

# We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

5,500

Open access books available

136,000

International authors and editors

170M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index  
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?  
Contact [book.department@intechopen.com](mailto:book.department@intechopen.com)

Numbers displayed above are based on latest data collected.  
For more information visit [www.intechopen.com](http://www.intechopen.com)



# Plant Root Enhancement by Plant Growth Promoting Rhizobacteria

*Metin Turan, Tuba Arjumend, Sanem Argın, Ertan Yıldırım, Hikmet Katırcıoğlu, Burak Gürkan, Melek Ekinci, Adem Güneş, Ayhan Kocaman and Parisa Bolouri*

## Abstract

Soil microorganisms perform a variety of functions, some of which are extremely helpful to the maintenance of ecological sustainability. Bacteria thriving in the plant rhizosphere drive plant development through a variety of ways, which are referred to as PGPR (plant growth-promoting rhizobacteria). Despite the fact that there are many different types of PGPR, their significance and applications in sustainable agriculture are still debated and limited. The performance of PGPR varies, which might be related to a variety of environmental conditions that impact their development and proliferation in plants. PGPR is a nonpathogenic, friendly bacterium that stimulates plant development by altering hormone concentrations and nutritional needs, as well as mitigating stress-related damage. PGPR colonizes root hairs and lateral roots in plants, where they may exhibit their beneficial characteristics. Rhizobacteria that promote plant development have the ability to control root system architecture (RSA), as well as the vegetative growth and physiology of the entire plant. The generation of hormones like Indole acetic acid (IAA) by PGPR has long been linked to RSA effects. This book chapter reviews to show PGPR affects on the growth, physiological, biochemical, and molecular characteristics of plant roots.

**Keywords:** Roots, growth, PGPR, plant

## 1. Introduction

Agriculture is vital to a country's economic well-being. Many biotic and abiotic stressors are plaguing the industry, which has resulted in massive plant productivity losses throughout the world. Nutrient shortage, heavy metal pollution, high temperature, diseases, plant invasions, pests, salt, and soil erosion are all stress factors. The absence of reliable and consistent traits has generally hampered crop breeding for abiotic stress resistance. Multiple genes operate collectively to promote stress tolerance. Furthermore, the use of agrochemicals to combat biotic stressors and nutritional shortages hastens environmental pollution and has a detrimental impact on the biogeochemical cycle system, and poses a health risk to humans. The potential consequences of the aforementioned stresses are substantial, implying the need for solid, cost-effective, and ecologically acceptable ways to reduce the negative impacts of these challenges on plants. As a result, interest in ecologically friendly

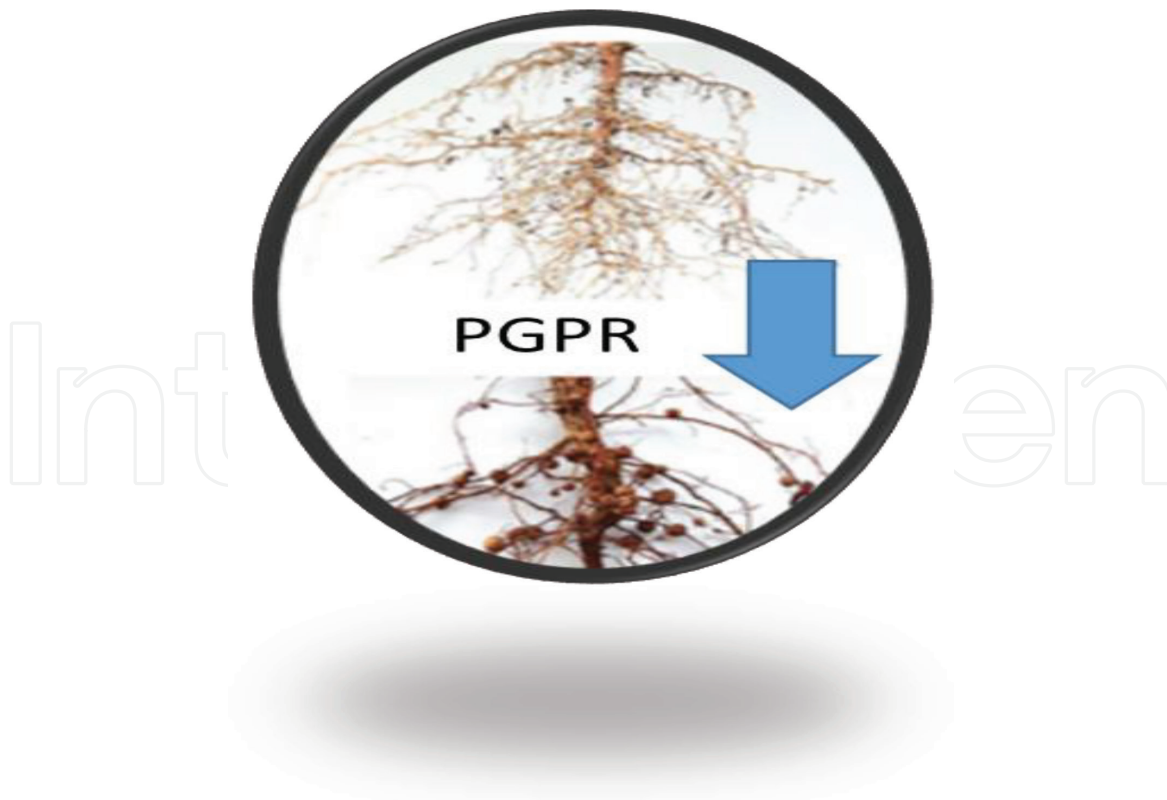
and organic agriculture techniques has surged [1]. Bio-fertilization, revitalizing root growth, rhizoremediation, disease resistance, and other methods of microbial revival employing plant growth stimulants have been used.

Plants, unlike animals, cannot employ avoidance and escape as stress-relieving techniques; as a result, their evolution has been distinguished by the development of extremely advantageous relationships with their more mobile partners, microorganisms. Interactions between plants and microbiomes including soil bacteria are in high demand all around the world. Microorganisms are considerably more prevalent in the rhizosphere, or soil/root contact than they are in bulk soil. This is due to the fact that roots release a large portion of their photo-assimilates, serving the primary food source for the rhizobacteria. In exchange, they are able to have a positive impact on plant development and play an important part in plant adaptation to the environment [2, 3].

Soil microorganisms perform a variety of functions, some of which are extremely helpful to the maintenance of ecological sustainability. Bacteria thriving in the plant rhizosphere drive plant development through a variety of ways, which are referred to as PGPR [4]. The rhizosphere is the confined zone of soil directly around the roots [5] whereas rhizobacteria refer to a group of rhizosphere bacteria capable of inhabiting the root environment [6]. PGPR is a nonpathogenic, friendly bacterium that stimulates plant development by altering hormone concentrations and nutritional needs, as well as mitigating stress-related damage [7, 8].

Plant growth could be boosted by PGPRs in both direct and/or indirect ways. Among the direct ways is 1) secreting growth regulators such as cytokinins, auxin, and gibberellins, 2) decreasing the levels of ethylene in plants, 3) solubilizing inorganic phosphate, 4) mineralising organic phosphate, 5) Non- Symbiotic nitrogen fixation, 6) forming organic matter, which comprises amino acids, 7) enzymes synthesizing and 8) activating disease-resistance pathways [9]. Indirectly, PGPRs may serve as biocontrol agents by controlling plant disease-causing organisms. They also help to relieve the effects of cold, drought, metal toxicity, and excessive salinity. Plants grown in arid and semi-arid climates might increase their drought resistance and water usage efficiency by inoculating them with beneficial PGPR which promotes plant abiotic stress tolerance with an osmotic component. Plant's biochemical changes resulting in improved tolerance to abiotic stress have been suggested as PGPR induced root growth, nutrient uptake efficiency, and systemic tolerance. They can also fix asymbiotic nitrogen, help with mineral phosphate and other nutrient solubilization; manage plant disease caused by other bacteria and fungi, and produce antibiotics, enzymes, and siderophores, among other functions. Certain PGPR may infer particular growth-promoting properties like abiotic stress tolerance, and phytopathogen and insect biological control [10]. The stimulation of disease tolerance of the inoculated plant, N<sub>2</sub> fixation, phosphorus solubilization, and/or phytohormone synthesis are all possible explanations for PGPR's growth-promoting effects on plants [9]. Phytohormones are chemical molecules that influence the development of plants. Plant growth regulators are another name for them. Auxins, gibberellins, ethylene, cytokinins, and abscisic acid are the five principal categories of phytohormones known by botanists. Indole acetic acid is a phytohormone that affects plant growth in a variety of ways, including organogenesis, tropic responses, cell division, and cell differentiation.

Despite the fact that there are many different types of PGPR, their significance and applications in sustainable agriculture are still debated and limited. The performance of PGPR varies, which might be related to a variety of environmental conditions that impact their development and proliferation in plants (**Figure 1**) [11]. Due to these effects, the use of PGPRs in agriculture has begun to be studied. In this work, we used the currently widely used databases and tools including Web



**Figure 1.**  
*PGPR in plant roots.*

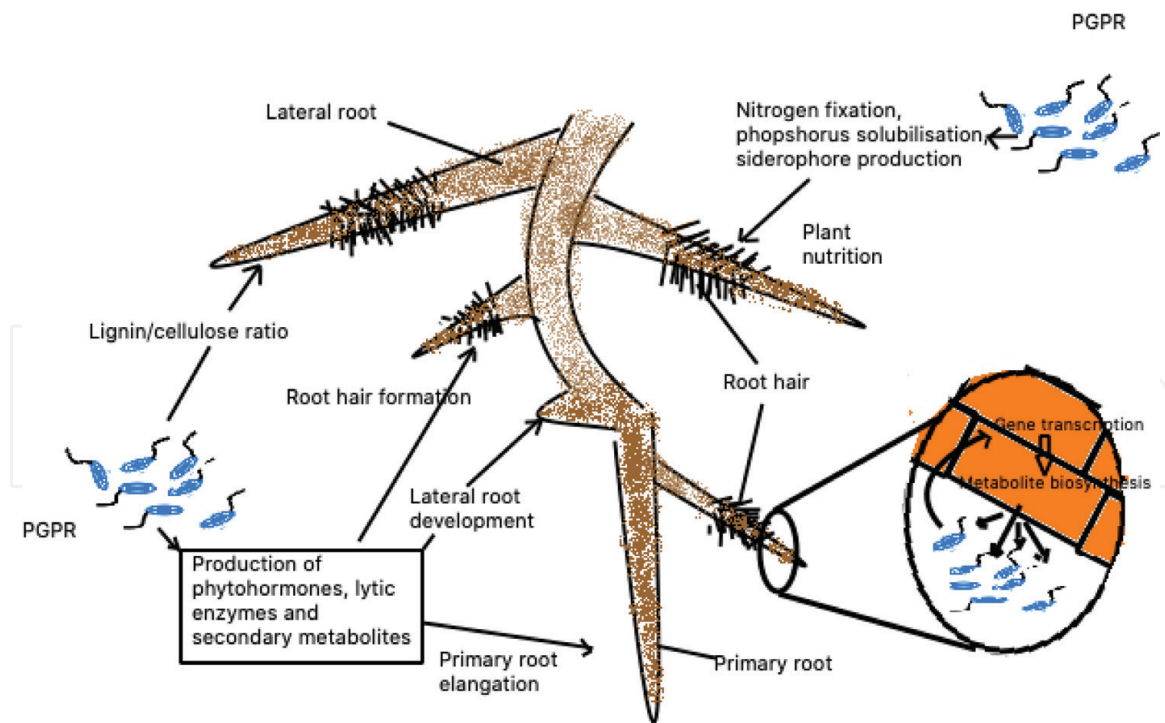
of Science, Science Direct, Google Scholar etc., and key words such as roots, PGPR, growth, development, root structure, chemical characteristics, genes etc.

## 2. PGPR's effect on the architecture and structure of root systems

The plant's aboveground development is heavily reliant on its underground root structure. The root system of most terrestrial plants develops to scrutinize soil and reach nutrients. Root comprises the root tip, differentiation and elongation zones, root meristem, and emerging lateral roots [12]. Each of these regions has a unique significance. According to gene expression research, root hairs are specialized epidermal cells that are crucial for nutrient uptake [13]. The functional specialization of roots is also reflected in plant-microbe interactions. The root tip, for example, is the most essential area for initiating the rhizobial colonization, which leads to the development of a nodule in the Fabaceae family [14]. PGPR colonizes roots in plants where they can exert their beneficial properties [15]. RSA encompasses spatial arrangement of primary and lateral roots, as well as the number and length of different root types. It can be affected by a variety of abiotic and biotic variables, including PGPR strains. The potential of PGPR to interfere with the plant hormones modifies root system architecture (**Figure 2**).

PGPR engages in some activities in the soil to keep it active in crop production and sustainability [16]. PGPR colonize roots systems competitively, regulate root development, surface area and enhance plant growth through and a variety of mechanisms, including phosphate solubilization [17], nitrogen fixation [18], production of siderophores [19], 1-amino-cyclopropane-1-carboxylate (ACC) deaminase and hydrogen cyanide [20].

Ironically, some microorganisms, such as PGPR, may trigger the synthesis of phytohormones in plants. Phytohormones are organic compounds that stimulate,



**Figure 2.**

*The influence of phyto-stimulating PGPR on nutrient uptake, root system architecture and root function.*

hinder, or change plant growth at low concentrations [21]. Gibberellins, cytokinins, abscisic acid, ethylene, brassinosteroids, and auxins are examples of phytohormones that cause the root cell to proliferate by overproducing lateral roots and root hairs [22]. Plant growth regulators may be given exogenously to plants or plant tissues as extracted hormones or synthetic counterparts. Phytohormones are classified according to where they act. This is critical for nutrient absorption regulation based on soil type and climatic conditions. The most prevalent effects are a slowdown in primary root development rate and an increased lateral roots and root hairs. The synthesis of growth metabolites by PGPRs may play a role in conferring resilience to water stress in host root colonization, leading to increased strategic crop output. By root repair, beneficial rhizobacteria may adapt to specific environmental circumstances and gain stress resistance.

Auxin, cytokinin, ethylene, and to a lesser extent gibberellin and abscisic acid (ABA) interactions with PGPR might induce variations in the root system [23]. Auxin-cytokinin balance is a fundamental regulator of plant organogenesis and influences root characteristics [24]. PGPR can alter the auxin to cytokinin ratio because they may produce a variety of phytohormones as well as secondary metabolites that might disrupt hormonal pathways. Several PGPRs generate phytohormones and secondary metabolites that interfere with auxin pathway in plants. PGPR can generate IAA, which promotes primary root elongation (**Figure 2**) [25, 26]. IAA is often produced by PGPR via various routes, which can be present in various quantities in root exudates depending on the plant genotype. Indirect activation of the plant auxin pathway by PGPR can also promote plant growth. Several PGPR strains, such as *Azospirillum brasilense*, for example, exhibit nitrite reductase activity and can thus generate NO during root colonization [27]. NO is engaged in the auxin signaling system, which controls the development of lateral roots [28]. Fluorescent pseudomonas generates 2,4-diacetylphloroglucinol (DAPG), which at lower doses can act as a signal molecule, causing systemic resistance [29], and increasing root forming [30]. DAPG can modify RSA by interfering with an auxin-dependent signaling pathway [31].

Cytokinin production has been shown by PGPR like *Azospirillum brasilense*, *Bacillus licheniformis*, *Bradyrhizobium japonicum*, *Pseudomonas fluorescens*, and *Paenibacillus polymyxa* [25, 32]. Cytokinins promote cell division, regulate root meristem differentiation, and drive root hair proliferation, however, reduce lateral root development and main root growth [33].

PGPR has been shown in several studies to be capable of producing ABA or gibberellic acid, as well as controlling the levels of these hormones in plants [34]. ABA, for example, plays an important role in drought stress. Elevated ABA levels under water stress induce stomata to close, reducing water loss [35]. ABA, on the other hand, has a variety of functions during lateral root growth [34]. In Arabidopsis, *Azospirillum brasilense* Sp245 resulted in an increase in ABA concentration, particularly when grown under osmotic stress [36]. Gibberellins encourage lateral root growth and primary root elongation [37]. Gibberellin production has been seen in PGPR from *Azospirillum* spp., *Azotobacter* spp., *Acinetobacter calcoaceticus*, *Gluconobacter diazotrophicus*, *Herbaspirillum seropedicae*, *Rhizobia* spp., and *Bacillus* spp. [34]. These two hormones are engaged in plant defensive systems in addition to their involvement in plant RSA. As a result, the hormonal balance involved in plant defense may be modulated by PGPR generating these hormones [38]. The role of bacterial hormones in modulating plant hormonal balance has yet to be shown.

### 3. The structural properties of the root by PGPR

PGPRs can alter the chemical composition and, as a result, the structural characteristics of root cell walls (**Figure 2**) [39]. The biocontrol agent *Bacillus pumilus* INR-7, for example, significantly increases lignin deposition in pearl millet epidermal tissues [40]. INR-7 inoculation was the sole cause of callose apposition. *Bacillus pumilus* and *Bacillus subtilis* resulted in increased fungal pathogen resistance in pea and melon roots [41]. In the case of PGPR, these cell wall changes have been found to protect plants against phytopathogens through the activation of induced systemic resistance (ISR) [41, 42]. ISR is not unique to a single pathogen, but it aids the plant in the management of a variety of diseases [43]. ISR includes ethylene hormone, which aids in the induction of a host plant's defense responses against a range of plant diseases. ISR can strengthen the cell wall by increased lignin synthesis and callose apposition [44], which limits phytopathogen progression in plant tissues [41]. PGPR also triggers modifications in the chemical makeup of root cell walls, which directly stimulate plant development (**Figure 2**).

Lower lignin concentration, on the other hand, may aid cell elongation and hence total root growth. *Azospirillum irakense* generates pectate lyases, which can degrade the pectate content of root cell walls, allowing it to move across root cortex cells [45]. Changes in plant gene expression caused by the PGPR are considered to be the primary cause of changes in root cell wall ultrastructure. *Bacillus subtilis* GB03 stimulates Arabidopsis development by generating volatile organic compounds (VOCs), which have been demonstrated to affect the expression of 38 genes related to cell wall construction [39]. Thirty of these were linked to cell wall expansion or loosening. Sekar et al. [46] found that the endophytic PGPR *Azospirillum irakense* up-regulated polygalacturonase genes in rice.

PGPR produces enzymes such ACC-deaminase, 1,3-glucanase, and chitinase, which are involved in the lysis of cell walls and pathogen neutralization [47]. Because most fungal cell wall components are made up of 1,4-N-acetylglucosamine and chitin, bacteria that produce 1,3-glucanase and chitinase regulate their development. *Fusarium oxysporum* and *Fusarium udum* cause fusarium wilt, which is caused by beta-glucanases and chitinases produced by *Pseudomonas fluorescens* LPK2

and *Sinorhizobium fredii* KCC5 [48]. PGPR also inhibits *Phytophthora capsici* and *Rhizoctonia solani*, two of the world's most devastating crop diseases [49].

#### 4. PGPR's systemic effects on the physiology and functioning of the whole plant

PGPR may alter the physiology and function of tissues far from colonized areas in plants. PGPR can improve plant root nutrient availability and absorption. Some PGPR, on the other hand, causes particular systemic reactions, most of which are triggered by unknown signaling pathways. PGPR has been shown to affect gene expression and metabolite accumulation in plants which have been demonstrated by studies of plant transcriptome and metabolomic. These findings show that PGPR has a broad impact on plant physiology and function, and they highlight ways to better understand PGPR's systemic impact.

##### 4.1 PGPR's effect on plant nutrition

Plant nutrition may be affected by PGPR through impacts on nutrient absorption and/or plant development [50]. Nutrient absorption can be improved as a result of the enhanced root growth induced by PGPR. To promote both higher nutrient uptake and plant growth, PGPR is involved in pathways that coordinate plant development and nutrition (**Figure 2**). Rhizobacteria that promote plant development can enhance nutrient supplies in the rhizosphere and/or activate root ion transport mechanisms. One of the most important effects of PGPR on plant nutrition is phosphate solubilization. Soils typically contain a lot of phosphorus, which builds up over time as a result of fertilizer treatments, but only a tiny quantity of it is available to plants. Plants may absorb mono and dibasic phosphate on their own; organic and insoluble phosphate must be mineralized or solubilized by microbes [51]. *Pseudomonas*, *Bacillus*, and *Rhizobium* may dissolve phosphate in insoluble forms [52].

Miller et al. [53] identified that various linked bacteria have the ability to fix  $N_2$  and so supply nitrogen to the plant. For some plants, particularly sugar cane, evidence of PGPR engagement in the plant N budget has been documented [54]. Also, non-fixing rhizobacteria can promote plant growth, indicating that external fertilizer application may not be necessary to increase plant growth and yield.

Only a few research on the influence of PGPR on nutrient absorption have been reported so far though.  $NO_3^-$  and K uptake have been shown to increase after canola was inoculated with *Achromobacter* sp. strain U80417 [55]. In *Arabidopsis*,  $NO_3^-$  inflow was enhanced after 24 hours of inoculation with *Phyllobacterium brassicacearum* [56]. Increases in transcripts of nitrate and ammonium transporters were substantially altered after *Phyllobacterium brassicacearum* STM196 treatment, with the exception of the RT2.5 and NRT2.6 genes [56]. The RT2.5 and NRT2.6 genes were recently discovered to be essential in *Arabidopsis* growth stimulation [57]. This result highlights the topic of the connections between N nutrition and plant growth in PGPR-inoculated plants, as these two genes control  $NO_3^-$  transporters [58]. In experiments using *Bacillus subtilis* GB03, evidence was found in favor of PGPR regulating ion transporters at the transcriptional level. This strain can modify HKT1 expression in *Arabidopsis* seedling [59]. HKT1 acts in phloem tissues in the shoots to extract  $Na^+$  from the xylem and is implicated in  $Na^+$  absorption [60]. Under salt-stress conditions, the differential control of HKT1 caused decreased  $Na^+$  uptake and enhanced  $K^+$  uptake in GB03-inoculated seedlings [59]. The plant's iron acquisition mechanism is also activated by the volatile organic chemicals released by GB03,

resulting in enhanced iron absorption [61]. PGPR affects nutrition through nitrogen fixation, phosphorus solubilization, and siderophore formation, as well as modify root physiology through gene transcription and metabolite synthesis.

#### 4.2 PGPR's effect on plant transcriptome

Effects of PGPR applications on gene expression in plants has been described. Inoculation of Arabidopsis leaves with *Pseudomonas putida* resulted in upregulation of 520 genes. These genes take part in several metabolic processes, chemical syntheses, ABA and Ca signaling, and ISR induction [62]. *Azospirillum brasilense* Sp245 on two rice cultivars with a contrasting capacity to acquire N via nitrogen fixation, the expression of ethylene receptors was monitored. Cultivar IR42 had greater ethylene receptor expression than IAC 4440 [63]. All ethylene receptor transcripts may be required for the formation of a favorable relationship between the plant and the bacterium [64]. *Herbaspirillum seropedicae* inoculation induced the expression of genes sensitive to auxin and ethylene, as well as the suppression of the defense-related proteins PBZ1 and thionins in rice [65]. Plants treated with the biocontrol PGPR are more resistant to bacterial and fungal pathogen infections. This rhizobacteria-mediated ISR in Arabidopsis necessitates ethylene and jasmonate sensitivity. *Pseudomonas fluorescens* WCS417r triggered a significant shift in the expression of 97 genes in roots [66]. Following investigations on Arabidopsis found that bacterized plant shoots had higher levels of defense-related transcripts [67]. The ISR generated by *Pseudomonas fluorescens* SS101 has been shown to be related to salicylic acid signaling rather than jasmonic acid [67]; moreover, a major function for camalexin and glucosinolates in the ISR was postulated. *Pseudomonas fluorescens* treatment resulted in enhancement of defense-related transcripts in wheat [68]. Beneficial relationships involve reciprocal considerable coordination of plant and PGPR, and beneficial microorganisms influence plant immunology as a result.

#### 4.3 PGPR's effect on plant metabolome

Researches have looked at the metabolomic changes caused by PGPR by examining the metabolite content in plants under non-stressed and stressed circumstances (Figure 2). PGPR has been found in certain studies to cause modifications in the activity of root enzymes, which play role in the synthesis of metabolites [69]. The level of carbon compounds released from roots was increased by up to one-third in several *Azospirillum* strains [70]. Furthermore, microbially produced chemicals such as phenazines and DAPG have the potential to increase total net amino acid outflow in plant species [71]. *Chryseobacterium balustinum* affects flavonoids exudation on soybean roots [72]. Flavonoid exudation by Fabaceae roots may be influenced by PGPR [72] or *Azospirillum* [73]. PGPR can cause changes in the metabolite composition of plants. Rice plants treated with *Herbaspirillum seropedicae*, for example, had greater malate and important amino acid levels in their shoots than the control ones [74]. Furthermore, other researches focused on secondary metabolite changes. Isoflavone accumulation was seen on soybean seedlings infected with different PGPR [75]. Following PGPR inoculation, medicinal plants showed enhancement in the concentration of numerous alkaloids and terpenoids of pharmacological importance [76]. *Azospirillum* strains caused qualitative and quantitative changes in secondary metabolite content in maize cultivars [30]. Similarly, the metabolic profile of two rice cultivars infected with two different strains of *Azospirillum* under gnotobiotic conditions showed that their secondary metabolite profiles changed [77]. Plant metabolic alterations changed depending on the *Azospirillum* strain-cultivar combination in both investigations, indicating



a unique response. Furthermore, PGPR applied to the roots has been shown to change the composition of metabolites in shoots [77]. *Pseudomonas*, *Azospirillum*, or *Rhizoglyphus/Glomus* strains, or all three strains together treatments resulted in qualitative and quantitative changes in root secondary metabolites in maize [78]. These changes were dependent on the degree of fertilization and the kind of microorganisms injected. When treated alone, the three strains produced different outcomes, yet all microbial consortia produced metabolic responses that were surprisingly comparable. Rhizobacteria that promote plant development can assist plants to survive saline stress, which could be connected to the buildup of particular metabolites. Infected *Bacopa monnieri* had a greater proline content, while rice inoculated with *Pseudomonas pseudoalcaligenes* had a larger accumulation of glycine betaine [76]. *Bacillus subtilis* GB03 caused an increase in glycine betaine and its precursor choline content in the *Arabidopsis* [79]. On the grapevine, *Burkholderia phytofirmans* PsJN, an endophytic strain, alleviated cold stress, improving cold acclimation [80]. This is accompanied by increased expression of defense and cold-related genes [81]. Bacterization increased starch content by 1.2 times and total soluble sugars by two times, with sugars implicated in low-temperature tolerance showing greater amounts in treated seedlings [82].

## 5. PGPR population ecology and impact on root system performance

PGPR's methods of action have been studied extensively utilizing only one strain and one host plant. However, PGPRs do not function in the rhizosphere as individuals. A diverse range of PGPR populations are interacting with the same host plant, and they may have antagonistic or synergistic effects. Different taxonomic groupings of plant growth-promoting rhizobacteria strains exist, and these groups may coexist in a particular soil [83]. PGPR strains from different taxonomic groups might coexist in soil and colonize the same rhizosphere. This potential has been recorded several times, particularly when determining the taxonomic identity of bacterial isolates chosen for their beneficial influence on plant growth [84]. It appears that this option is the rule rather than the exception. A functional group is made up of PGPR populations that perform the same function (for example, ISR, nitrogen fixation, plant growth promotion, and so on). When particular genes are documented, functional group methods can be used. The coexistence of genetically contrasting PGPR strains has two effects when examining the PGPR-plant connection in fields. If the PGPR populations have synergistic effects, the PGPR function may be higher than only one kind of strain. The higher the function leads to increased nutrient availability to the plant. Others, such as the generation of auxinic signals, will require fine-tuning of the functional group's performance to prevent production levels that are too small or too big [85]. Regulatory effects should also be considered to bridge the gap between the PGPR function and its actual execution [86]. Some interactions between various PGPR strains in the same rhizosphere are crucial. Interactions between different PGPR functional groups can be competitive and inhibitory [87] and positive signaling [15]. These interactions have the ability to influence PGPR effectiveness by modulating spatial colonization patterns on roots [87].

## 6. PGPR's effects on regulated Phyto and microbial beneficial protein interactions

PGPR efficacy is connected to mutual gene regulation between PGPR and plants during colonization. This regulation has positive effects on growth, nutrient

absorption, and metabolite upregulation, as well as on proteins and biological processes, and gene expression [88–90]. PGPR produces a number of phyto-beneficial and desirable features, including increased phytohormone production and resistance to biotic and abiotic stress [91]. Increases in gene expression and particular protein families, which interfere with hormone production, cellular breakdown, and signaling pathway modulation, are linked to the positive effect. The capacity of sulfatase to cycle ambient sulfur via degradation or cellular remodeling might explain the rise in element compositions after PGPR inoculation. Because of a rise in the Carbohydrate Kinases protein family the rise in biomass in plants is linked to the increased sugars and carbohydrates shown in their study [92].

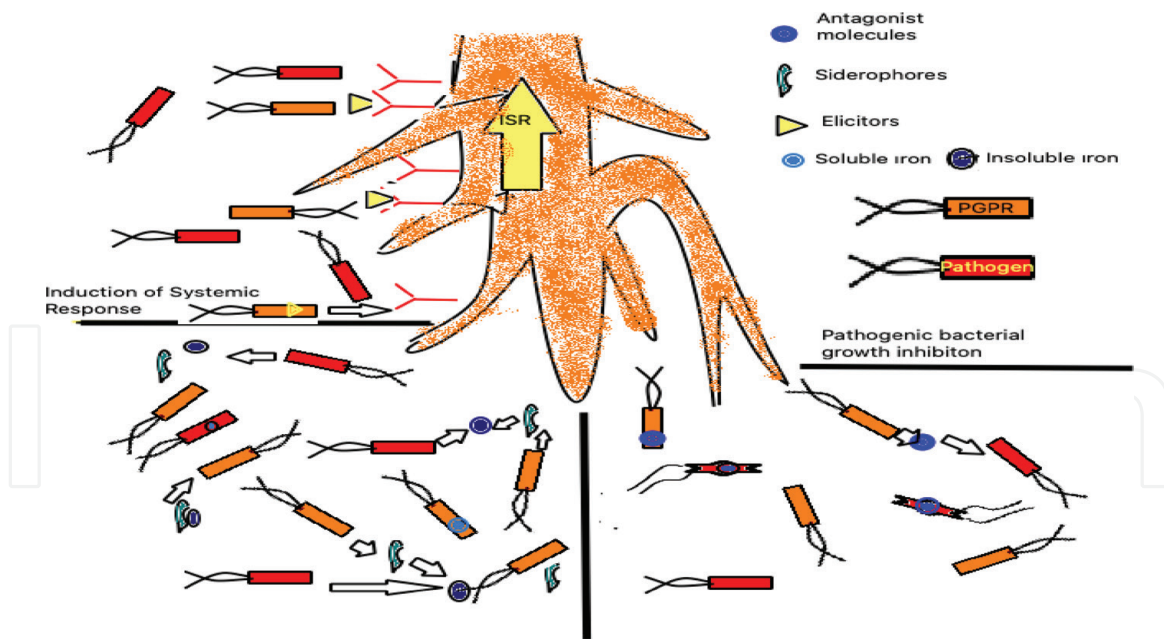
Heat Shock Protein 70 (Hsp70) is a family of conserved proteins that are found in the cytoplasm and in the chloroplasts. Hsp70 is involved in protein synthesis, stress protection, and protein translocation help. The preservation of cellular homeostasis and protection from various forms of stress. Phyto-beneficial characteristics were modulated by reciprocal protein activation via microbe–plant interactions during and after colonization by PGPR. Furthermore, bacterial gene regulators linked to bacterial signaling, DNA binding transcriptional regulators, and cell proliferation were induced by plant root exudates [93]. Climate change has a significant impact on the efficiency of PGPR, yet unfavorable growing circumstances in the field are to be expected as part of the routine operation of agriculture [94]. Multiple mechanisms, such as phosphate solubilization, dinitrogen fixation, ACC deaminase, and antifungal activity, IAA and siderophore biosynthesis, and others, are responsible for plant growth promotion and increased yield [95]. Following PGPR treatments, significant increases in yields of several agricultural plants have been seen in both natural agro-ecological niches and controlled soil conditions. Because there is a global aversion to eating foods made from genetically engineered plants, PGPR might be useful for encouraging plant development. The widespread use of PGPR might reduce the world's reliance on agricultural pesticides. Furthermore, it is a technology that farmers in both rich and poor nations may easily obtain [96].

## 7. PGPR as a growth enhancer

Plant development is aided by PGPR through both direct and indirect processes, which include improving plant physiology and resistance to diverse phytopathogens via a variety of modes and activities [97]. These include nutrition fixation, biotic and abiotic stress neutralization, and disease prevention through the production of volatile organic compounds and enzymes. However, depending on the kind of host plant (**Figure 3**), the manner of action of different kinds of PGPR differs [98]. Plant genotypes, developmental phases, defense systems, and other members of the microbial community are among the biotic and abiotic elements that impact them [99].

Auxin may be produced by a wide range of bacterial species (Indole acetic acid). *Mycobacterium*, *Sphingomonas* *Hizobium*, *Azospirillum*, *Microbacterium*, and *Burkholderia* spp. are examples of such bacteria [100]. PGPR treatments were found to have a considerable impact on the hormone content of cabbage seedlings in previous investigations. Inoculation with PGPR enhanced salicylic acid, gibberellic acid, and IAA levels. *P. agglomerans* RK-92 had the highest levels of gibberellic acid, salicylic acid, and IAA, whereas abscisic acid was highest in the control treatment [9].

*Pseudomonas aeruginosa*, *Pseudomonas putida*, *Paenibacillus polymyxa*, *Enterobacter asburiae*, *Mesorhizobium ciceri*, *Azotobacter chroococcum*, *Klebsiella oxytoca* and *Stenotrophomonas maltophilia*, *Rhizobium leguminosarum*, all of which are considered



**Figure 3.**  
*Rhizobacteria promotes plant development in a variety of ways.*

PGPR. Auxins, kinetin, ethylene and gibberellins are hormones generated exclusively by these bacteria and are vital for root growth (**Figure 3**) [101].

## 8. Conclusion

Plants have developed a variety of biotic relationships with microbial communities in the soil, ranging from commensalism to mutualism. Plant-PGPR collaboration plays a key part in this continuum of interactions, boosting the development and health of a wide range of plants. Recent research has aided in understanding important characteristics of plant-PGPR interactions, such as mechanisms of action and ecology, although substantial information gaps remain. Rhizobacteria that promote plant development have the ability to control RSA, as well as the growth and physiology of plant. The generation of IAA by PGPR has long been linked to RSA effects. Remarkably, bacterial regulation of auxin distribution and IAA signal pathways has also been discovered, independent of IAA synthesis by PGPR. Plant hormones control the expression of genes involved in the production of other hormones or hormonal pathway components. As a result, it explains why PGPR has such pleiotropic effects on plants.

Understanding how PGPR influences the plant hormonal balance and signaling pathways is one of the key ongoing scientific problems ahead. PGPR populations from different soils can work together to exhibit plant-beneficial characteristics. As previously stated, plant-rhizo-microbiome interactions are complicated and vary depending on plant genotypes and soil-inhabiting populations. The taxonomic and functional diversity of next-generation sequencing methods has begun to emerge. They've started to provide fresh information on the ecology of PGPR groupings. Metatranscriptomics and metaproteomics are likely to advance dramatically in the near future, allowing for greater knowledge of the ecological behavior of PGPR in the rhizosphere.

# IntechOpen

## Author details

Metin Turan<sup>1</sup>, Tuba Arjumend<sup>2</sup>, Sanem Argın<sup>3</sup>, Ertan Yıldırım<sup>4\*</sup>,  
Hikmet Katırcıoğlu<sup>5</sup>, Burak Gürkan<sup>5</sup>, Melek Ekinci<sup>4</sup>, Adem Güneş<sup>6</sup>,  
Ayhan Kocaman<sup>7</sup> and Parisa Bolouri<sup>1</sup>

1 Department of Genetics and Bioengineering, Faculty of Engineering,  
Yeditepe University, Istanbul, Turkey

2 Department of Plant Protection, Faculty of Agriculture, Uşak University, Uşak,  
Turkey

3 Department of Agricultural Trade and Management, Yeditepe University,  
Istanbul, Turkey

4 Department of Horticulture, Faculty of Agriculture, Atatürk University,  
Erzurum, Turkey

5 Secondary School Science and Mathematics Education, Gazi University, Ankara,  
Turkey

6 Department of Soil Science, Faculty of Agriculture, Erciyes University, Kayseri,  
Turkey

7 Department of Environmental Engineering, Faculty of Engineering,  
Karabük University, Karabük, Turkey

\*Address all correspondence to: [ertanyil@atauni.edu.tr](mailto:ertanyil@atauni.edu.tr)

## IntechOpen

© 2021 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/3.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 

## References

- [1] Esitken, A., Ercisli, S., Karlidag, H., Sahin, F., 2005. Potential use of plant growth promoting rhizobacteria (PGPR) in organic apricot production. In: Proceedings of the International Scientific Conference of Environmentally Friendly Fruit Growing, Tartu-Estonia, 7-9 September, pp. 90-97
- [2] Rodríguez, H., Fraga, R., 1999. Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnol. Adv*
- [3] Hardoim, P. R., van Overbeek, L. S., and Elsas, J. D. (2008). Properties of bacterial endophytes and their proposed role in plant growth. *Trends Microbiol.* 16, 463-471. doi: 10.1016/j.tim.2008.07.008
- [4] Vessey, J.K. (2003) Plant growth promoting rhizobacteria as biofertilizers, *Plant Soil* 255, 571-586.
- [5] Walker, J. D., Enache, M., & Dearden, J. C. (2003). Quantitative cationic-activity relationships for predicting toxicity of metals. *Environmental Toxicology and Chemistry: An International Journal*, 22(8), 1916-1935.
- [6] Kloepper, J. W., Rodríguez-Kábana, R., McINROY, J. A., & Collins, D. J. (1991). Analysis of populations and physiological characterization of microorganisms in rhizospheres of plants with antagonistic properties to phytopathogenic nematodes. *Plant and Soil*, 136(1), 95-102.
- [7] Miransari M (2014) Plant growth promoting rhizobacteria. *J Plant Nutr* 37:2227-2235. <https://doi.org/10.1080/01904167.2014.920384>
- [8] Ansari, R. A., Rizvi, R., Sumbul, A., & Mahmood, I. (2017). PGPR: current vogue in sustainable crop production. In *Probiotics and plant health* (pp. 455-472). Springer, Singapore.
- [9] Turan, M., Ekinçi, M., Yildirim, E., Güneş, A., Karagöz, K., Kotan, R., & Dursun, A. (2014). Plant growth-promoting rhizobacteria improved growth, nutrient, and hormone content of cabbage (*Brassica oleracea*) seedlings. *Turkish Journal of Agriculture and Forestry*, 38(3), 327-333.
- [10] Egamberdieva, D., & Lugtenberg, B. (2014). Use of plant growth-promoting rhizobacteria to alleviate salinity stress in plants. In *Use of Microbes for the Alleviation of Soil Stresses*, Volume 1 (pp. 73-96). Springer, New York, NY.
- [11] Gouda, S., Kerry, R. G., Das, G., Paramithiotis, S., Shin, H. S., & Patra, J. K. (2018). Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture. *Microbiological research*, 206, 131-140.
- [12] Scheres, B., Benfey, P., and Dolan, L. (2002). Root development. *Arabidopsis Book* 1, e0101. doi: 10.1199/tab.0101 PMCID:PMC3243376
- [13] Von Wirén, N., Khodr, H., & Hider, R. C. (2000). Hydroxylated phytosiderophore species possess an enhanced chelate stability and affinity for iron (III). *Plant Physiology*, 124(3), 1149-1158.
- [14] Desbrosses, G. J., & Stougaard, J. (2011). Root nodulation: a paradigm for how plant-microbe symbiosis influences host developmental pathways. *Cell Host & Microbe*, 10(4), 348-358.
- [15] Combes-Meynet, E., Pothier, J. F., Moënné-Loccoz, Y., & Prigent-Combaret, C. (2011). The *Pseudomonas* secondary metabolite 2, 4-diacetylphloroglucinol is a signal inducing rhizoplane expression of

Azospirillum genes involved in plant-growth promotion. *Molecular plant-microbe interactions*, 24(2), 271-284.

[16] Gupta, G., Parihar, S. S., Ahirwar, N. K., Snehi, S. K., & Singh, V. (2015). Plant growth promoting rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture. *J Microb Biochem Technol*, 7(2), 096-102.

[17] Ahemad, M., & Khan, M. S. (2012). Effect of fungicides on plant growth promoting activities of phosphate solubilizing *Pseudomonas putida* isolated from mustard (*Brassica campestris*) rhizosphere. *Chemosphere*, 86(9), 945-950

[18] Glick, B. R. (2012). *Plant growth-promoting bacteria: mechanisms and applications*. Scientifica, 2012.

[19] Jahanian, A., Chaichi, M. R., Rezaei, K., Rezayazdi, K., & Khavazi, K. (2012). The effect of plant growth promoting rhizobacteria (PGPR) on germination and primary growth of artichoke (*Cynara scolymus*). *International Journal of Agriculture and Crop Sciences (IJACS)*, 4(14), 923-929.

[20] Xie, J., Shi, H., Du, Z., Wang, T., Liu, X., & Chen, S. (2016). Comparative genomic and functional analysis reveal conservation of plant growth promoting traits in *Paenibacillus polymyxa* and its closely related species. *Scientific reports*, 6(1), 1-12.

[21] Damam, M., Kaloori, K., Gaddam, B., & Kausar, R. (2016). Plant growth promoting substances (phytohormones) produced by rhizobacterial strains isolated from the rhizosphere of medicinal plants. *International Journal of Pharmaceutical Sciences Review and Research*, 37(1), 130-136.

[22] Sureshbabu, K., Amaresan, N., & Kumar, K. (2016). Amazing multiple function properties of plant growth

promoting rhizobacteria in the rhizosphere soil. *Int J Curr Microbiol Appl Sci*, 5(2), 661-683.

[23] Overvoorde, P., H. Fukaki & T. Beeckman. 2011. Auxin control of root development. *Cold Spring Harbor Perspective in Biology*. 2 1537 -1542

[24] Aloni, R., Aloni, E., Langhans, M., & Ullrich, C. I. (2006). Role of auxin in regulating Arabidopsis flower development. *Planta*, 223(2), 315-328.

[25] Perrig, D., Boiero, M. L., Masciarelli, O. A., Penna, C., Ruiz, O. A., Cassán, F. D., & Luna, M. V. (2007). Plant-growth-promoting compounds produced by two agronomically important strains of *Azospirillum brasilense*, and implications for inoculant formulation. *Applied microbiology and biotechnology*, 75(5), 1143-1150.

[26] Remans, R., Beebe, S., Blair, M., Manrique, G., Tovar, E., Rao, I., & Vanderleyden, J. (2008). Physiological and genetic analysis of root responsiveness to auxin-producing plant growth-promoting bacteria in common bean (*Phaseolus vulgaris* L.). *Plant and soil*, 302(1), 149-161.

[27] Creus, C. M., Graziano, M., Casanovas, E. M., Pereyra, M. A., Simontacchi, M., Puntarulo, S., Barassi, C.A., Lamattina, L. (2005). Nitric oxide is involved in the *Azospirillum brasilense*-induced lateral root formation in tomato. *Planta* 221, 297-303. doi: 10.1007/s00425-005- 1523-

[28] Molina-Favero, C., Creus, C. M., Simontacchi, M., Puntarulo, S., & Lamattina, L. (2008). Aerobic nitric oxide production by *Azospirillum brasilense* Sp245 and its influence on root architecture in tomato. *Molecular plant-microbe interactions*, 21(7), 1001-1009.

[29] Bakker, P. A., Pieterse, C. M., & Van Loon, L. C. (2007). Induced systemic

resistance by fluorescent *Pseudomonas* spp. *Phytopathology*, 97(2), 239-243.

[30] Walker, V., Bertrand, C., Bellvert, F., Moënne-Loccoz, Y., Bally, R., & Comte, G. (2011). Host plant secondary metabolite profiling shows a complex, strain-dependent response of maize to plant growth-promoting rhizobacteria of the genus *Azospirillum*. *New Phytologist*, 189(2), 494-506.

[31] Brazelton, J. N., Pfeufer, E. E., Sweat, T. A., Gardener, B. B. M., & Coenen, C. (2008). 2, 4-Diacetylphloroglucinol alters plant root development. *Molecular Plant-Microbe Interactions*, 21(10), 1349-1358.

[32] García de Salamone, I. E., Hynes, R. K., & Nelson, L. M. (2001). Cytokinin production by plant growth promoting rhizobacteria and selected mutants. *Canadian Journal of microbiology*, 47(5), 404-411.

[33] Riefler, M., O. Novak, M. Strnad and T. Schmulling, 2006. *Arabidopsis* cytokinin receptor mutants reveal functions in shoot growth, leaf senescence, seed size, germination, root development and cytokinin metabolism. *Plant Cell*, 18: 40-54.

[34] Dodd, I. C., Zinovkina, N. Y., Safronova, V. I., & Belimov, A. A. (2010). Rhizobacterial mediation of plant hormone status. *Annals of Applied Biology*, 157(3), 361-379.

[35] Bauer, H., Ache, P., Lautner, S., Fromm, J., Hartung, W., Al-Rasheid, K. A., ... & Hedrich, R. (2013). The stomatal response to reduced relative humidity requires guard cell-autonomous ABA synthesis. *Current Biology*, 23(1), 53-57.

[36] Cohen, A. C., Bottini, R., & Piccoli, P. N. (2008). *Azospirillum brasilense* Sp 245 produces ABA in chemically-defined culture medium and increases ABA

content in *Arabidopsis* plants. *Plant Growth Regulation*, 54(2), 97-103.

[37] Yaxley, J. R., Ross, J. J., Sherriff, L. J., and Reid, J. B. (2001). Gibberellin biosynthesis mutations and root development in pea. *Plant Physiology*, 125, 627- 633. doi: 10.1104/pp.125.2.627 PMCID:PMC64864

[38] Pieterse, C. M., Leon-Reyes, A., Van der Ent, S., and Van Wees, S. C. (2009). Networking by smallmolecule hormones in plant immunity. *Nat. Chem. Biol.* 5, 308-316. doi: 10.1038/nchembio.164

[39] Zhang, H., Kim, M. S., Krishnamachari, V., Payton, P., Sun, Y., Grimson, M., Farag, M.A., Ryu, C.M., Allen, R., Melo, I.S., Pare, P.W. (2007). Rhizobacterial volatile emissions regulate auxin homeostasis and cell expansion in *Arabidopsis*. *Planta* 226, 839-851. doi: 10.1007/s00425-007-0530-2

[40] Raj, S. N., Lavanya, S. N., Amruthesh, K. N., Niranjana, S. R., Reddy, M. S., & Shetty, H. S. (2012). Histo-chemical changes induced by PGPR during induction of resistance in pearl millet against downy mildew disease. *Biological Control*, 60(2), 90-102.

[41] García-Gutiérrez, L., Zeriuoh, H., Romero, D., Cubero, J., de Vicente, A., & Pérez-García, A. (2013). The antagonistic strain *Bacillus subtilis* UMAF 6639 also confers protection to melon plants against cucurbit powdery mildew by activation of jasmonate- and salicylic acid-dependent defence responses. *Microbial Biotechnology*, 6(3), 264-274.

[42] Weller, D. M., Mavrodi, D. V., van Pelt, J. A., Pieterse, C. M., van Loon, L. C., and Bakker, P. A. (2012). Induced systemic resistance in *Arabidopsis thaliana* against *Pseudomonas syringae* pv. *tomato* by 2,4-diacetylphloroglucinol-producing

*Pseudomonas fluorescens*.

Phytopathology 102, 403-412. doi:  
10.1094/PHYTO-08-11-0222

[43] Kamal, R., Gusain, Y. S., & Kumar, V. (2014). Interaction and symbiosis of AM fungi, actinomycetes and plant growth promoting rhizobacteria with plants: strategies for the improvement of plants health and defense system. *Int J Curr Microbial Appl Sci*, 3(7), 564-585.

[44] Strömberg, A., & Brishammar, S. (1993). A histological evaluation of induced resistance to *Phytophthora infestans* (Mont.) de Bary in potato leaves. *Journal of Phytopathology*, 137(1), 15-25.

[45] Bekri, M. A., Desair, J., Keijers, V., Proost, P., Searle-van Leeuwen, M., Vanderleyden, J., & Vande Broek, A. (1999). *Azospirillum irakense* produces a novel type of pectate lyase. *Journal of bacteriology*, 181(8), 2440-2447.

[46] Sekar, C., Prasad, N. N., and Sundaram, M. D. (2000). Enhancement of polygalacturonase activity during auxin induced para nodulation and endorhizosphere colonization of *Azospirillum* in rice roots. *Indian J. Exp. Biol.* 38, 80-83.

[47] Goswami, D., Thakker, J. N., & Dhandhukia, P. C. (2016). Portraying mechanics of plant growth promoting rhizobacteria (PGPR): A review. *Cogent Food & Agriculture*, 2(1).

[48] Ramadan, E. M., AbdelHafez, A. A., Hassan, E. A., & Saber, F. M. (2016). Plant growth promoting rhizobacteria and their potential for biocontrol of phytopathogens. *African Journal of Microbiology Research*, 10(15), 486-504.

[49] Islam, S., Akanda, A. M., Prova, A., Islam, M. T., & Hossain, M. M. (2016). Isolation and identification of plant growth promoting rhizobacteria from cucumber rhizosphere and their effect

on plant growth promotion and disease suppression. *Frontiers in microbiology*, 6, 1360.

[50] Mantelin, S., and Touraine, B. (2004). Plant growth-promoting bacteria and nitrate availability: impacts on root development and nitrate uptake. *J. Exp. Bot.* 55, 27-34. doi: 10.1093/jxb/erh010

[51] Ramaekers, L., Remans, R., Rao, I. M., Blair, M. W., and Vanderleyden, J. (2010). Strategies for improving phosphorus acquisition efficiency of crop plants. *Field Crops Res.* 117, 169-176. doi: 10.1016/j.fcr.2010. 03.001

[52] Richardson, A. E., Baréa, J. M., McNeill, A. M., and Prigent-Combaret, C. (2009). Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant Soil* 321, 305-339. doi: 10.1007/s11104-009-9895-2

[53] Miller, S. H., Browne, P., PrigentCombaret, C., Combes-Meynet, E., Morrissey, J. P., and O'Gara, F. (2009). Biochemical and genomic comparison of inorganic phosphate solubilisation in *Pseudomonas* species. *Environ. Microbiol. Rep.* 2, 403– 411. doi: 10.1111/j.1758-2229.2009. 00105.x

[54] Boddey, R. M., Urquiaga, S., Alves, B. J., & Reis, V. (2003). Endophytic nitrogen fixation in sugarcane: present knowledge and future applications. *Plant and soil*, 252(1), 139-149.

[55] Bertrand H., Plassard C., Pinochet X., Touraine B., Normand P., Cleyet-Marel J. C. (2000). Stimulation of the ionic transport system in *Brassica napus* by a plant growth-promoting rhizobacterium (*Achromobacter* sp.). *Can. J. Microbiol.* 46 229-236 10.1139/cjm-46-3-229

[56] Mantelin, S., Desbrosses, G., Larcher, M., Tranbarger, T. J., Cleyet-Marel, J. C., and Touraine, B. (2006).



Nitratedependent control of root architecture and N nutrition are altered by a plant growth-promoting *Phyllobacterium* sp. *Planta* 223, 591-603. doi: 10.1007/s00425-005-0106-y

[57] Kechid, M., Desbrosses, G., Rokhsi, W., Varoquaux, F., Djekoun, A., and Touraine, B. (2013). The NRT2.5 and NRT2.6 genes are involved in growth promotion of *Arabidopsis* by the PGPR strain *Phyllobacterium brassicacearum* STM196. *New Phytol.* 198, 514-524. doi: 10.1111/nph. 12158

[58] Kotur, Z., Mackenzie, N., Ramesh, S., Tyerman, S. D., Kaiser, B. N., and Glass, A. D. (2012). Nitrate transport capacity of the *Arabidopsis thaliana* NRT2 family members and their interactions with AtNAR2.1. *New Phytol.* 194, 724– 731. doi: 10.1111/j.1469-8137.2012. 04094.x

[59] Zhang, H., Kim, M. S., Sun, Y., Dowd, S. E., Shi, H., and Paré, P. W. (2008). Soil bacteria confer plant salt tolerance by tissue-specific regulation of the sodium transporter HKT1. *Mol. Plant Microbe Interact.* 21, 737-744. doi: 10.1094/MPMI-21-6-0737

[60] Rus, A., Yokoi, S., Sharkhuu, A., Reddy, M., Lee, B. H., Matsumoto, T. K., Koiwa, H., Zhu, J.K., Bressan, R.A., Hasegawa, P.M. (2001). AtHKT1 is a salt tolerance determinant that controls Na<sup>+</sup> entry into plant roots. *Proc. Natl. Acad. Sci. U.S.A.* 98, 14150– 14155. doi: 10.1073/pnas.241501798 PMCID: PMC61183

[61] Zhang, H., Sun, Y., Xie, X., Kim, M. S., Dowd, S. E., and Pare, P. W. (2009). A soil bacterium regulates plant acquisition of iron via deficiency-inducible mechanisms. *Plant J.* 58, 568-577. doi: 10.1111/j.1365-313X. 2009.03803.x

[62] Srivastava, S., Chaudhry, V., Mishra, A., Chauhan, P. S., Rehman, A., Yadav, A., Narendra, T., Nautiyal, C.S. (2012).

Gene expression profiling through microarray analysis in *Arabidopsis thaliana* colonized by *Pseudomonas putida* MTCC5279, a plant growth promoting rhizobacterium. *Plant Signal. Behav.* 7, 235-245. doi: 10.4161/psb.18957 PMCID:PMC3405686

[63] Vargas, L., Gurjao de Carvalho, T. L., Gomes Ferreira, P. C., Baldani, V. L., Baldani, J. I., and Hemerly, A. S. (2012). Early responses of rice (*Oryza sativa* L.) seedlings to inoculation with beneficial diazotrophic bacteria are dependent on plant and bacterial genotypes. *Plant Soil* 356, 127-137. doi: 10.1007/s11104-012- 1274-8

[64] Miché, L., Battistoni, F., Gemmer, S., Belghazi, M., and ReinholdHurek, B. (2006). Upregulation of jasmonate-inducible defense proteins and differential colonization of roots of *Oryza sativa* cultivars with the endophyte *Azoarcus* sp. *Mol. Plant Microbe Interact.* 19, 502-511. doi: 10.1094/MPMI-19-0502

[65] Brusamarello-Santos, L. C. C., Pacheco, F., Aljanabi, S. M. M., Monteiro, R. A., Cruz, L. M., Baura, V. A., & Wasseem, R. (2012). Differential gene expression of rice roots inoculated with the diazotroph *Herbaspirillum seropedicae*. *Plant and Soil*, 356(1), 113-125.

[66] Verhagen, B. W., Glazebrook, J., Zhu, T., Chang, H. S., van Loon, L. C., and Pieterse, C. M. (2004). The transcriptome of rhizobacteria-induced systemic resistance in *Arabidopsis*. *Mol. Plant Microbe Interact.* 17, 895-908. doi: 10.1094/MPMI.2004. 17.8.895

[67] Van de Mortel, J. E., de Vos, R. C., Dekkers, E., Pineda, A., Guillod, L., Bouwmeester, K., Joop, J.A., Loon, V., Dicke, M., Raajmakers, J.M. (2012). Metabolic and transcriptomic changes induced in *Arabidopsis* by the rhizobacterium *Pseudomonas fluorescens* SS101. *Plant Physiol.* 160,

2173– 2188. doi: 10.1104/pp.112.207324  
PMCID:PMC3510139

[68] Maketon, C., Fortuna, A. M., and Okubara, P. A. (2012).

Cultivardependent transcript accumulation in wheat roots colonized by *Pseudomonas fluorescens* Q8r1-96 wild type and mutant strains. *Biol. Control* 60, 216-224. doi: 10.1016/j.biocontrol.2011.11.002

[69] Shaw, L. J., Morris, P., and Hooker, J. E. (2006). Perception and modification of plant flavonoid signals by rhizosphere microorganisms. *Environ. Microbiol.* 8, 1867-1880. doi: 10.1111/j.1462-2920.2006.01141.x

[70] Heulin, T., Guckert, A., and Balandreau, J. (1987). Stimulation of root exudation of rice seedlings by *Azospirillum* strains – carbon budget under gnotobiotic conditions. *Biol. Fertil. Soil* 4, 9-14

[71] Phillips, D. A., Fox, T. C., King, M. D., Bhuvaneshwari, T. V., & Teuber, L. R. (2004). Microbial products trigger amino acid exudation from plant roots. *Plant physiology*, 136(1), 2887-2894.

[72] Dardanelli, M. S., Manyani, H., Gonzalez-Barroso, S., Rodriguez Carvajal, M. A., Gil-Serrano, A. M., Espuny, M. R., Lopez-Baena, F.J., Bellogin, R.A., Megias, M., Oliero, F.J. (2010). Effect of the presence of the plant growth promoting rhizobacterium (PGPR) *Chryseobacterium balustinum* Aur9 and salt stress in the pattern of flavonoids exuded by soybean roots. *Plant Soil* 328, 483-493. doi: 10.1007/s11104-009-0127-6

[73] Burdman, S. A. U. L., Volpin, H. A. N. N. E., Kigel, J. A. I. M. E., Kapulnik, Y. O. R. A. M., & Okon, Y. A. A. C. O. V. (1996). Promotion of nod gene inducers and nodulation in common bean (*Phaseolus vulgaris*) roots inoculated with *Azospirillum brasilense* Cd.

Applied and environmental microbiology, 62(8), 3030-3033.

[74] Curzi, M. J., Ribaudó, C. M., Trincheró, G. D., Cura, J. A., and Pagano, E. A. (2008). Changes in the content of organic and amino acids and ethylene production of rice plants in response to the inoculation with *Herbaspirillum seropedicae*. *J. Plant Interact.* 3, 163-173. doi: 10.1080/17429140802255167

[75] Ramos-Solano, B., Algar, E., GarciaVillaraco, A., Garcia-Cristobal, J., Garcia, J. A. L., and GutierrezManero, F. J. (2010). Biotic elicitation of isoflavone metabolism with plant growth promoting rhizobacteria in early stages of development in *Glycine max* var. Osumi. *J. Agric. Food Chem.* 58, 1484-1492. doi: 10.1021/jf903299

[76] Bharti, N., Yadav, D., Barnawal, D., Maji, D., & Kalra, A. (2013). *Exiguobacterium oxidotolerans*, a halotolerant plant growth promoting rhizobacteria, improves yield and content of secondary metabolites in *Bacopa monnieri* (L.) Pennell under primary and secondary salt stress. *World Journal of Microbiology and Biotechnology*, 29(2), 379-387.

[77] Chamam, A., Sanguin, H., Bellvert, F., Meiffren, G., Comte, G., Wisniewski-Dyé, F., Bertrand, C., Combaret, C.P. (2013). Plant secondary metabolite profiling evidences strain-dependent effect in the *Azospirillum*–*Oryza sativa* association. *Phytochemistry*, 87, 65-77.

[78] Walker, V., Couillerot, O., Von Felten, A., Bellvert, F., Jansa, J., Maurhofer, M., Bally, R., Moenne-Loccoz, Y., Comte, G. (2012). Variation of secondary metabolite levels in maize seedling roots induced by inoculation with *Azospirillum*, *Pseudomonas* and *Glomus* consortium under field conditions. *Plant Soil* 356, 151-163. doi: 10.1007/s11104-011-0960-2

- [79] Zhang, H., Murzello, C., Sun, Y., Kim, M. S., Xie, X., Jeter, R. M., ... & Paré, P. W. (2010). Choline and osmotic-stress tolerance induced in *Arabidopsis* by the soil microbe *Bacillus subtilis* (GB03). *Molecular plant-microbe interactions*, 23(8), 1097-1104.
- [80] Ait Barka, E., Nowak, J., and Clement, C. (2006). Enhancement of chilling resistance of inoculated grapevine plantlets with a plant growth-promoting rhizobacterium, *Burkholderia phytofirmans* strain PsJN. *Appl. Environ. Microbiol.* 72, 7246-7252. doi: 10.1128/AEM. 01047-06
- [81] Theocharis, A., Bordiec, S., Fernandez, O., Paquis, S., Dhondt-Cordelier, S., Baillieul, F., Clement, C., Barka, E.A. (2012). *Burkholderia phytofirmans* PsJN primes *Vitis vinifera* L. and confers a better tolerance to low nonfreezing temperatures. *Mol. Plant Microbe Interact.* 25, 241-249. doi: 10.1094/MPMI-05-11- 0124
- [82] Fernandez, O., Theocharis, A., Bordiec, S., Feil, R., Jacquens, L., Clement, C., Florence, F., Barka, E.A. (2012). *Burkholderia phytofirmans* PsJN acclimates grapevine to cold by modulating carbohydrate metabolism. *Mol. Plant Microbe Interact.* 25, 496-504. doi: 10.1094/MPMI-09-11-0245
- [83] Almario, J., Kyselková, M., Kopecký, J., Ságová-Marečková, M., Muller, D., Grundmann, G. L., Moenne, L.Y. (2013). Assessment of the relationship between geologic origin of soil, rhizobacterial community composition and soil receptivity to tobacco black root rot in Savoie region (France). *Plant Soil*. doi: 10.1007/s11104-013-1677- 1671
- [84] Upadhyay, S. K., Singh, D. P., & Saikia, R. (2009). Genetic diversity of plant growth promoting rhizobacteria isolated from rhizospheric soil of wheat under saline condition. *Current microbiology*, 59(5), 489-496.
- [85] Spaepen, S., Versees, W., Gocke, D., Pohl, M., Steyaert, J., and Vanderleyden, J. (2007). Characterization of phenylpyruvate decarboxylase, involved in auxin production of *Azospirillum brasilense*. *J. Bacteriol.* 189, 7626-7633. doi: 10.1128/JB.00830-07 PMCID: PMC 216873
- [86] Prigent-Combaret, C., Blaha, D., Pothier, J. F., Vial, L., Poirier, M. A., Wisniewski-Dyé, F., Moenne-Loccoz, Y. (2008). Physical organization and phylogenetic analysis of *acdR* as leucine-responsive regulator of the 1-aminocyclopropane-1-carboxylate deaminase gene *acdS* in phytobeneficial *Azospirillum lipoferum* 4B and other proteobacteria. *FEMS Microbiol. Ecol.* 65, 202– 219. doi: 10.1111/j.1574-6941.2008. 00474.x
- [87] Couillerot, O., Combes-Meynet, E., Pothier, J. F., Bellvert, F., Challita, E., Poirier, M. A., Rohr, R., Comte, G., Moenne-Loccoz, Y., Prigent-Combaret, C. (2011). The role of the antimicrobial compound 2,4-diacetylphloroglucinol in the impact of biocontrol *Pseudomonas fluorescens* F113 on *Azospirillum brasilense* phytostimulators. *Microbiology* 157, 1694-1705. doi: 10.1099/mic.0.043943-0
- [88] Dhawi, F., Datta, R., & Ramakrishna, W. (2015). Mycorrhiza and PGPB modulate maize biomass, nutrient uptake and metabolic pathways in maize grown in mining-impacted soil. *Plant Physiology and Biochemistry*, 97, 390-399.
- [89] Dhawi, F., Datta, R., & Ramakrishna, W. (2017). Proteomics provides insights into biological pathways altered by plant growth promoting bacteria and arbuscular mycorrhiza in sorghum grown in marginal soil. *Biochimica et Biophysica Acta (BBA)-Proteins and Proteomics*, 1865(2), 243-251.
- [90] Dhawi, F., Datta, R., & Ramakrishna, W. (2018). Metabolomics, biomass and lignocellulosic total sugars

analysis in foxtail millet (*Setaria italica*) inoculated with different combinations of plant growth promoting bacteria and mycorrhiza. *Communications in Plant Sciences*, 8, 8.

[91] Etesami, H., & Maheshwari, D. K. (2018). Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture: Action mechanisms and future prospects. *Ecotoxicology and environmental safety*, 156, 225-246.

[92] Zhang, L.X., Gao, M., Li, S.Q., Li, S.X., Liang, Z.S. (2011). Modulation of plant growth, water status and antioxidative system of two maize (*Zea mays* L.) cultivars induced by exogenous glycinebetaine under long term mild drought stress. *Pak. J. Bot.*, 43(3): 1587-1594.

[93] Dhawi, F. (2020). Plant growth promoting Rhizobacteria (PGPR) regulated Phyto and microbial beneficial protein interactions. *Open Life Sciences*, 15(1), 68-78.

[94] Zaidi, A., Khan, M. S., Ahemad, M., Oves, M., & Wani, P. A. (2009). Recent advances in plant growth promotion by phosphate-solubilizing microbes. *Microbial strategies for crop improvement*, 23-50.

[95] Bashan, Y., & Holguin, G. (1997). *Azospirillum*-plant relationships: environmental and physiological advances (1990-1996). *Canadian Journal of Microbiology*, 43(2), 103-121

[96] Gamalero, E., Lingua, G., Berta, G., & Glick, B. R. (2009). Beneficial role of plant growth promoting bacteria and arbuscular mycorrhizal fungi on plant responses to heavy metal stress. *Canadian Journal of Microbiology*, 55(5), 501-514.

[97] Zakry, F.A.A., Z.H. Shamsuddin, K.A. Rahim, Z.Z. Zakaria and A.A. Rahim, 2012. Inoculation of *Bacillus*

*sphaericus* UPMB-10 to young oil palm and measurement of its uptake of fixed nitrogen using the <sup>15</sup>N isotope dilution technique. *Microbes Environ.*, 27: 257-262. DOI: 10.1264/jsme2.ME11309

[98] García-Fraile, P., Menéndez, E., & Rivas, R. (2015). Role of bacterial biofertilizers in agriculture and forestry. *AIMS Bioengineering*, 2(3), 183-205.

[99] Vacheron, J., Desbrosses, G., Bouffaud, M. L., Touraine, B., Moënnelocoz, Y., Muller, D., & Prigent-Combaret, C. (2013). Plant growth-promoting rhizobacteria and root system functioning. *Frontiers in plant science*, 4, 356.

[100] Uma Maheshwari, T.C., Sivagurunathan, P., Sangeetha, D. (2013). Performance of Bradyrhizobial isolates under drought conditions. *Int. J. Curr. Microbiol. Appl. Sci.* 2:228-232.

[101] Ahemad, M., & Kibret, M. (2014). Mechanisms and applications of plant growth promoting hizobacteria: current perspective. *Journal of King saud University-science*, 26(1), 1-20