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ROOT ASSOCIATED BACTERIA – FRIENDS OR ENEMIES? A REVIEW

GABRIELA MIHALACHE, MARIA-MAGDALENA ZAMFIRACHE and MARIUS ŞTEFAN

"Alexandru Ioan Cuza" University of Iaşi, Faculty of Biology, Iaşi, Romania
Corresponding author: Maria-Magdalena Zamfirache, magda@uaic.ro; magda_zamfirache@yahoo.com

Plant roots, due to their exudates, represent important ecological niches for bacteria, which can influence the plant growth by their both beneficial and deleterious effects. The positive effects of bacteria interaction with the plants roots consist in facilitating the nutrient uptake (N, P), producing phytohormones, enhancing their resistance to biotic and abiotic factors such as pathogenic fungi and bacteria, extreme temperatures, heavy metals, salinity. Regarding the harmful effects of bacteria on plants growth, production of phytotoxins, competition for nutrients or inducing diseases or even plants death represents examples of mechanisms by which bacteria can affect in a negative manner the growth of the plants.

Keywords: root exudates, bacteria, rhizosphere, colonization, beneficial interactions, and harmful interactions.

1. INTRODUCTION

Plants constantly interact with different types of microorganisms providing ideal habitats for microbial growth such as seeds and roots surfaces. According to Berendsen *et al*., 2012 [11] soil microbial communities are the greatest reservoir of biological diversity in the world, the interaction between them and the roots being the most intense. Frequently, interactions between microorganisms and plants take place in the rhizosphere – the area of soil surrounding the roots which is most exposed to the influence of specific substances exuded by the plant roots.

In the rhizosphere many important microbial processes occur, including growth promotion by facilitating nutrient uptake or by production of phytohormones, plant protection through synthesis of antibiotics or siderophores, pathogenesis, competition etc. [69]. Therefore, plant microbe interaction can be considered beneficial, harmful or neutral to the plants [7].

Here we review the cost and gains of the plants interacting with the associated microorganisms, with an emphasis on bacteria and their effect on the plant growth.

2. PLANT ROOTS EXUDATES IN THE RHIZOSPHERE

Plant roots represent important ecological niches that support microbial communities which can influence the plant growth by their beneficial or deleterious effects [77, 88]. The driving force for plant – microorganism interactions is represented by the organic compounds released by roots in a few mm of thickness of the surrounding soil, called rhizosphere [69, 99]. Broadly, in the rhizosphere there are three different, but interacting components: the rhizosphere (soil) or ectorhizosphere, the rhizoplane and the root itself or endorhizosphere. Thus, the rhizosphere or ectorhizosphere is the zone of soil whose chemical composition is influenced by the roots exudates which can stimulate or inhibit the microbial community and its activity. The rhizoplane is the root surface with the epidermis and mucilaginous layer and the strong adhering soil along with specific microorganisms. The root itself or the endorhizosphere is a very important component taking into account the fact that certain endophytic microorganism are capable of inner root tissues colonization including the endodermis and cortical layers [52, 63, 69, 101].

More than 40% of plants photosynthates are secreted into the rhizosphere [11]. Root exudation includes water, sugars and polysaccharides, amino acids, organic acids, fatty acids, sterols, growth factors, enzymes, flavonoids, proteins etc. [68, 88] which serves as signals and growth substrates for beneficial or pathogenic microbial partners [8]. Depending on their molecular weight, root exudates are often divided into two classes of compounds: low-molecular weight compounds as amino acids, organic acids, sugars, phenolics and high-molecular weight exudates such as polysaccharides and proteins [7].

The mechanisms of root exudation are not fully understood but it is known the fact that is a passive process mediated through three different pathways: diffusion, ion channels and vesicle transport [5, 21, 66]. If diffusion is a process of small polar molecules transportation depending on membrane permeability and cytosolic pH [5], ion channels mediate the release of specific carboxylates (citrate, malate, oxalate, phytosiderophores) [66]. Vesicle transport is involved in high molecular weight compounds excretion such as mucilage polysaccharides, mediated by Golgi vesicle, or exoenzymes such as acid phosphatase, phytase, peroxidase, phenoloxidase [5, 66]. Another mechanism, recently discovered, is related to the ATP-binding cassette (ABC) transporters [21, 32] which encompass a large protein family found in all the plants involved in root secretion processes [5].

The root exudates composition and concentration can vary with the plant species, cultivars, plant's age, soil properties, level of biotic and abiotic stress etc. [21, 68, 69]. For example, in a study conducted by De-La-Peña *et al*. (2010) the proteins exuded by *Arabidopsis* roots in various plant development stages in the presence of beneficial or pathogenic microorganisms were different [27]. Moreover, in maize root exudates, the N deficiency reduced the release of amino acids, P deficiency stimulated the release of *gamma*-aminobutyric acid and carbohydrates, K-deficiency led to a less sugars release and Fe deficiency increased the release of glutamate, glucose, ribitol and citrate [19]. As a consequence, plant roots exudates

have a strong influence on microbial population, which can differ between the same plant species growing in the same soil [61], the stage of plant development [88], ecotypes and even in the same root system within a plant [11, 21]. For example, the production of a single exogenous glucosinolate altered the microbial community structure of transgenic *Arabidopsis thaliana* rhizosphere [17]. The composition and the quantity of the rhizospheric microbial population were different in the case of maize in the vegetative growth comparing with the flowering and the fructification period [88].

Moreover, the same root exudates compound can initiate beneficial and pathogenic root-microbe interaction. For example, the same flavonoids from *Pisum sativum* L. attracted the beneficial nitrogen-fixing *Rhizobium leguminosarium* bv. *viciae* symbiont by inducing *nod* gene transcription and also the pathogenic *Nectria haematococca* MP 6 (*Fusarium solani*) by inducing spore germination [72].

Also the presence of beneficial or pathogenic bacteria can influence the root exudation. For example, the interaction between *Medicago trunculata* and its symbiont *Sinorhizobium meliloti* increased the secretion of some plant proteins such as hydrolases, peptidases and peroxidases, but these proteins were not induced when the plants interact with the pathogenic bacteria *Pseudomonas syringae*. Similar results were found when these two strains interacted with *Arabidopsis thaliana* [5].

The process of root exudation is not homogenous along the root axes, high amounts of exudates being released in the root collar and hair root zone in comparison to the root distal parts such as tips. As a result of heterogeneous released of exudates, the root microbial colonization is also spatially different distributed [25].

Besides exudates, in the rizosphere there are also other sources of organic C which consists in root debris and border cells [21]. Border cells are specialized root cells that contain mitochondria, Golgi stacks and Golgi-derived vesicles that become detached from the root cells and enmeshed in the mucilage surrounding the root surface [32]. Along with the root debris and root exudates, border cells build up the rhizodeposition whose function is to attract beneficial microorganisms that service the plant through production of growth promoting hormones, acquiring nutrients, preventing diseases [21], to either entrap pathogenic bacteria and nematodes in the mucilage surrounding the roots [32] or to stimulate their growth [63].

3. RHIZOSPHERE COLONIZATION

The structure of rhizosphere microbial communities differs from that of the bulk soil, [61] suggesting that plants are able to shape their microbiome [103]. However, the rhizosphere microbiome is very diverse comprising bacteria, fungi, nematodes, protozoa, algae and microarthropods. Though, the dominant population of the rhizosphere is made up by species belonging to Proteobacteria and Actinobacteria [69].

Because of the significant amounts of rhizodeposits (10 to 250 mg/g root) microbial biomass and activity are generally much higher in the rhizosphere, than in the bulk soil [37]. The concentration of bacteria per gram of soil can reach here between 10^{10} and 10^{12} cells. Therefore, plant roots, through their rhizodeposits, can be seen as initiators of crosstalked with soil microbes, which in turn produce signals that initiate colonization [69].

Rhizosphere colonization is an important aspect of plant-bacteria beneficial or pathogenic interactions involving different steps: movement of microbes to root surface, adsorption, anchoring and gene expression [37].

A widespread mechanism used by bacteria to sense and respond to their environment stimuli such as rhizodeposits, refers to a system that comprise two components: a membrane-bound sensor histidine protein kinase and a response regulator most often mediating differential gene expression [33]. An example of such mechanism is chemotaxis. This is a primitive sensing mechanism activated by changes in pH, temperature, osmolarity, viscosity or environment chemical composition [4]. Chemotaxis is mediated by two-component regulatory system consisting of a sensor kinase -CheA and a response regulator -CheY. Chemoreceptors, methyl-accepting proteins (MCPs), localized in the cytoplasmatic membrane, monitor the concentration of the chemicals in the environment. Through the methylation of the MCPs a signal transduction occurs and auto-phosphorylation of CheA takes place. Subsequently, P-CheA donates the phosphate group to CheY and P-CheY will interact with the flagellar motor. Whenever the signal drops below a certain threshold, CheY will be phosphorylated, and clockwise rotation will occur. In this case, bacteria will start to tumble to change swimming direction. If this signal rises above the threshold value, CheY will be dephosphorylated and counter clockwise rotation will occur, resulting in a run of the bacterial cell [29].

The capacity of the microorganisms to colonize the rhizosphere can be stimulated by the presence of root exudates [4], but in the same time depends on the genetic traits of the host plant and the colonizing microorganisms [22]. Moreover, recent genomic studies have demonstrated that root exudates modulate the expression of some bacterial genes involved in rhizosphere colonization and competitiveness [33]. For example, *Rhizobium* genes responsible for nodulation are activated in the presence of flavonoids and izoflavonoids which can be found in the root exudates of many leguminous plants [6]. In addition, a mutant strain of *Pseudomonas fluorescens* with plant growth promoting abilities, which lacked the *cheA* gene responsible for chemotaxis, showed reduced movement towards root exudates and also decreased root colonization in tomato rhizosphere [25]. Moreover, the presence of some genes such as *sss* or *colR*/*cols* is necessary for efficient competitive root colonization [22].

In addition to chemotaxis, bacterial movement toward attractants can occur through flagella. However, their presence is not always necessary for colonization as it has been shown for fluorescent *Pseudomonas* and *Serratia* strains and wheat.

Therefore, cell density-dependent quorum sensing is a highly important process for intra- and inter-specific communication and for rhizosphere and rhizoplane colonization [25] mediated by small diffusible signaling molecules (autoinducers) [99]. The most studied quorum-sensing signal among bacteria is the N-acyl-homoserine lactones (AHLs), which can be synthesized by a large number of Gram-negative bacteria, both beneficial and deleterious. The AHL synthesis is dependent on synthases belonging to two classes: the LuxI and AinS homologs. Signal perception relies on a sensor protein, a LuxR homolog, which is also a transcriptional regulator controlling the expression of quorum-sensing-regulated genes [33]. Root colonization through quorum-sensing mechanism have been demonstrated for beneficial *Pseudomonas fluorescent* strain carrying a mutation in a gene of LuxR-LuxI family [25]. Quorum-sensing has been also demonstrated in the case of pathogenic bacteria such as *Erwinia carotovora*. For this strain, quorum-sensing controls the expression of pathogenicity factors conferred by the population density, such as extra-cellular enzymes and the Hrp secretion system, as well as carbapenem antibiotic production [98]. Moreover, it has been shown that plants can interfere with bacterial quorum-sensing by producing so called AHL mimics [9] that can stimulate or repress quorum regulate behavior, affecting gene expression and chemical signal production in both beneficial and pathogenic soil bacteria [72]. For example the production of quorum-sensing active compounds by *Medicago truncatula* stimulated or inhibited the quorum-sensing responses in the LasR, LuxR or LuxP reporters [39].

Regarding the Gram-positive bacteria, the intra-specific communication is mediated by peptide-signaling molecules [99]. This peptide is secreted via ATP-binding cassettes (ABC) transporters. For detection of the autoinducers, Gram-positive bacteria use two-component sensor kinases [62]. Therefore, at the beginning the extracellular stimuli modulates the activity of a histidine protein kinase [72], which transfers a phosphoryl group to the response regulator protein (RR) in a reaction catalyzed by the RR. Phosphotransfer to the RR results in activation of a downstream effector domain that elicits the specific response [92].

Migration of microorganisms towards the roots is followed by movement along the roots, agglutinability by root exudates and adherence [4].

Because of the heterogeneous release of exudates along the root axis, bacterial distribution and colonization on the root is not uniform, the rich areas in organic compounds being preferred [25]. Therefore, a high number of bacteria is founded at the root base: 10^7-10^8 CFU/ cm [58] and rapidly decrease to 10^3–10^4 CFU/cm at the root tip. Furthermore, it is estimated that less than 10% of the root surfaces are colonized by microorganisms. For example, *Pseudomonas* cells on the tomato root are mainly present on junctions between epidermal cells and the deeper parts of the root epidermis and root hairs [22].

Agglutination and attachment of microorganisms to plant roots are very important for a successful colonization. Compounds that can mediate these processes

are adhesins, fimbriae, pili, cell surface proteins and polysaccharides. It has been demonstrated that the number of 4 type fimbriae on bacterial cells of *Pseudomoans fluorescens* WCS365 influence the degree of attachment to tomato roots. In addition, the outer membrane protein OprF of *P. fluorescens* OE28.3 is involved in attachment to plant roots. Also, the lack of the O-antigen side chain of lipopolysaccharide (LPS) in *Pseudomonas* mutants resulted in a deficient colonization of the plant roots, because of the affected outer membrane which didn't allow an optimal functioning of nutrient uptake systems [22].

Another important step in colonization is invasion which is specific only for endophytes and pathogens. A successful invasion suppose that bacteria, after being recognized by plant, must overcome the plant defense responses which implies antioxidant systems, ethylene biosynthesis inhibitors etc. [42]. To escape the plant defense responses, pathogenic bacteria are able to produce some proteins called effectors which interfere with the host defense system provoking infection [71]. Bacterial effectors contribute to pathogen virulence by mimicking or inhibiting plants cellular functions [50]. For example, strains of *Pseudomonas syringae* secrete two effectors AvrPto and AvrPtoB which inhibit the kinase activity of the receptor proteins called pattern recognition receptors (PRRs) of the host cells [15].The aim of these PRRs is to recognize the conserved microbial elicitors (molecules that induce an immune defense response in plants) called pathogen-associated molecular patterns (PAMPs), which are typical components found in all type of pathogens such as bacterial flagellin or fungal chitinase [31]. Also, pathogens can produce effectors that mimic plant hormones. For instance, *Pseudomonas syringae* can produce coronatine that mimic jasmonic acid suppressing the salicylic-acid-mediated defence to biotrophic pathogens, inducing stomatal opening, helping pathogenic bacteria gain access to the apoplast [50]. Important pathogenic bacteria for plants, that provoke yield losing include: *Ralstonia solanacearum*, *Xanthomonas campestris, Agrobacterium tumefaciens, Erwinia stewartii, E. carotovora, Pseudomonas syringae* [98].

4. PLANT-BACTERIA INTERACTION IN THE RHIZOSPHERE

The presence of the bacteria in the rhizosphere can affect the plants by many ways including growth promotion and pathogenesis. Therefore the plant-bacteria interaction can be considered beneficial, harmful or neutral [7].

4.1. BENEFICIAL INTERACTION

Beneficial interactions between plants and microorganisms are frequent in nature and usually take place in the rhizosphere, where the nutrient abundance favor the microorganisms development, improving plant growth or helping the plant to overcome biotic or abiotic stress [14, 103]. The best known example of beneficial microorganisms is the mycorrhizal fungi that form symbiosis with

approximately 80% of all terrestrial plant species by delivering nutrients for the plants in return for photosynthates. Beneficial interactions also occur between symbiotic bacteria belonging to *Rhizobium* genus and leguminous plants in which the *Rhizobium* bacteria fix atmospheric nitrogen for the plant. Besides symbiotic beneficial association, free living rhizosphere microorganisms that include plant growth promoting rhizobacteria (PGPR) can positively affect the plant growth [103]. The benefits of plant-PGPR interaction include increases in seed germination rate, root growth, yield, leaf area, chlorophyll content, nutrient uptake, protein content, hydraulic activity, tolerance to abiotic stress, shoot and root weights, biocontrol, and delayed senescence [2, 25]. For example, the inoculation of runner bean seeds (*Phaseolus coccineus* L.) with *Bacillus pummilus* and *Bacillus mycoides* alone or in combination increased the rate of photosynthesis, the transpiration, the water use efficiency, the chlorophyll content, the grain yield, the nutritive value of the beans, but also enhanced the stress tolerance [90]. Stimulatory effects of rhizobacteria on the growth of the plants have been also observed in the case of maize, soybean or sunflower. For this plants a better development of stem length, photosynthesis, catalase activity, protein content have been seen [88].

The mechanisms of plant growth promotion mediated by rhizobacteria are not fully understood [36, 43] but it is know that these processes take place either by direct interaction between beneficial bacteria and their host plants or indirectly due to their antagonistic effects against plant pathogens [12]. Examples of direct mechanisms are phytohormones production, phosphate solubilization or nitrogen fixation. The indirect mechanisms are represented by reduction or prevention of the harmful effect of pathogenic organisms, production of substances such as antibiotics, siderophores, various enzymes (chitinase, protease, lipase, etc.) or stimulation of the plant systemic resistance [3, 40, 55]. Rhizobacteria can possess more than one mechanism through which it can influence the growth of the plants as in the case of *Bacillus pummilus* strain isolated from the rhizosphere of *Phaseolus coccineus* L. which was found positive for phosphate solubilization but also for siderophore production [91].

Due to their beneficial effects on plant growth, these bacteria can be used as inoculants in agriculture. According to the goal of their application, they can be classified as biofertilizers (such as rhizobia, which have been applied commercially for over a century), phytostimulators (such as auxin-producing, root-elongating *Azospirillum*), rhizoremediators (pollutant degraders which use root exudate as their carbon source) and biopesticides [57].

Direct mechanisms used by rhizobacteria for plant growth promotion

Nitrogen fixation

Nitrogen is an essential element for the plants growth, being required in some important processes as synthesis of enzymes, proteins, chlorophyll, DNA and RNA [43]. Although there is about 78% in the atmosphere, N_2 is a limiting factor for

the growing plants due to the low accessibility [3, 13, 96]. Important for atmospheric N_2 transformation into plant-utilizable forms are the nitrogen fixing bacteria, which changes nitrogen to ammonia by using a complex enzyme system called nitrogenase [3]. Bacteria with nitrogen fixing abilities can either form symbiosis with the leguminous plants (*Rhizobium* genus), with the trees (*Frankia* genus) or can live free in the soil [2, 3, 100, 102]. Among the free living bacteria with nitrogen fixation capabilities are the rhizobacteria [13, 55], also known as diazotrophs being capable of forming non-obligate interaction with the non-leguminous plants [3]. Examples of nitrogen fixing rhizobacteria are: *Azoarcus, Azospirillum, Herbaspirillum, Azotobacter, Burkholderia, Gluconobacter, Pseudomonas, Enterobacter* [13, 14, 78]. Beneficial effects of inoculation with *Azospirillum* on wheat yields in both greenhouse and field conditions have been reported. Also an increase in the yield of rice, cotton and wheat has been seen after the application of *Azotobacter* species. However, in many cases the yield increasing was mainly attributed to PGPR ability to improve the root development due to phytohormones production, which led to a better water and mineral uptake compared to biological N_2 fixation [43].

The mechanism of nitrogen fixation by PGPR is based on the activity of nitrogenase enzyme, a two component metallo-enzyme composed of: dinitrogenase reductase, a dimer of two identical subunits that contains the sites for MgATP binding and hydrolysis, and supplies the reducing power to the dinitrogenase and the dinitrogenase component that contains a metal cofactor [38]. Although, dinitrogenase reductase provides electrons with high reducing powers while dinitrogenase uses these electrons to reduce N_2 to NH_3. Three different N fixing systems have been identified depending on the metal cofactor: Mo-nitrogenase, V-nitrogenase and Fe-nitrogenase. Structurally, the N_2 fixation system is not the same for all the bacteria. Anyway, most of nitrogen fixation is carried out by the activity of the molybdenum nitrogenase which is found in all diazotrophs [3]. The genes responsible for nitrogen fixation and nitrogenase biosynthesis are the *nif* genes found in both symbiotic and free living bacteria [3, 55]. Regarding the diazotroph, *nif* genes were first described in *Klebsiella pneumoniae* by using a combination of genetic and biochemical techniques [81]. The *nif* genes can be carried on plasmids as in *Rhizobium* genus or frequently in the chromosome as in free living bacteria [38]. Most of the diazotrophs has the *nif* genes arranged in a single cluster of almost 20–24 kb with seven separate operons that encode 20 different proteins [3, 38, 40], as in the *Klebsiella* species [81]. Alternatively, for other bacterial species as those belonging to *Azoarcus* genus, which have three differently codified nitrogenase systems [14], *nif* genes are grouped into two different chromosomal linkage groups. This thing may be happening due to the different physiological conditions done by nitrogenase sensitivity to oxygen [81], taking into account the fact that *nif* genes expression and nitrogenase activity is inhibited by the oxygen presence [38].

Nitrogen fixation is an energy consumer process requiring at least 16 moles of ATP for each mole of reduced nitrogen [3]. For bacteria belonging to *Azotobacter* and *Beijerinkia* genus, the energy required for nitrogen fixation can be produced only in aerobic conditions which affect the nitrogenase activity. For this reasons, mechanisms needed for nitrogenase protection are present. Regarding the facultative microaerophilic bacteria such as *Azospirillum, Klebsiella* or *Bacillus*, such mechanisms are not necessary because the energy needed in the form of ATP for nitrogen fixation is produced by oxidative pathways [55].

Albeit many PGPR has the ability to fix nitrogen, it seems that this is not the only mechanism of plant growth promoting [97]. Therefore, mutants deficient in nitrogenase activity (*Azospirillum brasilense*, *Azoarcus* sp. and *Pseudomonas putida*) have been constructed observing that they kept their ability to promote the plant growth, questioning the contribution of nitrogen fixation in this process [78]. Moreover, free living bacteria with nitrogen fixation abilities are thought to contribute only in a small proportion to nitrogen assimilation by plants, most of the nitrogen being retain within the cells in the form of ammonia [65].

Phytohormones production

For growth and development of plants, phytohormones such as auxins, gibberellins, cytokinins, ethylene and abscisic acid play a very important role, contributing to the coordination of some important physiological processes (seed germination, root formation, florescence, branching, fruit ripening), increasing the plant resistance to environment factors, inducing or suppressing the expression of some genes or the synthesis of enzymes, pigments and metabolites [94]. These hormones can be produced by plants or by microorganisms such as bacteria or fungi [87]. Symbiotic and free living bacteria are known for their ability to produce phytohormones, influencing plants hormonal balance [94].

Auxin production

Besides the important role on plants cells division, extension and differentiation, auxins stimulate seed and tuber germination, root development, initiate the formation of lateral and adventitious roots, mediate responses to light and gravity, florescence, and fructification, affect processes as photosynthesis, pigment formation, biosynthesis of various metabolites, increase the resistance to stressful conditions [38, 94]. Most of the plants auxin belongs to indole derivates [94], the most frequent and studied being indole-3-acetic acid (IAA) which is used as interchangeable term for auxin [38]. In plants, IAA is mainly found in conjugated forms (amide linked IAA forms bound to one or more amino acids and ester-linked forms bound to sugars) involved in the transport of IAA in plants, storage and subsequent reuse of it, protection against enzymatic destruction, control of IAA levels, as an entry route intro the subsequent catabolism of IAA and only in small amounts as free acid [83].

The optimal auxin concentration needed for the plant growth varies according to plants species, tissues involved and plant development stage. Moreover, it has been seen that concentrations below the optimal levels has no effects on plants, whereas higher concentrations inhibit the growth. For example, in *Arabidopsis thaliana* seedlings, the primary root elongation took place only at exogenous IAA concentration situated between 10^{-10} and 10^{-12} M. The endogenous pool of auxin is influenced by exogenous factors such as bacteria capable of auxin production. In this case, the endogenous concentration of IAA in the roots can exceed the optimal amount stimulating or suppressing the plant growth [38]. Therefore, in the case of the two weeks seedlings of *Arabidopsis thaliana* inoculated with *Pseudomonas thivervalensis* MLG45 strain in a concentration of less than 10 CFU/ml no significant differences in the root length could be observed compared with the sterile control. When the concentration was above 10^2 CFU/ml a 30% reduction of the root size could be observed, from 10^2 to 10^5 CFU/ml the relationship between inoculum density and root length was proportional with a maximum root size reduction of 70% and at concentrations above 10^6CFU/ml the bacterization caused irreversible damage to plants [73].

The inhibitory effect of the auxin can be the result of the interaction of IAA with 1-aminocyclopropan-1-carboxylate synthase [34]. The production of high amounts of IAA by bacteria along with the endogenously produced plant IAA activates ACC synthase, leading to production of ACC, a precursor of ethylene. Ethylene is an inhibitory hormone of root growth, especially of the primary root length. However, there are bacteria such as *Pseudomonas putida* GR12-2 that can produce ACC deaminase which converts ACC to ammonium and 2-ketobutirate lowering the ethylene concentration and also the inhibitory effect on the root growth [87].

More than 80% of the soil bacteria are capable of auxin production [38]. This ability has been detected to many rhizospheric and epiphytic bacteria such as: *Azospirillum* spp., *Agrobacterium* spp., *Azotobacter* spp., *Alcaligenes* spp., *Enterobacter* spp., *Erwinia* spp., *Acetobacter* spp., *Rhizobium* spp., *Bradyrhizobium* spp., and *Herbaspirillum* spp. In addition, the IAA production is widespread among bacteria of the genera: *Pseudomonas, Bacillus* and *Xanthomonas* as well as in *Achromobacter*, *Flavobacterium, Arthrobacter, Klebsiella, Rhodococcus, Mycobacterium, Sphingomonas, Stenotrophomonas, Microbacterium, Flavobacterium, Acinetobacter, Corynebacterium*, and *Micrococcus* [94]. The synthesis of this hormone by rhizobacteria is frequently dependent on the presence of IAA precursor in the root exudates [54]. As in plants, the auxin biosynthesis in bacteria relies on an amino acid called tryptophan [38, 54, 87, 94]. The tryptophan concentration in exudates differs strongly among plants, the amount of IAA produced by bacteria depending on this characteristic. For example the inoculation of seeds with the auxin-generating *Pseudomonas fluorescens* WCS365 resulted in a significant increase in the root weight of radish, but not in the root and shoot weight of cucumber,

sweet pepper or tomato. The explanation is that radish roots produces at least nine times more tryptophan in its exudates per seedling than cucumber, sweet pepper, or tomato [56].

IAA synthesis pathways in bacteria are similar to those which occur in plants, being related to tryptophan, but there are also independent routes. Depending on the mediators involved, five different IAA synthesis ways using tryptophan as precursor were identified [38, 87]. The best characterized IAA synthesis pathway in bacteria is the indole-3-acetamide (IAM), in which tryptophan is converted to IAM by the enzyme tryptophan-2-monooxygenase (IaaM), encoded by the *iaaM* gene and IAM is converted to IAA by an IAM hydrolase (IaaH), encoded by *iaaH*. The genes that encode IaaM and IaaH was cloned and characterized in many bacterial species such as: *Agrobacterium tumefaciens, Pseudomonas syringae, Pantoea agglomerans, Rhizobium* and *Bradyrhizobium* [87].

The indole-3-pyruvate (IPyA) pathway is considered to be a major way of IAA synthesis in plants, even if the key genes and enzymes were not yet discovered. This pathway frequently occurs in beneficial bacteria such as *Bradyrhizobium, Azospirillum*, *Rhizobium* spp. and *Enterobacter cloacae*. In this pathway, tryptophan is converted to IPyA by an aminotransferase, decarboxilated to indole-3-acetaldehyde (IAAld) by indole-3-pyruvate decarboxylase (IPDC) and finally oxidized to IAA. The encoded gene for IPDC enzyme was isolated and characterized in *Azospirillum brasilense, Enterobacter cloacae*, *Pseudomonas putida* and *Pantoaea agglomerans* [87].

The tryptamine pathway (TAM) detected also in plants, was found in *Bacillus cereus* by identification of tryptophan decarboxylase activity and in *Azospirillum* by detection of the conversion of exogenous tryptamine to IAA [87].

IAA synthesis through tryptophan side-chain oxidase (TSO) activity has only been characterized in *Pseudomonas fluorescens* CHA0 and not in plants. In this pathway tryptophan is directly converted to IAAld, which can be oxidized to IAA [87].

The last pathway dependent on tryptophan is indole-3-acetonitrile (IAN). For this route, found also in plants, only the last step is known: the conversion of IAN to IAA by a nitrilase. The identification of nitrilase in *Alcaligenes faecalis* was possible due to the specificity for indole-3-acetonitrile [87].

The tryptophan independent pathways for IAA synthesis are not very well known, but it was demonstrated at *Azospirillum brasilense* using labeled precursors. This pathway is used when tryptophan is not added in the environment. The results showed that 90% of IAA is synthesized via the tryptophan-independent pathway, while 0.1% is produced via the IAM pathway. Moreover it has been observed that the same bacteria can possess several ways of IAA production [87].

Auxin synthesis is affected by either environmental factors as well as genetic factors. Therefore, medium pH, osmotic and matrix stress, carbon starvation and the composition of the root exudates influence the bacterial abilities to produce

IAA [38]. For example, in the case of *Azospirillum brasilense* strains it has been shown that the amount of IAA is increased and the expression of *ipdC* genes take place only in environments with limited carbon concentration, acid pH and only when the bacterial cells enter in the stationary phase [70].

Genetic factors that may affect the amount of IAA synthesized by bacteria are related to the location of the genes: on plasmid (especially for phytopathogenic bacteria) or on chromosome (saprophytic bacteria) or to their way of expression: constitutive or inducible [87, 94]. Therefore, when the genes are located on plasmids, as in the case of *Pseudomonas savastavoi*, the amount of IAA is significantly higher compared with the situations when are situated on the chromosome, as in the case of *Pseudomonas syringae*. This is happening because the plasmids are generally present in various copies in the bacterial cells, providing a higher number of IAA biosynthesis genes [87].

Expression of the genes responsible of IAA synthesis in a constitutive or inducible mode differs among the bacterial species and the biosynthesis pathway. Therefore, in *Agrobacterium tumefaciens* and *Agrobacterium rhizogenes* the region of the Ti plasmid containing *iaaM* and *iaaH* is transferred and integrated into the plant genome and expressed under control of constitutive promoters, resulting in an increase IAA production inside the plants. For *Pseudomonas fluorescens* CHA0 IpyA pathway is usually constitutive, whereas TSO pathway is active only in the stationary phase. Moreover, expression of IAA biosynthesis gene is influenced by two transcriptional regulators *RpoS* which regulates the transcription of genes in response to stress conditions and starvations and the two-component system GacS/GacA, which controls the expression of genes of which are induced during a late logarithmic growth phase and have a role in maintaining the competitiveness of the bacterium in the rhizosphere [87].

Gibberellins production

Gibberellins are the largest class of phytohormones comprising more than 100 compounds synthesized by plants, bacteria and fungi [94]. Therefore, it has been identified 136 gibberellins produced by plants, 28 by fungi that belongs to 7 species and only 4 by bacteria (GA_1, GA_3, GA_4 and GA_{20}) [51]. In plants, gibberellins are involved in many processes as seed germination, steam and leaf growth, flowering and fructification, root growth, root hair abundance, senescence delay. In these processes gibberellins act synergistically with other hormones, affecting the plants hormonal balance. Regarding their role in fungi and bacteria it seems that gibberellins are secondary metabolites that play an important role as signaling factors towards the host plant [16].

Chemically, gibberellins are tetracyclic diterpenoid acids made up by isoprene residues that form four rings (A, B, C, D). The best studied gibberellins that are widespread in nature and exhibit maximum biological activity are GA_1, GA_3, GA_4 and GA_7 [94].

The ability of bacteria to synthesize gibberellins was first described in *Azospirillum brasilense* and *Rhizobium*, but since then they were detected in many bacterial genera such as: *Azotobacter, Arthrobacter, Azospirillum, Pseudomonas, Bacillus, Acinetobacter, Flavobacterium, Micrococcus, Agrobacterium, Clostridium, Rhizobium, Burkholderia, and Xanthomonas*. Usually, the positive effects on plants biomass is associated with an increase content of gibberellins in plant tissues [38].

Cytokinins production

Another group of phytohormones synthesized by both plants and rhizobacteria are cytokinins. Cytokinins are adenine derivates[94] which depending on the chemical structure of their molecule fulfill various important roles in the physiological processes of plants such as: protein synthesis, cellular division, seed germination, stabilization of photosynthetic apparatus under the conditions of water stress, root development, delay of senescence, increased resistance against plant pathogens [38, 44, 94].

Microorganisms are capable of synthesizing various cytokinins derivates such as zeatin, kinetin, isopentenyladenine [94]. The gene responsible of cytokinins production was first described in *Agrobacterium tumefaciens* [38], but it can also be produced by *Rhizobium, Azotobacter, Azospirillum, Arthrobacter, Bacillus, Proteus, Escherichia, Klebsiella* [48, 94]. As in the case of IAA, a high concentration of cytokinins in plants can have an inhibitory effect on the root elongation as a result of plant ethylene levels increasing. The factors that can lead to a cytokinins accumulation are related to the presence of bacteria or to some environmental stresses as drought [38].

Ethylene

Ethylene is a phytohormone produced by most of the plants, but also by different biotic and abiotic processes in soil which can induce changes in the physiological status of the plants [3]. Usually, ethylene inhibit the plant growth when is produced in high amounts, but it can also stimulate it when the concentration inside the plant tissues is low (below $0.1 \mu l \cdot 1^{-1}$) [74]. Therefore, ethylene is involved in fruit ripening, flower senescence, leaf and petal abscission. High amounts of ethylene are synthesized in the condition of environmental stresses such as extreme temperatures, flooding, drought, the presence of toxic metals and organic pollutants, radiation, wounding, insect predation, high salt, and various pathogens including viruses, bacteria, and fungi [38].

The negative effects of the ethylene can be reduced due to the presence of rhizobacteria that possess the enzyme ACC deaminase that can degrade its immediate precursor, L-aminocyclopropane-L-carboxylic acid [34], found in the root exudates and used as a carbon source. Under such conditions re-uptake by roots is prevented and the level of the ethylene inside the roots is highly reduced [95]. Genes responsible for ACC deaminase synthesis have been identified in many bacterial genera such as: *Azospirillum, Rhizobium, Agrobacterium, Achromobacter,*

Burkholderia, Ralstonia, Pseudomonas and *Enterobacter* [38]. These bacteria take up the ethylene precursor ACC and convert it into 2-oxobutanoate and NH_3 [3]. The main effect of seeds inoculated with ACC deaminase producing bacteria refers to root elongation [38], nodulation and N, P and K uptake [3].

Phosphate solubilization

Phosphorus (P) is one of the major plant growth nutrient, which is abundant in soils in both inorganic and organic forms [55]. The biggest reserves of P in soil are represented by mineral forms as apatite, hydroxyapatite and oxyapatite which are insoluble. Moreover, the mineral phosphates can be found associated with the surface of hydrated oxides of Fe, Al, and Mn, which are poorly soluble and assimilable. Another significant amount of P (30–50% of the total phosphorus in soil) is found in organic forms. One of the most stable organic phosphates synthesized by both plants and microorganisms is inositol phosphate. Other organic phosphates present in soil are in the form of phosphomonoesters, phosphodiesters including phospholipids and nucleic acids and phosphotriesters [79].

Most of the agricultural soils contains large reserves of P, especially because of the application of chemical fertilizers [49], their presence being at levels of 400–1200 $mg \cdot kg^{-1}$ of soil [79]. However, a high amount of the P added in the soil is rapidly precipitated by metal–cation complexes, becoming insoluble [38]. P fixation and precipitation is dependent on soil type and pH. Therefore, in the acid soils, P is fixed by free oxides and hydroxides of aluminum and iron, while in alkaline soils it is fixed by calcium [41, 49, 55, 79]. As a result of these processes the availability of the P in soil is very low (less than 10 M $H_2PO_4^-$) [41, 79]. The only forms of phosphate that plants can absorb are the monobasic ($H_2PO_4^-$) and diabasic ($H_2PO_4^{2}$) ions [3, 97].

Taking into account the fact that most of the P compounds are insoluble with a high molecular weight that cannot be assimilated by plants, a biological transformation to either soluble ionic phosphate (Pi, HPO_4^{2-}, $H_2PO_4^{2-}$) or low molecular-weight organic phosphate is necessary [79]. Capable of this process are bacteria that have the ability to solubilize the precipitated phosphates or to mineralize the organic phosphates and make it available to plants [3]. Most of the phosphates solubilizing bacteria are found in the rhizosphere, where the metabolic activity is higher than in the bulk soil [53, 79].

The main mechanism of phosphate solubilization by rhizobacteria is the production of low molecular weight organic acids such as gluconic acid, citric acid, oxalic acid, lactic acid, acetic acid etc. These acids, that are the result of the bacterial metabolism mostly by oxidative respiration or by fermentation of organic carbon sources [85], bind phosphate with their hydroxyl and carboxyl groups thereby chelating cations and also inducing soil acidification, both resulting in the release of soluble phosphate [38]. The rhizosphere pH decreasing occurs due to protons production, biocarbonate release or gaseous (O_2/CO_2) exchanges [53].

However, medium acidification is not the only mechanism used by rhizobacteria for phosphate solubilization [85]. Other mechanisms are related to H^+ excretion originating from NH_4^+ assimilation or respiration [85], production of chelating substances and inorganic acids [38]. The ability of the inorganic acids such as carbonic, sulphidric, nitric [79] or hydrochloric acid is less effective compared to organic acids at the same pH [53].

Regarding the organic phosphate solubilization (mineralization) an important role is played by a number of enzymes as phosphatases (also known as phosphohydrolase), phytases, phosphonatases and C-P lyases [43, 84].

Half of the soil microorganisms have the ability to solubilize the organic phosphorus under the action of phosphatases [53]. The most abundant and best studied phosphatases produced by rhizobacteria are phosphomonoesterases [84] which as phosphodiesterase and phosphotriesterase, catalyze the hydrolysis of phosphoric esters [64, 79]. A high phosphatases activity has been seen in the rhizosphere compared with the non-rhizospheric soil. Moreover, it has been demonstrated that when the level of the available phosphorus in soil decreases the phosphatase activity increases [64]. Other factors that influence the phosphatases activity are: soil properties, soil biocenosis, temperature and presence of inhibitors or activators [64, 79].

Depending on the optimal catalytic activity, phosphomonoesterases can be acid or alkaline [79, 84]. Alkaline phosphatase activity has not been detected in plants, most of the alkaline phosphatase being synthesized by soil microorganisms. The situation is different with respect to acid phosphatase, which in the soil can be derived from plants, fungi and bacteria[64]. However, several studies suggest that microbial phosphatases have a greater affinity for organic phosphate compounds than those from plants [85]. There are situations when fosfomonoesterases act in combination with phosphodiesterases to remove phosphorus from phosphate diesters. In this case phosphodiesterases and fosfomonoesterases act sequentially (one after another). Thus, after the hydrolysis of phosphodiesters results phosphate monoesters that are further hydrolyzed by phosphomonoesters with free phosphate releasing that can be biologically assimilated [64].

Regarding the presence of inhibitors or activators, toluene usage does not affect phosphodiesterase or acid and alkaline phosphomonoesterase activities but increases the phosphotriesterase activity of soil. Application of inorganic P can repress the synthesis of phosphomonoesterases in soil because it inhibits the expression of PHO genes or it may not affect their activity [64].

Another group of enzymes that mineralized phosphorus relates to phytases which degrades phytates. These are the primary source of inositol and the major stored form of P in plant seeds and pollen and are a major component of organic P in soil. Since the ability of plants to obtain P directly from phytate is very limited, the presence of the microorganisms is very important [84].

Regarding the phosphonatases and C-P lyases, they cleave the C-P bond of organophosphonates [80].

Bacterial genera capable of phosphate solubilization or mineralization include: *Pseudomonas, Bacillus, Rhizobium, Burkholderia, Enterobacter, Klebsiella, Serratia, Xanthomonas, Azotobacter, Azospirillum, Citrobacter, Proteus* etc. [20, 38]. Moreover, there are bacterial strains which have the ability to both solubilize and mineralize phosphates such as *Burkholderia caryophylli, Pseudomonas cichorii, Pseudomonas syringae, Bacillus cereus* or *Bacillus megaterium*.

Phosphorus derived from phosphate solubilization or mineralization contributes to the root development, stem elongation, flowers and seed formation, higher yielding of crops, nitrogen fixation or disease resistance [53].

Indirect mechanisms used by rhizobacteria

Siderophore production

Another essential element for all the organisms is the iron. Even though is the fourth most abundant element on earth the amount of iron available for plant assimilation is very low ranging from $10^{-7}$and 10^{-23} M at pH 3.5 and 8.5 [38].The most frequent iron ions found in the well aerated soil are the ferric (Fe^{3+}) ions which are usually precipitated in iron-oxide forms hard to be uptake by plants. The iron preferred by the plant roots to be absorbed is the more reduced ferrous (Fe^{2+}) ion [97]. Plants have developed two strategies for iron uptake. The first strategy used by mono- and dicotyledonous plants relies on rhizosphere acidification through H^+ excretion leading to the reduction of Fe^{3+} to Fe^{2+} and its transport inside the root tissues. The second strategy used by herbaceous and graminaceous plants such as wheat (*Triticuma estivum*), barley (*Hordeum vulgare*), rice (*Oryza sativa*), and maize (*Zea mays*) is based on synthesis of Fe^{3+} chelators called phytosiderophores and absorption of Fe-phytosiderophore complex in root cells mediated by specific transporter molecules [38].

To survive in an iron deficient habitat, bacteria have developed the ability to synthesize siderophores. Sirerophores are non-ribozomal peptides with low molecular weight secreted in the absence of sufficient amounts of iron in the environment [93] with high affinity for Fe^{3+} ions as well as membrane receptors able to bind the Fe–siderophore complex, thereby allowing iron uptake by microorganisms [38].

Siderophores production by bacteria can be influenced by various factors such as pH, the level of iron and the form of iron ions, an adequate supply of carbon, nitrogen and phosphorus. Furthermore, siderophore production is stimulated by $(NH_4)_2SO_4$ and amino acids and an optimum siderophore yield is obtained with urea[82]. The main groups of siderophores include the catecholatesor phenolates (enterobactins, mycobactins, tropolone), hydroxamates (aerobactin, arthrobactin), carboxylates (cepabactin, rhizbactin) and pyoverdines (pyoverdine, pseudobactin) [26]. Most of the siderophores producing bacteria belongs to *Pseudomonas* and *Enterobacter* genera, which are Gram-negative bacteria, but also to *Bacillus* and *Rhodococcus*, Gram-positive bacteria [82].

There are controversial opinions regarding the contribution of bacterial siderophores to plant nutrition. Some authors believe that their role in iron acquisition by plants is insignificant while other authors suggest a vital role, mainly in calcareous soil [97].

The importance of soil bacteria on improving iron nutrition of plants is demonstrated in the case of exposure to heavy metals. Metals mobility in the soil can be influenced by microbial metabolites, especially by siderophores that can bind to magnesium, manganese, chromium (III), gallium (III), cadmium, copper, nickel, arsenic, lead and zinc and radionuclides, such as plutonium (IV) as well as to iron [38].

Moreover, siderophores are known to mediate the competition for iron between microorganisms and to protect the plants against pathogens. For example the siderophores produced by fluorescent pseudomonads lead not only to competition between pseudomonads and pathogenic fungi such as *Fusarium* and *Pythium* suppresing their development but also between different bacterial species and strains of pseudomonads [26].

Antibiotics production

Antibiotics production is usually associated to the ability of rhizobacteria to suppress the soil borne pathogens [38]. The antibiotics produced by rhizobacteria are oligopeptides that inhibit synthesis of pathogens walls, influence the cell membrane structure, inhibit the formation of initiation complex on ribosomes small subunit or inhibit the functions of ribosomes [59].

Bacteria that have an important role in suppressing the activity of pathogenic microorganisms belong, especially, to *Pseudomonas* and *Bacillus* genera. These bacterial antagonists suppress the plant pathogens by secretion of extracellular metabolites that are inhibitory at low concentration. Antibiotics produced by *Pseudomonas* genus are divided into antibiotics that act on fungi, bacteria, anti-tumor and anti-viral compounds. Examples of antibiotics which have an inhibitory effect on phytopathogenic fungi are phenazine (produced by *Burkholderia*, *Streptomyces*, *Brevibacterium* genera), pyrrolnitrin, pyoluteorin (with also bactericidal and herbicidal effects), 2,4-diacetylphloroglucinol, oomycin A, ecomycin, butyrolactones, sulphonamide. Among the antibacterial antibiotics can be mentioned mupirocin (pseudomonic acid) that express an efficient activity against staphylococci and streptococci, *Neisseria gonorrhoeae* and *Haemophilus influenzae*, but are less effective on Gram-positive anaerobes. As antitumor compounds we can mention FR901463 and cepafungins and as antiviral antibiotic – karalicin [35].

Bacillus species produces over 167 different types of antibiotics of which more than 12 are synthesized by *B. subtilis*. These include: iturin, bacillomycin, mycobacilin, fungistatin, surfactin, plipastatina, bacilizina etc. Most *Bacillus* antibiotics are active on both Gram-positive and Gram-negative bacteria (for example colistin, polymixin) and on phytopathogenic fungi such as: *Alternaria solani, Aspergillus*

flavus, Botryosphaeria ribis, Colletotrichum gloeosporioides, Fusarium oxysporum, Helmintho sporiummaydis, Phomopsis gossypii, Penicillium roqueforti, Rosellinane catrix, Pyricularia oryzae etc. [35, 59].

Most antibiotics, that have a vital role in suppressing phytopathogens, are grouped into non-volatile antibiotics (those above) and volatile antibiotics such as hydrogen cyanide, aldehydes, alcohols, ketones and sulfides. Cyanide is a secondary metabolite produced by Gram-negative bacteria (*Pseudomonas fluorescens, P. aeruginosa, Chromobacterium violaceum*) with inhibitory effect on phytopathogenic fungi [35].

Antifungal volatile that belongs to aldehydes such as alcohols, ketones and sulfides can be produced by *Pseudomonas chlororaphis* (PA23) isolated from the root of soybean plants, having inhibitory effect on the development of *Sclerotinia sclerotiorum* [35].

Competition

Another indirect mechanism used by microorganisms for plant growth is competition. Beneficial rhizobacteria competes with pathogens for nutrients and a suitable niche to be colonized. Bacteria that colonize the plant roots consume the nutrients derived the exudates limiting the amount of available nutrients for pathogens. This mechanism is often used by *Pseudomonas fluorescens* due to its nutritional versatility and high rate of multiplication in the rhizosphere [75].

Enzyme production

Production of enzymes by PGPR such as chitinase, cellulose, β-1,3 glucanase, protease or lipase, that induce lysis of fungal cell walls represents another mechanism of suppressing the soilborne pathogens and simultaneously enhancing plant growth processes. Among these enzymes, chitinase is considered to be essential for controlling phytopathogenic fungi such as *Botrytis cinerea, Sclerotium rolfsii, Fusarium oxysporum* var. *cucumerinum*, *Phytophthora* sp. β-glucanase can damage the cell walls of *Rhizoctonia solani* and *Pythium ultimum* [38].

Induced systemic resistance (ISR)

Rizobacteria stimulate indirectly the plant growth by increasing the resistance against pathogens by activating the induced systemic resistance. Beside the local defense response (production of reactive oxygen species) that plants can have in the case of a pathogenic attack, plants can also trigger a systemic response. In this situation, genes encoding pathogenesis-related proteins are activated both in the cells around the affected area and in the whole plant (systemic), limiting the growth of the pathogen. Activation of plant defense genes (called systemic resistance) provides resistance to a broad spectrum of pathogens in the non-infected plant organs. This can be viewed as a form of “plant immunization” [86].

There are two types of systemic resistance depending on the signaling molecules involved in the response: systemic acquired resistance (SAR) that occurs when salicylic acid accumulates inside the plants tissues and induced systemic resistance (ISR), which is performed on a salicylic acid-independent pathway involving jasmonic acid (JA) and ethylene (ET) signals that activates the P1 defense genes [86].

If systemic acquired resistance occurs after an initial infection with a pathogen, induced systemic resistance occurs without a pathogenic attack, being stimulated by the presence of rhizobacteria [24].

The way PGPR increase plant resistance to pathogens, often, does not involve defense mechanisms that are activated in the plant tissues at the perception of induced signal, but rather these tissues are sensitized to express faster and stronger defense responses to pathogen attack, a phenomenon known as priming [28]. Bacterial determinants of induced systemic resistance (elicitors) refer to lipopolysaccharide, siderophores, flagella, diacetilfloroglucinol, pyocianin, bio-surfactants, volatile organic compounds [10]. These induce the expression of a group of genes involved in the plants defense against pathogen attack encoding enzymes involved in the synthesis of phytoalexins, as well as phenolic substances. It is believed that the virulent pathogen species does not determine phytoalexins biosynthesis, thus favoring the expansion of pathogen attack [18].

Therefore, PGPR that induce the systemic resistance fortify the cell wall (*e.g.* by storing callose) and modify the physiological and metabolic responses of the host, leading to the production of defense substances (such as phenolic compounds) to the site of pathogen attack. Biochemical and physiological changes relates to the accumulation of pathogenesis related proteins including antifungals (chitinases, glucanases), oxidative enzymes (peroxidase, lipoxygenase that stimulates the process of lignification and accumulation of volatile compounds and antifungal products) and phytoalexins with antimicrobial properties [24].

Increased resistance to abiotic factors

Rhizobacteria, apart from improving the plants ability to uptake nutrients from the soil or to fight pathogens, can also increase tolerance to various abiotic factors.

Therefore, as a response to water deficiency the production of glycine betaine by osmo-tolerant bacteria can act synergistically with plant produced glycine betaine increasing the plant tolerance to drought. For example, the growth of the rice plants inoculated with osmo-tolerant rhizobacteria was significant under drought stress as compared to non- inoculated plants. The differences were related to shoot dry weight, roots dry weight and numbers of tillers. The growth of groundnut under saline field conditions in the presence of ACC deaminase-producing *Pseudomonas fluorescens* TDK1 was significant compared with the plants growth in the presence of strains lacking the enzyme. In the conditions of extreme temperatures rhizo-

bacteria can improve the plants adaptability to overcome this factor. Therefore, the inoculation with *Burkholderia phytofirmans* PsJN of 18 clones of potato grown under two different temperatures (20°C day, 15°C night; 33°C day, 25°C night) resulted in a plant adaptation to heat and increase of the tubers formation by 63% as compared to the control. Inoculation of grape vines with the same strain resulted in an increased resistance to low temperatures (4°C) due to the accumulation of large amounts of carbohydrate when compared to the control. Moreover, the growth of the barley plants in soils contaminated with cadmium has led to a 120% higher grain yield and twofold decreased cadmium contents in grains when inoculated with *Klebsiella mobilis* CIAM 880 strain. This can be explained by the fact that rhizobacteria has the ability to produce substances that can chelate metals [30].

4.2. HARMFUL INTERACTIONS

Root exudates can equally attract beneficial microorganism and pathogenic population that can have negative effects on plant growth [63, 69]. Microorganisms that are deleterious to plant health include pathogenic fungi, bacteria and nematodes. The number and diversity of these microbial communities depends on the quantity and quality of the rhizodeposits and the microbial interaction that occur in the soil. As the beneficial microorganisms, phtytopathogens can grow in the bulk soil, but rhizosphere is the place where their activity is increased and where the infection occur [77]. The most important plant pathogens are fungi, followed by bacteria and viruses [57]. The strategy used by pathogenic bacteria to proliferate in intercellular spaces (the apoplast) is to enter through as or water pores (stomata and hydathodes, respectively), or gain access via wounds [50]. Only a few groups of bacteria are pathogenic for plants such as *Ralstonia solanacearum* which can cause bacterial wilt of tomato, *Agrobacterium tumefaciens* known as crown gall agent, *Pantoaea stewartii* – cause of Stewart's wilt of corn, *Xanthomonas campestris* – a vascular pathogen that causes black rot of cabbage and other cruciferous plants etc. [98]. There are also some filamentous bacteria (*Streptomyces*) that are adapted to survive in the soil and to infect the plants. The low number of soilborne bacteria may be related with low survival capacity of then on-spore forming bacteria in soil. Moreover, for a successful infection, bacteria need a wound or a natural opening to penetrate into the plants [77]. The mechanisms by which rhizobacteria affect the plant growth relates to the production of phytotoxins and phtyohormones, competition for nutrients, inhibition of myccorhizal fungi [63].

A successful infection depends on the ability of pathogen to avoid or suppress the plant defense responses. Pathogenicity factors that have been identified in bacteria refer to type III effectors and toxins [1]. Type III effectors, also known as TTSS for type three secretion system, are molecules (proteins or nucleic acids) that are directly introduced into the host cell. The TTSS is not generally encountered in non-pathogenic agents, being specific for few pathogenic bacteria. The genes

encoding TTSS are the *hrp* genes (hypersensitive response and pathogenicity), arranged in clusters and located in pathogenicity islands (PAIs), which are regions that vary in G+C content and are flanked by insertion sequences, bacteriophage genes and transposable elements. The *hrp* genes encode proteins that either regulate synthesis or assembly of the TTSS, are structural components of the TTSS, or are extracellular proteins (e.g. harpins) secreted by the TTSS. The mechanisms by which TTSS effector proteins act refers to an increase in the pH and nutrient content of the plant apoplast, making the apoplastic fluids suitable for bacterial development, activate the host defense system through recognition by corresponding host R protein, inhibiting the activation of host defense responses that are signals by other TTSS avirulence effectors, inhibiting the basal resistance mechanisms of plants[76]. For example, the DC3000 type III effector AvrPto overexpressed in transgenic *Arabidopsis* limited the callose deposition and papillae formation [1].

Other important bacterial virulence factors include phytotoxins such as coronatine, syringomycin or pectatelyases [57]. Coronatine, which can be produced by *Pseudomonas* bacteria is a toxin that mimics jasmonic acid and interferes with salicylic acid that mediates the defense response in plants [23]. Regarding syringomycin, it acts through the formation of ion channels in plant plasma membranes which lead to a cascade of intercellular signaling events [57].

Bacterial auxin production can either stimulate the plant growth or can enhance the bacterial gall formation, its synthesis being sometimes associated with pathogenesis. Bacteria such as *Agrobacterium tumefaciens, Agrobacterium rhizogenes, Pseudomonas savastanoi* and *Pantoaea agglomerans* pv. *gypsophilae* possess the IAM pathways involved in IAA synthesis and pathogenesis. The mechanism of gall or tumor formation and the role of IAA are different depending on the species involved. Therefore, for *Agrobacterium tumefaciens* tumor formation involves the transfer of T-DNA, which possesses genes encoding the IAM pathway for IAA formation, from the bacteria into the host genome of infected cells. An auxin overproduction of the transformed plant cells results in the typical crown gall or tumor. Regarding, the mechanism of gall formation by *Pantoaea agglomerans* pv. *gypsophilae* on *Gypsophila* it doesn't involve a DNA transfer as in *Agrobacterium tumefaciens.* Gall formation by *Pantoaea agglomerans* requires a constant presence of the living bacteria. Only the pathogenic *Pantoaea agglomerans* carry the genes encoding the IAM pathway on the pPATHPag plasmid, whereas the non-pathogenic strains possess chromosomal genes encoding the IPyA pathway for IAA biosynthesis.

In addition, a new, but still unclear way of IAA implication in phytopathogenesis relates to a link between the TTSS and phytohormone production in the plant pathogen *Ralstonia solanacearum* was established through a host responsive regulator of the TTSS activation cascade -HrpG. It seems that HrpG controls some virulence determinants and genes probably involved in adaptation to life in the host which includes IAA and ethylene biosynthesis genes [87].

Another mechanism by which rhizobacteria can affect in a negative manner the growth of the plants is the competition for nutrients. In soil, nutrients are distributed in a heterogeneous way, plant roots being under the necessity of competing with microorganisms and other root systems to capture them [45]. In nutrient-rich zones with high microbial activity and density, microbes may initially sequester the available nutrients before roots can gain access to them. Ultimately some of the sequestered nutrients will become available through microbial turnover and be released back into the rhizosphere [47]. For example, in a study in which the grassland soil was inoculated with ^{15}N label in the form of $^{15}NH_4^+$ and $^{15}NO_3^-$, most of labeled nitrogen was recovered in the microbial biomass [46]. When *Glycine max* L. seeds were treated with rhizobacteria an inhibition in the germination process of the seeds was seen, probably due to a nutrient competition [89]. Moreover, microorganisms appear to be more competitive for Fe compared to plants roots. Thus, in a medium were both bacterial and plants siderophores are present at similar concentrations, Fe mostly bounds to the bacterial siderophores, than to phytosiderophores. Regarding another essential element for the plants growth such as phosphorus, rhizosphere microorganisms can reduce its availability to plants by immobilization in the microbial biomass, decomposition of P-mobilizing root exudates and by inhibition of root growth [60]. Zn and Mn deficiency caused by bacterial immobilization can lead to the emergence of diseases of the fruit trees or of the oats [88]. However microbial competitiveness is strongly affected by carbon availability [60]. Therefore, on a short timescale, soil microorganisms compete better than plants for the added N [46]. But in the long term plants outcompete microorganisms maybe because their turnover times [45].

However, bacteria can behave as pathogens or symbionts depending on the environmental conditions [32] such as light, nutrient, water or temperature stress, size of inoculums, host developmental signals. For example, the symptoms associated with the infection with *Pseudomonas syringae* on tomato appear only when the population size exceeds a quorum-sensing threshold, triggering the formation of lesions. Moreover, the bacterial pathogen *Erwinia artroseptica* can be beneficial for its hosts due to its nitrogen-fixing genes, but in the same time, in certain agricultural conditions, it can be harmful by provoking diseases such as potato blackleg [67].

5. CONCLUSIONS

The rhizosphere is the zone of plant-bacteria beneficial and harmful interaction due to root exudates that attract them. The positive effects of bacteria interaction with the plant roots consist in facilitating the nutrient uptake (N, P), producing phytohormones, enhancing their resistance to biotic and abiotic factors such as pathogenic fungi and bacteria, extreme temperatures, heavy metals,

salinity. Bacteria that colonize the rhizosphere can also have a negative impact on the plant growth by production of phytotoxins, competition for nutrients or by inducing diseases or even plants death. However, the abundance of beneficial bacteria in the rhizosphere is considerably higher than that of pathogenic bacteria. But being a friend or a foe to plants depends on many factors such as root exudates composition, the ability of bacteria to overcome the plant defense system, the plants ability to fight against pathogenic attack, the plant species and the genetic traits that can influence the microbial diversity and its influence on the plants growth and health, the environmental conditions etc. Anyway a better understanding of the plant-bacteria interaction is necessary for the bacteria to be considered a friend or an enemy to plants since there are many mechanisms and factors involved.

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REFERENCES

1. ABRAMOVITCH R.B., MARTIN G.B., *Strategies used by bacterial pathogens to suppress plant defenses*, Current Opinion in Plant Biology, 2004, **7**, *4*, 356–364.
2. ADESEMOYE A., KLOEPPER J., *Plant–microbes interactions in enhanced fertilizer-use efficiency*, Applied Microbiology and Biotechnology, 2009, **85**, *1*, 1–12.
3. AHEMAD M., KIBRET M., *Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective*, Journal of King Saud University – Science, 2014, **26**, *1*, 1–20.
4. BACILIO-JIMÉNEZ M., AGUILAR-FLORES S., VENTURA-ZAPATA E., PÉREZ-CAMPOS E., BOUQUELET S., ZENTENO E., *Chemical characterization of root exudates from rice (Oryza sativa) and their effects on the chemotactic response of endophytic bacteria*, Plant and Soil, 2003, **249**, *2*, 271–277.
5. BADRI D.V., VIVANCO J.M., *Regulation and function of root exudates*, Plant, Cell & Environment, 2009, **32**, *6*, 666–681.
6. BAIS H.P., PARK S.-W., WEIR T.L., CALLAWAY R.M., VIVANCO J.M., *How plants communicate using the underground information superhighway*, Trends in Plant Science, 2004, **9**, *1*, 26–32.
7. BAIS H.P., WEIR T.L., PERRY L.G., GILROY S., VIVANCO J.M., *The Role of Root Exudates in Rhizosphere Interactions with Plants and Other Organisms*, Ann. Rev. Plant Biol., 2006, **57**, 233–266.
8. BAKKER M., MANTER D., SHEFLIN A., WEIR T., VIVANCO J., *Harnessing the rhizosphere microbiome through plant breeding and agricultural management*, Plant and Soil, 2012, **360**, *1–2*, 1–13.
9. BAKKER P.A.H.M., BERENDSEN R., DOORNBOS R., WINTERMANS P.A., PIETERSE C.M.J., *The rhizosphere revisited: root microbiomics*, Front. Plant Sci., 2013, **4**, 1–5.
10. BAKKER P.A.H.M., DOORNBOS R.F., ZAMIOUDIS C., BERENDSEN R.L., PIETERSE C.M.J., *Induced Systemic Resistance and the Rhizosphere Microbiome*, Plant Pathol. J., 2013, **29**, *2*, 136–143.
11. BERENDSEN R.L., PIETERSE C.M.J., BAKKER P.A.H.M., *The rhizosphere microbiome and plant health*, Trends in Plant Science, 2012, **17**, *8*, 478–486.
12. BERG G., *Plant–microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture*, Appl Microbiol Biotechnol, 2009, **84**, 11–18.

13. BHATTACHARYYA P.N., JHA D.K., *Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture*, World Journal of Microbiology and Biotechnology, 2012, **28**, *4*, 1327–1350.
14. BLOEMBERG G.V., LUGTENBERG B.J.J., *Molecular basis of plant growth promotion and biocontrol by rhizobacteria*, Current Opinion in Plant Biology, 2001, **4**, *4*, 343–350.
15. BOLLER T., HE S.Y., *Innate Immunity in Plants: An Arms Race Between Pattern Recognition Receptors in Plants and Effectors in Microbial Pathogens*, Science, 2009, **324**, *5928*, 742–744.
16. BOTTINI R., CASSÁN F., PICCOLI P., *Gibberellin production by bacteria and its involvement in plant growth promotion and yield increase*, Appl Microbiol Biotechnol 2004, **65**, 497–503.
17. BRESSAN M., RONCATO M.-A., BELLVERT F., COMTE G., HAICHAR F.E.Z., ACHOUAK W., BERGE O., *Exogenous glucosinolate produced by Arabidopsis thaliana has an impact on microbes in the rhizosphere and plant roots*, ISME J, 2009, **3**, *11*, 1243–1257.
18. BURZO I., DELIAN E., DOBRESCU A., VOICAN V., BĂDULESCU L., *Fiziologia plantelor de cultură –Vol. I. Procesele fiziologice din plantele de cultură*, Ed. Ceres, Bucuresti, 2004.
19. CARVALHAIS L.C., DENNIS P.G., FEDOSEYENKO D., HAJIREZAEI M.-R., BORRISS R., VON WIRÉN N., *Root exudation of sugars, amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency*, Journal of Plant Nutrition and Soil Science, 2011, **174**, *1*, 3–11.
20. CHAIHARN M., LUMYONG S., *Screening and optimization of indole-3-acetic acid production and phosphate solubilization from rhizobacteria aimed at improving plant growth.*, Curr Microbiol, 2011, **62**, *1*, 173 – 181.
21. CHAPARRO J., SHEFLIN A., MANTER D., VIVANCO J., *Manipulating the soil microbiome to increase soil health and plant fertility*, Biology and Fertility of Soils, 2012, **48**, *5*, 489–499.
22. CHIN-A-WOENG T.C., LUGTENBERG B.J., *Root Colonisation Following Seed Inoculation*, in *Plant Surface Microbiology* (A. Varma *et al.*, eds.), Springer, Berlin, Heidelberg, 2004.
23. CHISHOLM S.T., COAKER G., DAY B., STASKAWICZ B.J., *Host-Microbe Interactions: Shaping the Evolution of the Plant Immune Response*, Cell, 2006, **124**, *4*, 803–814.
24. CHOUDHARY D., PRAKASH A., JOHRI B.N., *Induced systemic resistance (ISR) in plants: mechanism of action*, Indian Journal of Microbiology, 2007, **47**, *4*, 289–297.
25. COMPANT S., CLÉMENT C., SESSITSCH A., *Plant growth-promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms involved and prospects for utilization*, Soil Biology and Biochemistry, 2010, **42**, *5*, 669–678.
26. CROWLEY D., *Microbial Siderophores in the Plant Rhizosphere*, in *Iron Nutrition in Plants and Rhizospheric Microorganisms* (L. Barton, J. Abadia, eds.), Springer, Netherlands, 2006.
27. DE-LA-PEÑA C., BADRI D.V., LEI Z., WATSON B.S., BRANDÃO M.M., SILVA-FILHO M.C., SUMNER L.W., VIVANCO J.M., *Root Secretion of Defense-related Proteins Is Development-dependent and Correlated with Flowering Time*, Journal of Biological Chemistry, 2010, **285**, *40*, 30654–30665.
28. DE VLEESSCHAUWER D., HÖFTE M., *Rhizobacteria-Induced Systemic Resistance*, in *Advances in Botanical Research* (L. C. V. Loon, eds.), Ac. Press, Amsterdam, 2009.
29. DE WEERT S., VERMEIREN H., MULDERS I.H.M., KUIPER I., HENDRICKX N., BLOEMBERG G.V., VANDERLEYDEN J., DE MOT R., LUGTENBERG B.J.J., *Flagella-Driven Chemotaxis Towards Exudate Components Is an Important Trait for Tomato Root Colonization by Pseudomonas fluorescens*, Molecular Plant-Microbe Interactions, 2002, **15**, *11*, 1173–1180.
30. DIMKPA C., WEINAND T., ASCH F., *Plant–rhizobacteria interactions alleviate abiotic stress conditions*, Plant, Cell and Environment, 2009, **32**, 1682–1694.
31. DODDS P.N., RATHJEN J.P., *Plant immunity: towards an integrated view of plant–pathogen interactions*, Nat Rev Genet, 2010, **11**, *8*, 539–548.
32. DOORNBOS R., LOON L., BAKKER P.H.M., *Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. A review*, Agronomy for Sustainable Development, 2012, **32**, *1*, 227–243.

33. FAURE D., VEREECKE D., LEVEAU J.J., *Molecular communication in the rhizosphere*, Plant and Soil, 2009, **321**, *1–2*, 279–303.
34. FELICI C., VETTORI L., GIRALDI E., FORINO L.M.C., TOFFANIN A., TAGLIASACCHI A.M., NUTI M., *Single and co-inoculation of Bacillus subtilis and Azospirillum brasilense on Lycopersicon esculentum: Effects on plant growth and rhizosphere microbial community*, Applied Soil Ecology, 2008, **40**, *2*, 260–270.
35. FERNANDO W.G.D., NAKKEERAN S., ZHANG Y., *Biosynthesis of Antibiotics by PGPR and its Relation in Biocontrol of Plant Diseases*, in *PGPR: Biocontrol and Biofertilization* (Z. Siddiqui, eds.), Springer, Berlin, Heidelberg, 2006.
36. FIGUEIREDO M., SELDIN L., ARAUJO F., MARIANO R., *Plant Growth Promoting Rhizobacteria: Fundamentals and Applications*, in *Plant Growth and Health Promoting Bacteria* (D. K. Maheshwari, eds.), Springer, Berlin, Heidelberg, 2011.
37. FRANS A.A.M.D.L., JAMES M.L., MELISSA J.B., *Rhizodeposition and Microbial Populations*, in *The Rhizosphere: Biochemistry and organic substances at the soil-plant interface* (R. Pinton *et al.*, eds.), CRC Press, New York, 2007.
38. GAMALERO E., GLICK B.R., *Mechanisms Used by Plant Growth-Promoting Bacteria*, in *Bacteria in Agrobiology: Plant Nutrient Management* (D. K. Maheshwari, eds.), Springer, Berlin, Heidelberg, 2011.
39. GAO M., TEPLITSKI M., ROBINSON J.B., BAUER W.D., *Production of Substances by Medicago truncatula that Affect Bacterial Quorum Sensing*, Molecular Plant-Microbe Interactions, 2003, **16,** *9*, 827–834.
40. GLICK B.R., *Plant Growth-Promoting Bacteria: Mechanisms and Applications*, Scientifica, 2012, **2012**, 15.
41. GYANESHWAR P., NARESH KUMAR G., PAREKH L.J., POOLE P.S., *Role of soil microorganisms in improving P nutrition of plants*, Plant and Soil, 2002, **245**, *1*, 83–93.
42. HARTMANN A., SCHMID M., TUINEN D., BERG G., *Plant-driven selection of microbes*, Plant and Soil, 2009, **321**, *1–2*, 235–257.
43. HAYAT R., ALI S., AMARA U., KHALID R., AHMED I., *Soil beneficial bacteria and their role in plant growth promotion: a review*, Annals of Microbiology, 2010, **60**, *4*, 579–598.
44. HEYL A., SCHMÜLLING T., *Cytokinin signal perception and transduction*, Current Opinion in Plant Biology, 2003, **6**, *5*, 480–488.
45. HODGE A., *The plastic plant: root responses to heterogeneous supplies of nutrients*, New Phytologist, 2004, **162**, *1*, 9–24.
46. HODGE A., ROBINSON D., FITTER A., *Are microorganisms more effective than plants at competing for nitrogen?*, Trends in Plant Science, 2000, **5**, *7*, 304–308.
47. HODGE A., STEWART J., ROBINSON D., GRIFFITHS B.S., FITTER A.H., *Plant N capture and microfaunal dynamics from decomposing grass and earthworm residues in soil*, Soil Biology and Biochemistry, 2000, **32**, *11–12*, 1763–1772.
48. HUSSAIN A., HASNAIN S., *Cytokinin production by some bacteria: its impact on cell division in cucumber cotyledons.*, African Journal of Microbiology Research, 2009, **3(11)**, 704–712.
49. IGUAL J.M., VALVERDE A., CERVANTES E., VELÁZQUEZ E., *Phosphate-solubilizing bacteria as inoculants for agriculture: use of updated molecular techniques in their study*, Agronomie, 2001, **21**, *6–7*, 561–568.
50. JONES J.D.G., DANGL J.L., *The plant immune system*, Nature, 2006, **444**, *7117*, 323–329.
51. JOO G.-J., KIM Y.-M., KIM J.-T., RHEE I.-K., KIM J.-H., LEE I.-J., *Gibberellins-Producing Rhizobacteria Increase Endogenous Gibberellins Content and Promote Growth of Red Peppers*, The Journal of Microbiology, 2005, **43**, *6*, 510–515.
52. JOSHI P., BHATT A.B., *Diversity and function of plant growth promoting Rhizobacteria associated with wheat Rhizosphere in North Himalayan Region*, International Journal of Environmental Sciences, 2011, **1**, *6*, 1135–1143.

53. KHAN A.A., JILANI G., AKHTAR M.S., NAQVI S.M.S., RASHEED M., *Phosphorus solubilizing bacteria: occurrence, mechanisms and their role in crop production*, J. Agric. Biol. Sci., 2009, **1**, *1*, 48–58.
54. KRAVCHENKO L.V., AZAROVA T.S., MAKAROVA N.M., TIKHONOVICH I.A., *The Effect of Tryptophan Present in Plant Root Exudates on the Phytostimulating Activity of Rhizobacteria*, Microbiology, 2004, **73**, *2*, 156–158.
55. KUHAD R., KOTHAMASI D., TRIPATHI K.K., SINGH A., *Diversity and Functions of Soil Microflora in Development of Plants*, in *Plant Surface Microbiology* (A. Varma *et al.*, eds.), Springer, Berlin, Heidelberg, 2004.
56. LUGTENBERG B., KAMILOVA F., *Plant-Growth-Promoting Rhizobacteria*, Annual Review of Microbiology, 2009, **63**, *1*, 541–556.
57. LUGTENBERG B.J., CHIN-A-WOENG T.C., BLOEMBERG G., *Microbe–plant interactions: principles and mechanisms*, Antonie van Leeuwenhoek, 2002, **81**, *1–4*, 373–383.
58. MACMILLAN J., *Occurrence of gibberellins in vascular plants, fungi, and bacteria*, J Plant Growth Regul., 2002, **20**, 387–442.
59. MAKSIMOVA I.V., ABIZGIL'DINAA R.R., PUSENKOVAB L.I., *Plant growth promoting rhizobacteria as alternative to chemical crop protectors from pathogens (Review)*, Applied Biochemistry and Microbiology, 2011, **47**, 333–345.
60. MARSCHNER P., CROWLEY D., RENGEL Z., *Rhizosphere interactions between microorganisms and plants govern iron and phosphorus acquisition along the root axis – model and research methods*, Soil Biology and Biochemistry, 2011, **43**, *5*, 883–894.
61. MARSCHNER P., CROWLEY D., YANG C., *Development of specific rhizosphere bacterial communities in relation to plant species, nutrition and soil type*, Plant and Soil, 2004, **261**, *1–2*, 199–208.
62. MILLER M.B., BASSLER B.L., *Quorum sensing in bacteria*, Annual Review of Microbiology, 2001, **55**, *1*, 165–199.
63. MORGAN J.A.W., BENDING G.D., WHITE P.J., *Biological costs and benefits to plant–microbe interactions in the rhizosphere*, Journal of Experimental Botany, 2005, **56**, *417*, 1729–1739.
64. NANNIPIERI P., GIAGNONI L., LANDI L., RENELLA G., *Role of Phosphatase Enzymes in Soil*, in *Phosphorus in Action* (E. Bünemann *et al.*, eds.), Springer, Berlin, Heidelberg, 2011.
65. NEHL D., KNOX O.G., *Significance of Bacteria in the Rhizosphere*, in *Microbial Activity in the Rhizoshere* (K. G. Mukerji *et al.*, eds.), Springer, Berlin, Heidelberg, 2006.
66. NEUMANN G., RÖMHELD V., *The release of root exudates as affected by the plant physiological status*, in *The Rhizosphere: Biochemistry and Organic Substances at the Soil-Plant Interface.* (R. Pinton *et al.*, eds.), CRC Press, New York, 2007.
67. NEWTON A.C., FITT B.D.L., ATKINS S.D., WALTERS D.R., DANIELL T.J., *Pathogenesis, parasitism and mutualism in the trophic space of microbe–plant interactions*, Trends in Microbiology, 2010, **18**, *8*, 365–373.
68. NICHOLAS C.U., *Types, Amounts, and Possible Functions of Compounds Released into the Rhizosphere by Soil-Grown Plants*, in *The Rhizosphere: Biochemistry and Organic Substances at the Soil-Plant Interface* (R. Pinton *et al.*, eds.), CRC Press, New York, 2007.
69. NIHORIMBERE V., ONGENA M., SMARGIASSI M., THONART P., *Beneficial effect of the rhizosphere microbial community for plant growth and health*, Biotechnol. Agron. Soc. Environ., 2011, **15**, *2*, 327–337.
70. ONA O., VAN IMPE J., PRINSEN E., VANDERLEYDEN J., *Growth and indole-3-acetic acid biosynthesis of Azospirillum brasilense Sp245 is environmentally controlled*, FEMS Microbiology Letters, 2005, **246**, *1*, 125–132.
71. PEL M.J.C., PIETERSE C.M.J., *Microbial recognition and evasion of host immunity*, Journal of Experimental Botany, 2013, **64**, *5*, 1237–1248.

72. PERRY L., G. , ALFORD É., R. , HORIUCHI J., PASCHKE M., W., VIVANCO J., M., *Chemical Signals in the Rhizosphere*, in *The Rhizosphere: Biochemistry and Organic Substances at the Soil-Plant Interface* (R. Pinton *et al.*, eds.), CRC Press, New York, 2007.
73. PERSELLO-CARTIEAUX F., DAVID P., SARROBERT C., THIBAUD M.-C., ACHOUAK W., ROBAGLIA C., NUSSAUME L., *Utilization of mutants to analyze the interaction between Arabidopsis thaliana and its naturally root-associated Pseudomonas*, Planta, 2001, **212**, *2*, 190–198.
74. PIERIK R., THOLEN D., POORTER H., VISSER E.J.W., VOESENEK L.A.C.J., *The Janus face of ethylene: growth inhibition and stimulation*, Trends in Plant Science, 2006, **11**, *4*, 176–183.
75. PODILE A., KISHORE G.K., *Plant growth-promoting rhizobacteria*, in *Plant-Associated Bacteria* (S. Gnanamanickam, eds.), Springer, Berlin, Heidelberg, 2006.
76. PONCIANO G., ISHIHARA H., TSUYUMU S., LEACH J.E., *Bacterial Effectors in Plant Disease and Defense: Keys to Durable Resistance?*, Plant Disease, 2003, **87**, *11*, 1272–1282.
77. RAAIJMAKERS J., PAULITZ T., STEINBERG C., ALABOUVETTE C., MOËNNE-LOCCOZ Y., *The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms*, Plant and Soil, 2009, **321**, *1–2*, 341–361.
78. RICHARDSON A., BAREA J.-M., MCNEILL A., PRIGENT-COMBARET C., *Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms*, Plant and Soil, 2009, **321**, *1–2*, 305–339.
79. RODRIGUEZ H., FRAGA R., *Phosphate solubilizing bacteria and their role in plant growth promotion*, Biotechnology Advances, 1999, **17**, *4–5*, 319–339.
80. RODRÍGUEZ H., FRAGA R., GONZALEZ T., BASHAN Y., *Genetics of phosphate solubilization and its potential applications for improving plant growth-promoting bacteria*, Plant and Soil, 2006, **287**, *1–2*, 15–21.
81. RUBIO L.M., LUDDEN P.W., *Biosynthesis of the Iron-Molybdenum Cofactor of Nitrogenase*, Annual Review of Microbiology, 2008, **62**, *1*, 93–111.
82. SAHARAN B.S., NEHRA V., *Plant Growth Promoting Rhizobacteria: A Critical Review*, Life Sciences and Medicine Research, 2011, **2011**, *LSMR-21*, 1–30.
83. SEIDEL C., WALZ A., PARK S., COHEN J.D., LUDWIG-MÜLLER J., *Indole-3-Acetic Acid Protein Conjugates: Novel Players in Auxin Homeostasis*, Plant Biology, 2006, **8**, *3*, 340–345.
84. SHARMA B.C., SUBBA R., SAHA A., *In vitro solubilization of tricalcium phosphate and production of IAA by phosphate solubilizing bacteria isolated from tea rhizosphere of Darjeeling Himalaya*, Plant Sciences Feed, 2012, **2**, *6*, 96–99.
85. SHARMA S., SAYYED R., TRIVEDI M., GOBI T., *Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils*, SpringerPlus, 2013, **2**, *1*, 587.
86. SMITH M.A., COUPLAND G., DOLAN L., HARBERD N., JONES J., MARTIN C., SABLOWSKI R., AMEY A., *Plant Biology*, Garland Science, New York, 2010.
87. SPAEPEN S., VANDERLEYDEN J., REMANS R., *Indole-3-acetic acid in microbial and microorganism-plant signaling*, FEMS Microbiology Reviews, 2007, **31**, *4*, 425–448.
88. STEFAN M., *Biologia microorganismelor rizosferice. Aplicații biotehnologice.*, Technopress, Iaşi, 2008.
89. STEFAN M., MIHASAN M., DUNCA S., *Plant growth promoting rhizobacteria can inhibit the in vitro germination of Glycine max L. seeds.*, Analele Ştiințifice ale Universității „Alexandru Ioan Cuza", Secțiunea Genetică şi Biologie Moleculară, 2008, **IX**, 105–110.
90. STEFAN M., MUNTEANU N., STOLERU V., MIHASAN M., *Effects of inoculation with plant growth promoting rhizobacteria on photosynthesis, antioxidant status and yield of runner bean*, Romanian Biotechnological Letters, 2013, **18**, *2*, 8132–8143.
91. STEFAN M., MUNTEANU N., STOLERU V., MIHASAN M., HRITCU L., *Seed inoculation with plant growth promoting rhizobacteria enhances photosynthesis and yield of runner bean (Phaseolus coccineus L.)*, Scientia Horticulturae, 2013, **151**, *0*, 22–29.

92. STOCK A.M., ROBINSON V.L., GOUDREAU P.N., *Two-component signal transduction.*, Annual Review of Biochemistry, 2000, **69**, *1*, 183–215.
93. TAILOR A.J., JOSHI B.H., *Characterization and optimization of siderophore production from Pseudomonas fluorescens strain isolated from sugarcane rhizosphere.*, Journal of Environmental Research and Development 2012, **6**, 688.
94. TSAVKELOVA E.A., KLIMOVA S.Y., CHERDYNTSEVA T.A., NETRUSOV A.I., *Microbial producers of plant growth stimulators and their practical use: A review*, Applied Biochemistry and Microbiology, 2006, **42**, *2*, 117–126.
95. VAN LOON L.C., *Plant responses to plant growth-promoting rhizobacteria*, European Journal of Plant Pathology, 2007, **119**, *3*, 243–254.
96. VANCE C.P., *Symbiotic Nitrogen Fixation and Phosphorus Acquisition. Plant Nutrition in a World of Declining Renewable Resources*, Plant Physiology, 2001, **127**, *2*, 390–397.
97. VESSEY J.K., *Plant growth promoting rhizobacteria as biofertilizers*, Plant and Soil, 2003, **255**, *2*, 571–586.
98. VON BODMAN S.B., BAUER W.D., COPLIN D.L., *Quorum sensing in plant-pathogenic bacteria*, Annual Review of Phytopathology, 2003, **41**, *1*, 455–482.
99. WALKER T.S., BAIS H.P., GROTEWOLD E., VIVANCO J.M., *Root Exudation and Rhizosphere Biology*, Plant Physiology, 2003, **132**, *1*, 44–51.
100. ZAMFIRACHE M., TOMA C., *Semnificații ecologice ale relațiilor simbiotice în lumea vegetală.*, Buletinul Grădinii Botanice, Iaşi, 1997, **6**, *1*, 105–114.
101. ZAMFIRACHE M., TOMA C., *Simbioza în lumea vie*, Ed. Univ. "Al. I. Cuza", Iaşi, 2000.
102. ZAMFIRACHE M., TOMA C., *Simbioza în regnul vegetal*, Mem. Sect. St. Acad. Rom., 2002 (2005), **XXV,** 37–84.
103. ZAMIOUDIS C., PIETERSE C.M.J., *Modulation of Host Immunity by Beneficial Microbes*, Molecular Plant-Microbe Interactions, 2011, **25**, *2*, 139–150.

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