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

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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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4	Ewa Oleńska <sup>1*</sup> , Wanda Małek <sup>2</sup> , Małgorzata Wójcik <sup>3</sup> , Izabela Swiecicka <sup>1</sup> , Sofie Thijs <sup>4</sup> , Jaco Vangronsveld <sup>4</sup>
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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 underlaying 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.







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

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  $10^8$ - $10^9$ bacteria, 10<sup>6</sup>-10<sup>8</sup> archaea, 10<sup>7</sup>-10<sup>8</sup> actinomycetes, 10<sup>5</sup>-10<sup>6</sup> fungi, 10<sup>3</sup>-10<sup>6</sup> algae, 10<sup>3</sup>-10<sup>5</sup> protozoa, and 10 nematodes 61 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; Truyens 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).

The bacterial mechanisms of plant growth promotion and communication are still being studied (Bharti et al., 2016). There is a diverse number of PGPR-induced changes in plants, and the promotion of growth is most likely a result of a complex combination of a plethora of pathways, which affect both plant development and nutrition (Bharti et al., 2016). PGPB exert positive effects on plant growth both in direct and indirect ways (Weyens et al., 2009b; Asad et al., 2019). Plant growth under the rhizobacteria influence is a multigene process, which is specific to the individually participating bacteria and plants. This "additive hypothesis" is a complex phenomenon that involves a cumulative effect of changes in expression of various genes, which ultimately influences the global plant multifactor metabolic system (Bharti et al., 77 2016; Meena et al., 2017). Direct mechanisms of plant growth stimulation by bacteria rely on facilitating the uptake of 78 nutrients, and synthesizing or regulating the hormonal status of plants (Kong and Glick, 2017; Backer et al., 2018). 79 Indirect mechanisms of PGPB influence plant growth and comprise a whole range of mechanisms that prevent or suppress 80 plant diseases (Goswami et al., 2016; Asad et al., 2019). As an example, the phosphorus solubilizing, nitrogen fixing and 81 auxins producing PGP Providencia rettgeri strain P2, Advenella incenata strain P4, Acinetobacter calcoaceticus strain 82 P19, and Serratia plymuthica strain P35 as inoculants significantly increased (i) growth parameters, e.g. dry weight, plant 83 height, root length, root average diameter, root surface area, root volume, and chlorophyll content of oat (Avena sativa), 84 alfalfa (Medicago sativa), and cucumber (Cucumis sativus), and (ii) the activity of antioxidative enzymes, e.g. peroxidase, 85 catalase, superoxide dismutase, as well as (iii) soil conditions, e.g. soil urease, invertase, alkaline phosphatase, catalase 86 activity, available nitrogen, phosphorus, potassium, and organic carbon (Li, H. et al., 2020).

87 The above mentioned positive PGPB pathways occur as the bacterial reply to plant carbon-rich exudates, constituting the 88 investment of almost 20% of the photosynthetically fixed carbon-sources in the maintenance of the rhizosphere microbiota 89 (Philippot et al., 2013; Stringlis et al., 2018a). Using Arabidopsis thaliana - PGP Pseudomonas fluorescens strain 90 WCS417 as a model system, it was revealed that the WCS417-induced early root response ISR is not an effect of plant 91 defense costs, but is a defense priming phenomenon that does not rule out the WCS417 by local root immune responses 92 (Martinez-Medina et al., 2016; Moreau et al., 2019; Zhang, S. et al., 2019). PGPB are recognized by plants because of 93 molecules with a specific and conserved chemical structure/pattern termed microbe-associated molecular patterns 94 (MAMPs), which are detected by members of a large family of plant pattern recognition receptors (PRRs). These PRRs 95 activate the signaling cascades to induce the first line of plant defense, called MAMP-triggered immunity (MTI) (Choi 96 and Klessing, 2016; Offor et al., 2020). Among the best characterized MAMPs are flagellin (flg22), a bacterial flagella 97 component recognized by the PRR flagellin-sensitive2 receptor FLS2, and chitin, a fungal carbohydrate cell wall 98 component that is recognized by the PRR chitin elicitor receptor kinase1 (CERK1) (Jelenska et al., 2017; Lawrence II et 99 al., 2020). It is worth to mention that flagellins, specifically flg22<sup>417</sup> isolated from PGP *P. fluorescens* WCS417, flg22<sup>Pa</sup> 100 from the pathogen P. aeruginosa, and the living WCS417 strain reflected similar patterns of gene expression in 101 Arabidopsis upon their influence (Stringlis et al., 2018a). Upon MAMPs the genes involved in immunity, such as those 102 responding to bacteria, fungi, chitin, wounding, hypoxia, salicylic acid, ethylene, or abscisic acid were found to be 103 upregulated. Genes related to growth and development, like those having to do with amino acid export, ion transport, 104 glucosinolate biosynthetic process, metabolism of terpenoids, and secondary metabolic processes were downregulated. It 105 is notable that MAMP-repressed genes which were not affected by the elicitors have a strong auxin signature. In this 106 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 107

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-defcient 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).

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

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#### 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 microorganisms by blocking essential functional groups of organic molecules and modifying their active conformations
(Li et al., 2017), hence disturbing metabolism and inducing oxidative damage or genotoxicity (Epelde et al., 2015). These
disruptions lead to a decrease in the total amount of soil microbial biomass (Ayangbenro and Babalola, 2017) and a
reduction in genetic polymorphism in populations (Oleńska and Małek, 2015; Zhang et al., 2018; Oleńska and Małek,
2019). For example, under severe metal exposure where toxic ions compete with essential nutrients like iron, magnesium,
phosphorus, calcium, or zinc during root uptake, plant associated bacteria can improve nutrient acquisition by enhancing
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  $1.6 \times 10^{17}$  t. Most of it is found in the atmosphere  $(3.86 \times 10^{15} \text{ t})$ , the lithosphere  $(1.64 \times 10^{15} \text{ t})$ , and the biosphere  $(2.8 \times 10^{11} \text{ t})$  (Stevens, 2019). 151 152 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<sub>2</sub>, N<sub>2</sub>O, NO, NO<sub>2</sub>), soil (NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, humic acids) (circa  $3 \times 10^{11}$  t), and detritus ( $10^{11}$  t). Plants mainly use nitrate (NO<sub>3</sub><sup>-</sup>) and ammonium (NH<sub>4</sub><sup>+</sup>) and, to a lesser extent a few 156 157 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).

Mineralization involves a cascade of microbial and enzymatic activities which leads to conversion of soil organic N to inorganic forms (Zhang et al., 2019). The soil organic matter decomposition is accomplished through aminization (from macromolecules of organic N compounds to simple organic N compounds such as amino acids, amino sugars, and nucleic acids) and further through ammonification (from simple organic N compounds to ammonium) (Kemmit et al. 2008). The resulting NH<sub>4</sub><sup>+</sup> can be readily taken up by plants.

The ammonia pool in soils may undergo a nitrification process. Nitrification consists of the oxidation of ammonia to nitrite  $(NO_2^-)$  and subsequently to nitrate  $(NO_3^-)$ . Nitrification is a dominant pathway of nitrogen input in agricultural systems, since nitrates account for more than 95% of the total nitrogen uptake by plants (Subba et al., 2017). The twostep reaction is performed by consortia of aerobic chemoautotrophic bacteria catabolizing ammonia to nitrite (*e.g.*  *Nitrosomonas* spp., *Nitrosococcus* spp., *Nitrosospira* spp., *Nitrosolobus* spp., and *Nitrosovibrio* spp.), and then
transforming nitrite into nitrate (*e.g. Nitrobacter* spp., *Nitrococcus* spp., *Nitrospira* spp., and *Nitrospina* spp.) (Hagopian
and Riley, 1998).

Atmospheric nitrogen (N<sub>2</sub>), comprising almost 78% of the atmosphere, can be transformed into ammonia due to natural events (*e.g.* lightning, fires) but most of what is transferred to the biota is biologically fixed by diazotrophs (Mus et al., 2016; Smercina et al., 2019). Diazotrophic microorganisms transform the diatomic trivalent N<sub>2</sub> molecule into ammonia (NH<sub>3</sub>), that is useful and available to most organisms, using a nitrogenase enzyme complex consisting of two components, nitrogenase and nitrogenase reductase (Mahmud et al., 2020).

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

184 Rhizobia are Gram-negative bacteria of the family *Rhizobiaceae* (class  $\alpha$ - and  $\beta$ -*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 N<sub>2</sub> 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 N<sub>2</sub> 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).

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

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 (NO<sub>3</sub><sup>-</sup>) and 203 ammonium ( $NH_4^+$ ) 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 by. 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 melilotistrain 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 celluar 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 wilde 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* 

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

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<sup>-1</sup> 265  $(0.01-0.2\% P_2O_5)$  (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% P<sub>2</sub>O<sub>5</sub>), igneous rocks 267 (about 2.0% P<sub>2</sub>O<sub>5</sub>), and metamorphic rocks (about 1.3% P<sub>2</sub>O<sub>5</sub>). 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<sup>+</sup> 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<sup>+</sup> substitution. Among many diverse organic acid excretes, 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 Ca<sub>3</sub>(PO<sub>4</sub>)<sub>2</sub>, AlPO<sub>4</sub>, and FePO<sub>4</sub>. 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 inststance: 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 phosphonatases 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 brakii, 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 metal ions (Mn<sup>2+</sup>, Zn<sup>2+</sup>, Fe<sup>2+</sup>, Co<sup>2+</sup>, Cu<sup>2+</sup>, Hg<sup>2+</sup>, Cd<sup>2+</sup>) (Kumar et al., 2016; Rocky-Salimi et al., 2016). 352

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

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

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 exists as ferric Fe(III) ions which accumulate in mineral phases as highly stable hydroxide [Fe(OH)<sub>3</sub>] and oxyhydroxide 368 [FeO(OH)] complexes, leading to free Fe(III) concentrations in soils of  $10^{-9}$ - $10^{-18}$  M, which are not sufficient to meet the 369 370 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 are three possible mechanisms of iron uptake by plant roots using the siderophore-metal complexes: (i) chelate
degradation and iron release, (ii) uptake of the siderophore-Fe(III) complexes, or (iii) a ligand exchange reaction (Zhang,
X et al., 2019).

389 Siderophores, formerly mycobactins, are low molecular mass (400-1500 Da) chelators of a high affinity for ferric Fe(III) 390 (formation constant  $K \ge 10^{30}$ ), 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  $(\alpha$ -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 ( $\alpha$ -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 staphylloferrin 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).

Siderophores of bacterial origin influence host-plant iron homeostasis, immune function, and growth (Yu et al., 2017;
Hesse et al., 2018). For example, the *Pseudomonas fluorescens* strain C7R12 siderophore pyoverdine analog (apopyoverdine) 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 HBI1, 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

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

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 µg mL<sup>-1</sup> of IAA while *P. fluorescens* produces 28 µg mL<sup>-1</sup> (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-acetalaldehyde (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  $\alpha$ -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, 1999). At low concentrations, bacterial auxins stimulate elongation of primary plant roots, but at higher doses auxins 491 492 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. aryabhattai strain RSO25 lowered the levels of these antioxidative enzymes. 523 The alleviation of the metal exposure enhanced expression of the PAL gene, encoding for phenyloalanine 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 aryabhattai 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 (Patel and Saraf, 2017). In Bacteria, the cytokinin synthesis pathway is initiated by a transfer of the isopentenyl moiety 537 538 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

production by transferring the isopentenyl moiety from HMBDP (1-hydroxy-2-methyl-2(E)-butenyl 4-diposphate) to
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-7a-566 hydroxykaurenoic acid. Finally, oxidation of ent- $7\alpha$ -hydroxykaurenoic acid at C- $6\beta$  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).

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

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 levels of jasmonic acid and salicylic acid were upregulated in soybean plants inoculated with this strain SSB07 and 583 584 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 fulfils 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,

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

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 Azospirillium brasiliense strains Cd and Az39, Achromobacter xylosoxidans, Bacillus lycheniformis, 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 aryabhattai 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 and drought tolerance to their host-plants by altering morpho-physiological and biochemical properties and modulating 614 615 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. Nevertheless, the exact mechanisms of decrease amounts of ABA *in planta* and its effects on plant growth is still unclear. Although it was reported that plants such as *Gossypium hirsutum* inoculated with *Raoultella planticola* strain Rs-2, or *Solanum tuberosum* inoculated with *Promicromonospora* spp. strain SE188 showed decreased ABA concentrations, more data are required to better understand the mechanisms of how bacterial ABA-utilizers influence plant biomass (Kang et al., 2012; Wu et al., 2012). ABA-catabolizing *Rhodococcus quingshengii* associated with *Arabidopsis* under heavy metal stress significantly increased the expression of Cd, Zn, and Ni-related transporters, and increased the accumulation of metal ions possibly via ABA-mediated mechanisms (Lu et al., 2020).

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 the synthesis of ethylene through the production of rhizobitoxine, a competitive inhibitor of ACC synthetase (Yasuta et 655 656 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  $\beta$ -658 cystathionase in the methionine biosynthesis pathway (Sugawara, 2006) and ACC-synthase in the ethylene biosynthesis 659 pathway (Yasuta et al., 1999).

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

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 NiCl<sub>2</sub> 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<sup>+</sup> transporters (NHX1, SOS1), calmodulin (Cam1-1), antioxidant enzymes (Cw/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).

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### 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 Vleesschauwer 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 cenocepacia, 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 subtilosin 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 compounds, e.g. 2,4 diacetyl phloroglucinol (DAPG), phenazine-1-carboxylic acid (PCA), phenazine-1-carboxamide 710 711 (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 karalicins (Goswami et al., 2016).

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

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

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 phenylopropanoids 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 phenyloalanine 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 tobacco (Wang et al., 2009). 2,3-BD significantly reduced symptoms caused by fungal and bacterial pathogens, which 753 754 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, acetoin synthesized by Bacillus subtilis strain FB17 as inoculum of Arabidopsis thaliana, was found to be an ISR inducer, 756

which protects plants from infection in an ethylene-dependent manner against the pathogenic *Pseudomonas syringae* pv. tomato strain DC3000 (Ali et al., 2015). It is noteworthy that, the ISR plant response to PGPR may be induced also in the absence of any physical contact with plants via VOCs emissions. In P-deficient conditions, *Arabidopsis thaliana* enhanced salicylic acid and jasmonic acid mediated immunity and hyper-sensitivity to phosphate deficiency, under the influence of a VOC-type diacetyl, synthesized by *B. amylologuefaciens* 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 activities to enhance the availability of nutrients, synthesis of phytohormones, and decrease pathogenic infections, is of 767 768 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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## 1516 List of Tables and Figures

Plant	Bacterium	Abiotic stressor	Feature of plant growth promotion <sup>#</sup>
Alvssum bertolonii	Staphylococcus spp.	nickel pollution	siderophores
	Microbacterium spp.,	mener ponation	siderophores
	Pseudomonas spp.		
Acacia gerrardii	Bacillus subtilis	sodium chlorite	IAA
8		excess	
Brassica juncea	Azotobacter chroococcum strain	chromium pollution	nitrogen fixation
5	HKN-5	1	C
	Pseudomonas spp.	chromium pollution	siderophores, IAA
	Achromobacter xylosoxidans	copper pollution	P-solubilisation, IAA
Brassica napus	<i>Mycobacterium</i> spp. strain	cadmium, nickel, and	siderophores, IAA
•	ACC14	copper pollution	•
	Pseudomonas chlororaphis strain	copper pollution	ACC deaminase, P-solubilisation,
	SZY6		siderophores, IAA
Brassica oxyrrhina	Pseudomonas spp. strain SR12	nickel pollution	ACC deaminase, P-solubilisation,
-		-	siderophores, IAA
Cicer arietinum	Pseudomonas spp.	nickel pollution	siderophores
	Serratia spp.	nutrient deficience	IAA
Cucumis sativus	Trichoderma asperellum	sodium chlorite	IAA, GA, ABA
		pollution	
Helianthus annuus	Bacillus weihenstephanensis	copper, zinc, and	P-solubilisation, IAA
	strain SM3	nickel pollution	
Oryza sativa	Methylobacterium oryzae strain	nickel, and cadmium	ACC deaminase,
	CBMB20	pollution	
Pisum sativum	Pseudomonas marginalis strain	cadmium pollution	nutrient uptake, ACC deaminase
	Dp1	_	_
Ricinus communis	Pseudomonas spp.	nickel, zinc, and	ACC deaminase, siderophores, IAA
		copper pollution	_
Salix caprea	Serratia marcescens	cadmium, zinc, and	siderophores, IAA
		lead pollution	
Solanum nigrum	Bacillus spp. strain SLS18	cadmium pollution	siderophores, IAA, ACC deaminase
Sorghum vulgare	Bacillus spp. strain J119	cadmium pollution	siderophores, IAA, ACC deaminase
var. <i>sudanense</i>			
Thlaspi goesingense	Methylobacterium spp.	nickel pollution	siderophores, IAA
Trifolium repens	Bacillus cereus	iron, manganese, zinc,	IAA, nutrient uptake
		and cadmium	
		pollution	
Trifolium pratense	Brevibacillus spp.	lead pollution	IAA
Triticum aestivum	Bacillus lycheniformis	sodium chlorite	IAA
		excess	
Vigna radiata	Pseudomonas putida strain KNP9	cadmium, and lead	siderphores
		pollution	
Vinca rosea	Bacillus megaterium	ickel pollution	IAA
Vitis vinifera	Bacillus lycheniformis,	flooding	ABA
	Pseudomonas fluorescens		
Zea mays	Burkholderia spp. strain J62,	cadmium, and lead	IAA, siderophores, ACC deaminase
	Leifsonia spp., Bacillus spp.	pollution	

1517 Table 1. Examples of plant growth promoting rhizobacteria and features alleviating abiotic stress in plants

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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- 1529 Figure 2. Examples of main categories of siderophores: (A) enterobactin as catecholate, (B) desferrioxamine B as
- 1530 hydroxamate, and (C) staphylloferrin A as (α-hydroxy)-carboxylate





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



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



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



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



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