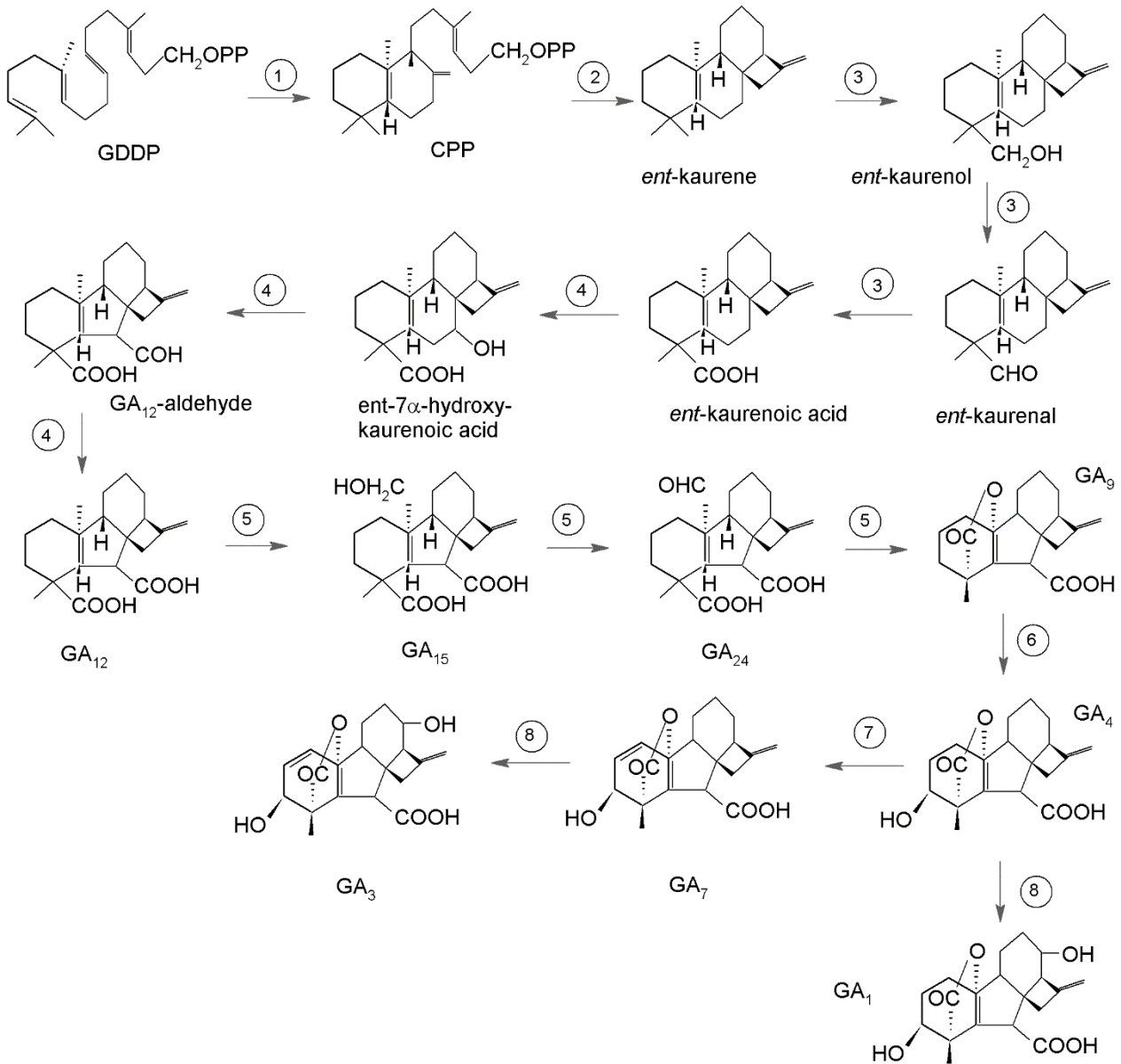
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1535 **Figure 3.** Scheme of tryptophan-dependent pathways of IAA biosynthesis in bacteria. Numbers in circles correspond to:
 1536 1 – nitrile hydratase, 2 – tryptophan monooxygenase, 3 – tryptophan decarboxylase, 4 – nitrilase, 5 – indole-3-acetamide
 1537 (IAM) hydrolase, 6 – amine oxidase, 7 – aminotransferase, 8 – IPDC, indole-3-pyruvate decarboxylase, 9 – indole-3-
 1538 acetaldehyde (IAAld) dehydrogenase. Based on Patten and Glick, 1996; Spaepen and Vanderleyden, 2011; Lin et al.,
 1539 2015; Goswami et al., 2016



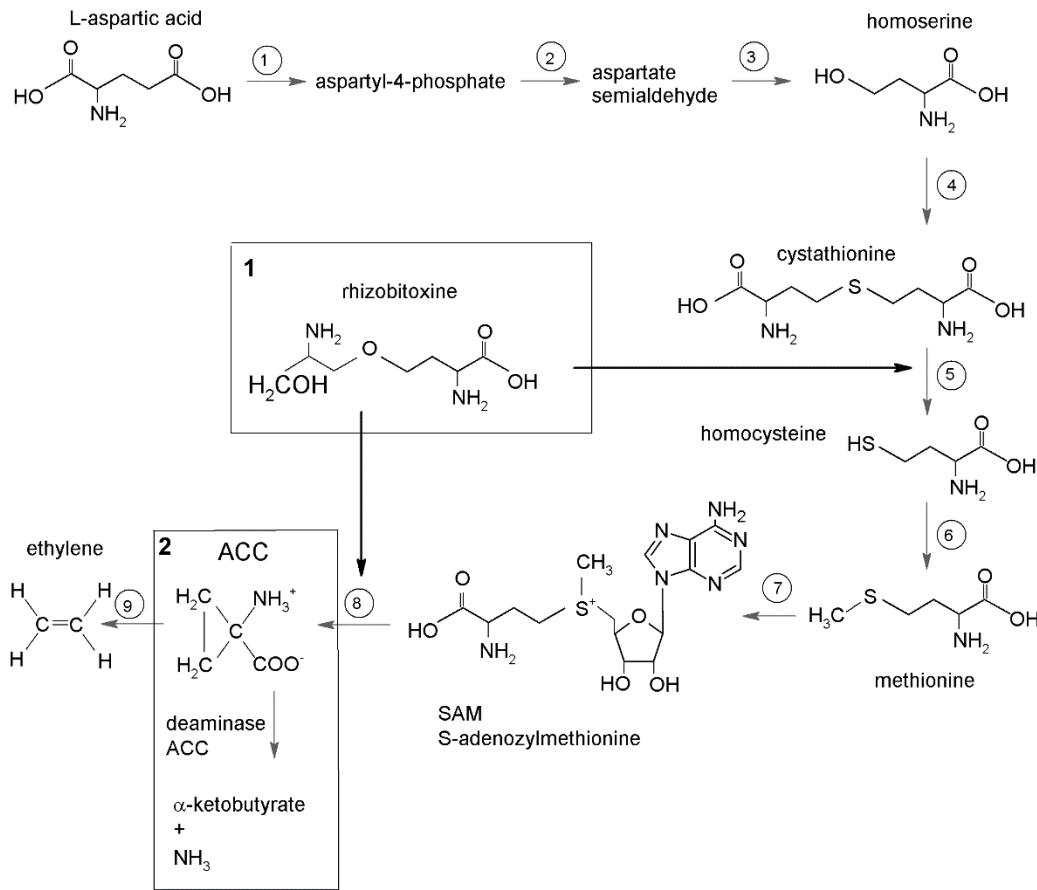
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1553 **Figure 4.** Pathway of gibberellins synthesis in bacteria. Numbers in circles correspond to: 1 – *ent*-copalyl diphosphate
 1554 synthase, 2 – *ent*-kaurene synthase, 3 – *ent*-kaurene oxidase, 4 – *ent*-kaurenoic acid oxidase, 5 – 20-oxoglutarate-
 1555 dependent dioxygenase, 6 – 3-oxidase, 7 – cytochrome 450 monooxygenase 1, 8 – cytochrome 450 monooxygenase 2.
 1556 Abbreviations correspond to: GGPP – geranyl-geranyl diphosphate, CPP – *ent*-copalyl diphosphate. Based on Hayashi et
 1557 al., 2014; Salazar-Cerezo et al., 2018



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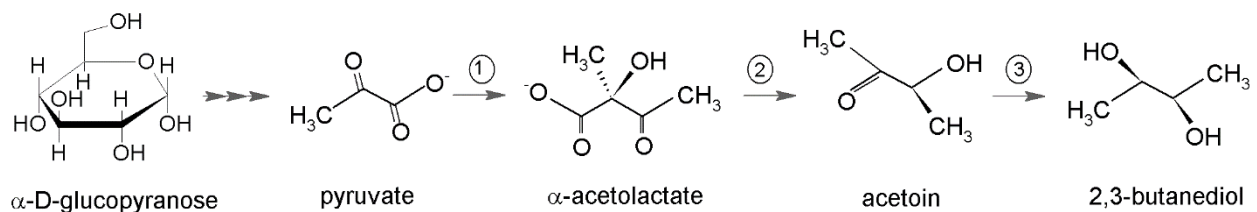
1564 **Figure 5.** Ethylene biosynthesis in plants and the mechanisms of affecting this pathway by bacteria: 1 – suppression of a
 1565 ACC synthetase by a rhizobitoxine, and 2 – degradation of ethylene intermediate ACC with ACC deaminase. Numbers
 1566 in circles correspond to: 1 – aspartokinase (AspK), 2 – aspartate semialdehyde dehydrogenase (AspSD), 3 – homoserine
 1567 dehydrogenase (HSD), 4 – cystathionine β -synthase, 5 – β -cystathionase, 6 – methionine synthetase, 7 – S-
 1568 adenosylmethionine (SAM) synthase, 8 – 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, 9 – ACC oxidase.
 1569 Based on Yashuta et al., 1999; Sugawara, 2006; Ong et al., 2015



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1572 **Figure 6.** Simplified diagram of 2,3-butanediol biosynthesis in bacteria. Numbers in circles correspond to: 1 – α -
 1573 acetolactate synthase (ALS), 2 – α -acetolactate decarboxylase (ALDC), 3 – 2,3-butanediol dihydrogenase (acetoin
 1574 reductase). Based on Ji et al., 2011; Kandasamy et al., 2016; Ji et al., 2018



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