Interactions in Soil-Microbe-Plant System: Adaptation to Stressed Agriculture

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6.1 Introduction

In the last decades, the intensive agriculture faces serious problems originated by the necessity of higher yield and quality of the agricultural products. Expecting the number of world population to reach almost nine billion by 2050, the necessity of more quantity and more secure food is evident. As a result, in all industrialized countries an intensive fertilization is applied as a method for yield increase. All these applications, incl. pesticide application, conducted to changes in the agroecosystem having as a result accumulation of chemicals in soil, water and plant production, and decreasing crop productivity. On the other hand, the climate change conducted to aggravation of unfavorable environmental conditions, such as drought, nutrient scarcity, high temperature, between others. In that situation, the agricultural

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sector is trying to find other approaches, more suitable and more acceptable, in order to reach the objectives.

One unique alternative of the conventional method is the improvement of naturally occurring interactions between plant roots and soil microbial communities, such as mycorrhizal fungus and PGPR. Stimulation of the development of these communities could help the plants to battle the environmental stresses that lead to reduced plant quality and productivity. It is known that diverse microbial genera are vital for soil fertility, also because they are involved in different biotic activities and occupy plenty of environmental niches related to nutrient cycles. Their activity could be defined as very important for sustainable crop production (Kidd et al. 2009).

This very interesting, natural, and applicable strategy for improving agricultural production is more visible and more investigated during the last decade (Fig. 6.1). More than 830 papers indexed in Scopus were published for the last 10 years, while their citations for that time are almost 8000.

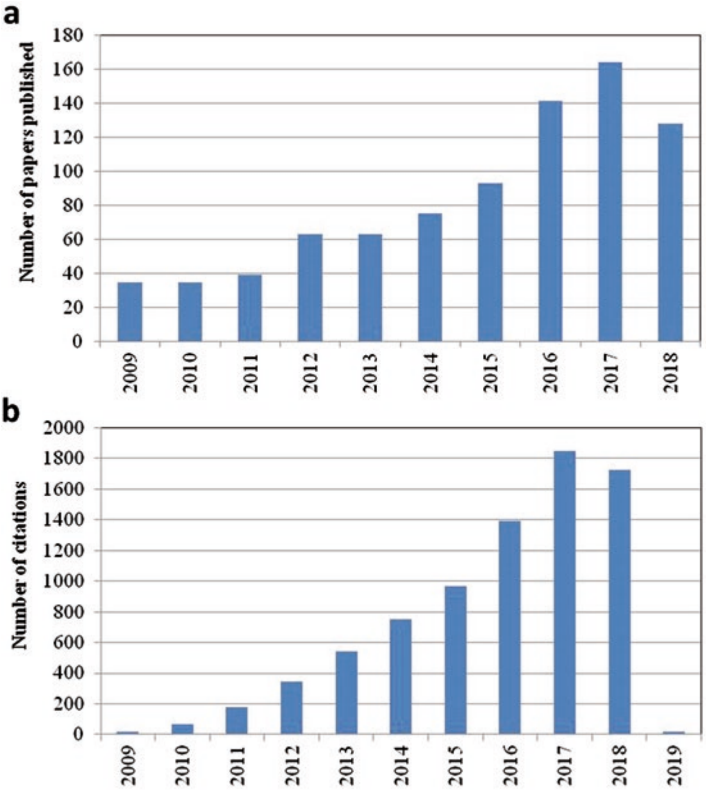

Fig. 6.1 Publications featuring the use of beneficial microorganisms in agriculture (**a**) and their citation (**b**) during the last 10 years. Source: *Scopus*; search parameters: ("plant growth-promoting" or "beneficial microorganisms") and (agriculture). The search was performed in the end of September 2018

On the other hand, a number of review papers collected plenty of information concerning the beneficial microorganisms and their investigation, abilities, habitats, and ecology (Vejan et al. 2016; Gupta et al. 2015; de Souza et al. 2015; Kong and Glick 2017; Gouda et al. 2018; Kidd et al. 2009). In the present review paper, we aimed to give an additional and recent focus on beneficial microorganisms from the point of view of the important mechanisms and agricultural applications.

6.2 Interactions of Root Exudates and Rhizosphere and the Role of Beneficial Microorganisms for Healthy Plants

It is well known that plant roots release different compounds in order to attract and select microbial consortium in their rhizosphere environment, where these plants associated microorganisms, use different mechanisms to influence plant health and growth. The rhizosphere microbes help the plant roots to uptake soil nutrients from the soil matrix. Therefore, the processes of root growth in rhizosphere have an enormous impact on soil nutrient transformations and mobilizations and the efficient usage by the different plant species. Plant roots regulate their morphologies to suite environmental conditions in the soils. In addition, they significantly modify rhizospheric processes through their physiological activities, specially by the exudation of different small molecules, namely, organic acids, sugars, phosphatases, signaling compounds, proteins, and redox compounds (Hinsinger et al. 2009; Zhang et al. 2010; Marschner 2012). Root exudates are divided into two main classes: low molecular weight compounds, such as amino acids, organic acids, sugars, phenolics, hormones, and other secondary metabolites, and high molecular weight compounds, such as carbohydrates, proteins, and others (Bais et al. 2006; Badri and Vivanco 2009). In addition, root exudation includes the secretion of various ions, free oxygen and water, enzymes, mucilage, and diverse organic compounds to attract special rhizosphere microbes (Bais et al. 2006). The microbes live in the rhizosphere and interact with living entities with the diverse metabolites released by plant roots. These interactions influence the plant growth and development and change nutrient dynamics, which may change the plants' susceptibility toward diseases and abiotic stresses which affect plant health as well as plant growth (Yadav et al. 2015). The root produces different chemical signal molecules that attract different microbes toward it. Positive interactions include growth regulation mimicking molecules that support plant growth, development, and cross-species signaling with other rhizospheric microorganisms. The plant roots excrete almost 10–40% of their photosynthetically fixed carbon in the form of exudates and certain signaling molecules or antimicrobials for soil microorganisms. Such exudates contribute to the selection of the specific microbial consortium adapted to the specific rhizosphere of certain plant species (Guttman et al. 2014). The qualitative and quantitative composition of the root exudates is specified by the plant species and cultivars, their developmental stages, different environmental conditions and the presence of different microbial communities associated with the roots (Badri and

Vivanco 2009). These differences specify microbial community structure in the rhizosphere microenvironment that generates certain degree of specificity for plant species to gain mutual interactive benefits.

The root-induced rhizosphere mechanisms help plants in mobilization and acquisition of soil nutrients and at the same time regulate nutrient use efficiency by different species. The phenomenon is supposed to significantly contribute to crop production and plant health and sustainability (Zhang et al. 2010). Plant roots respond to environmental stimuli through the secretion of a diverse range of compounds depending upon their nutritional status and soil conditions (Cai et al. 2012; Carvalhais et al. 2013). These exudates interfere with the interacting plant-microbial species and constitute a significant proportion of efficiency of the microbial consortium in the rhizosphere (Cai et al. 2009, 2012; Carvalhais et al. 2013).

6.2.1 How Plants Are Able to Shape Their Associated Microbial Communities for Their Benefit?

The consortium of the microbial community in the rhizosphere is affected by the physicochemical conditions in the rhizospheric soil due to plant exudation; therefore, it differs considerably from those microbes present in the bulk soil because of root activities which mainly involve exudation which substantially affects their types. The efficiency of root/rhizosphere is mainly managed through (1) manipulating plant root growth, (2) regulating rhizosphere processes of the interaction between plant and microbes, and (3) optimizing root zone management of the different cropping systems (Shen et al. 2013).

It is well known that roots of soil plants are colonized by a diverse consortium of microbes that collectively function for the benefits of the plants and the microbes. Various studies have pointed out the influence of the microbiome on the host plants. The mechanisms by which plants select and shape associated microbial communities have been worked out but with little pace and attention. What are the drivers for the composition of the root-associated microbial communities? Different studies have shown that soil type was identified as the major factor affecting the composition of microbial communities in the rhizosphere (Schreiter et al. 2014), as the soil is a diverse reservoir for microorganisms that can be a potential source to colonize roots. However, under identical environmental conditions and soils, the plant genotype is the main factor which affects the structural and the functional diversity of root communities, where the plant is controlling and selecting its own microbial consortium (Reinhold-Hurek and Hurek 2011). When grown side by side in the same soil, different plant species harbor partially different microbiome consortiums despite they are grown under the same conditions and the same soil type. Several observations showed that root communities varied in different plant genera and species. However, root microbiome composition can diversify at the subspecies level, as was documented for cultivars of potato (Andreote et al. 2010) and rice, *Oryza sativa* (Hardoim et al. 2011). Functional diversity is also affected by variety: Remarkable varietal differences in root-associated nitrogenase gene fragment (nifH)-expressing communities were detected in rice; even cultivars representing sister lineages from the same crossing differed in their active diazotrophic microbiome (Knauth et al. 2005). Therefore, plant influence appeared to be heritable, as an interspecies rice hybrid showed an intermediate profile of the parental species. Differences in patterns of plant root exudation, which can have positive or negative effects on microbial population (Bais et al. 2006), are likely to play an important role in the development of plant type- and developmental of stage-specific microbiomes (Berg et al. 2014). For example, in a comparison of wheat, maize, rape, and barrel clover plants, root exudates significantly shaped the microbial consortium structure in the rhizospheric soil which is controlled by the plant genotype (Haichar et al. 2008). Root exudates of rice plants collected under sterile conditions induced a global transcriptomic response in the endophytic bacterium *Azoarcus* sp. strain BH72, and expression of genes required for endophytic colonization were elevated, suggesting that the bacterium was primed for the endophytic lifestyle by exudates (Shidore et al. 2012).

Brachypodium species are important in investigation of grasses due to the growing availability of genetic resources including a fully sequenced genome and the availability of a large collection of accessions. The *Brachypodium* rhizospheric microbial community and the root exudation profiles showed similar profile to those reported for wheat rhizospheres and different to *Arabidopsis* type; therefore, it was proposed that *Brachypodium* is a good model to investigate the microbiome of wheat (Kawasaki et al. 2016b).

6.2.2 Factors Affecting Plant Exudation and Beneficial Microbes

Several factors are influencing the production of root exudates including plant type, age, light type and intensity, soil microflora, soil fertilizer, soil pH, and other environmental factors and their interactions. Composition of root-associated microbial communities is controlled by factors arising from interactions with other microbes as well as regulated at an environmental condition (e.g., pH, temperature) or host level (plant species) (Wagner et al. 2016; Widder et al. 2016; Wemheuer et al. 2017). In addition to the rhizosphere pH changes induced by cation-anion imbalance, other processes such as root organic acid release, root and microbial respiration, and redox-coupled pH changes are involved in the change of the pH level (Hinsinger et al. 2003). Although many carboxylic acids are released from roots, the primary acids contributing to pH shifts are mainly citric and malic acid (Jones et al. 2003), which are mainly investigated under hydroponic conditions; however, there is lack of information under field conditions.

Despite there are many exudates that can potentially indirectly enhance nutrient acquisition through activation of the rhizosphere microbial biomass, there are few cases where these mechanisms have been proven to be of direct significance under field conditions. This is the case due to the lack of available techniques, and the difficulties in performing rhizosphere experimentation under field conditions. The released organic acids as an example can directly affect the behavior of inorganic P in the soil in several ways which cause in the end for the release of P into solution (Jones 1998). Changes of rhizospheric pH and/or exudation by using complexing agents allow to stimulate desorption of nutrients (e.g., Fe, P) from the soil growth matrix and increase their solubility in soil solution and subsequently their uptake and translocation into the plant (Duffner et al. 2012; Römheld 1987; Vance et al. 2003; Briat 2008); in addition, plant roots react to different environmental conditions through the secretion of various compounds which interfere in the plant-microbial interaction, being considered as an important factor in the efficiency of the inoculants to stimulate plant growth through different mechanisms (Bais et al. 2006; Cai et al. 2009, 2012; Carvalhais et al. 2013).

Endophytic bacteria consisting of different genera have been detected in a wide range of plant species, which can promote plant growth and/or resistance to diseases as well as environmental stresses by a variety of mechanisms including the fixation of atmospheric nitrogen for the benefits of the plants (Stoltzfus et al. 1997; Reinhold-Hurek and Hurek 1998) or the production of antibiotics and phytohormones required for protection against diseases and for better plant growth (Lodewyckx et al. 2002; Lugtenberg et al. 2002; Sturz et al. 2000); therefore, nowadays, many endophytes are used in agricultural cropping systems as biofertilizers and/or biological control agents for sustainable agriculture (Sturz et al. 2000; Lugtenberg et al. 2002). Analyzing the influence of fertilizer application and mowing frequency on bacterial endophytes in several grass species showed that management regimes influenced endophytic communities structure, and the observed responses were grass species-specific (Wemheuer et al. 2017). This might be attributed to several microbial specifically associated with a single grass species, and the structural and functional community patterns showed no correlation to each other, indicating that plant species-specific selection of endophytes is controlled by functional rather than phylogenetic traits (Wemheuer et al. 2017). Based on the comparison of microbiome data for the different root-soil zones and on knowledge of bacterial functions, a three-step enrichment model for shifts in community structure from bulk soil toward roots was suggested (Reinhold-Hurek et al. 2015).

Several studies have shown that exudates can select the microbial communities, so they are specific to certain plant species or even plant genotype stimulating or inhibiting particular microbial populations associated with the plant roots of particular species (Chaparro et al. 2014; Alegria Terrazas et al. 2016; Kawasaki et al. 2016b; Martin et al. 2017). In seagrass species, it was found that bacteria isolated from the roots of *Zostera marina* and *Halodule wrightii* showed positive chemotactic responses and preferential substrate utilization to root exudates and root extracts (Kilminster and Garland 2009). Other studies using 13C or 14C labeling have directly followed the flow of carbon source from the specific seagrasses into certain sediment bacteria (Holmer et al. 2001; Kaldy et al. 2006). Since there is very importance of the root microbiomes to host plant health, therefore, there is a need to better understand the controls and drivers of microbial compositions in seagrass systems, where the light availability controls primary productivity, reduced light may impact root exudation amount and type and consequently the composition of the root microbiome, where using 16S rDNA sequencing revealed that microbial diversity and composition strongly influenced by the presence of the specific seagrass roots, and the root microbiomes and were unique to each seagrass species under investigation (Martin et al. 2018).

Seagrasses uptake inorganic and organic nutrients through leaves and roots, where fixation of atmospheric N into ammonia by diazotrophic bacteria is considered as an important additional source of N covering the nutrient requirements of these plant species (Garcias-Bonet et al. 2016). Seagrass roots are also colonized by a diverse microbial community that are important for N fixation (Bagwell et al. 2002; Garcias-Bonet et al. 2016), sulfate reduction and oxidation (Küsel et al. 2008), phosphate solubilization (Ghosh et al. 2012), and nutrient processing (Trevathan-Tackett et al. 2017). Rhizospheric microbial community and their interaction with the plant can influence the productivity of the crops, where the microbial consortium can benefit plant growth by increasing nutrient supply to plants, suppressing pathogens, and by carrying out other roles. Plant growth-promoting (PGP) strains of *Azospirillum* and *Herbaspirillum* colonize *Brachypodium* roots and enhance the growth of some *Brachypodium* genotypes under low or no N conditions (Amaral et al. 2016). Inoculations with the PGP strain *Bacillus subtilis* B26 increased *Brachypodium* biomass and also enhanced plant drought resistance.

Plants release exudates into the rhizosphere which can alter the rhizosphere microbial community structure and diversity compared to the bulk soil where each plant species harbors specific rhizospheric microbial consortium depending on plant species as well as plant-microbial interaction (Berg and Smalla 2009). Root exudation is also influenced by various biotic and abiotic factors in the surrounding environment, which may lead to a significant shift in the rhizosphere microbiota composition (Lakshmanan et al. 2012; Kawasaki et al. 2012, 2016a). There is a requirement to understand the plant-soil interface sufficiently well to allow the rhizosphere to be engineered and adapted to benefit plant fitness in cereals (Zhang et al. 2015; Ryan et al. 2009). Characterizing the core microbial communities in the rhizosphere and identifying the major root exudates are critical inputs to such models. This information was collected in model plants such as *Arabidopsis* (Lundberg et al. 2012) and in crop species such as wheat (Ai et al. 2015; Donn et al. 2015), rice (Edwards et al. 2015), and maize (Peiffer et al. 2013). An interesting study using *Arabidopsis*, *Brachypodium*, and *Medicago* to investigate the shifts in the microbial populations in the soil over successive plantings, which lead to suggest three models, modified the soil microbiomes differently (Tkacz et al. 2015).

Plant age affects the composition of rhizosphere microorganism consortium and the stage of plant maturity controls the significance of rhizosphere effect and the degree of response to specific microorganisms (Buée et al. 2009). The flowering stage of plants is the most active period of plant metabolism and growth, where the mycorrhizosphere microorganism level increases during this stage and leads to increase of exudates content and composition (Walker et al. 2003; Tahat et al. 2008). Some microbes were found to be more effective at the flowering stage than in the seedling stage or at the full maturity stage (Bais et al. 2006). The effect of light type and intensity on the production of pectin and polygalacturonase (PG) in the root exudates of *Trifolium alexandrinum* showed that the pectin methyl esterase and PG increased with an increase in the duration of light to which plants were exposed during the experiment which indicates the importance of light and intensity (Chhonkar 1978).

Phosphorus (P) is a major yield-determining nutrient in legume, where the major problem with P nutrition is not the P content present in soil but its bioavailability to plants, as inorganic P gets immobilized in acid soils with Fe^{3+} and Al^{3+}, whereas in calcareous soils, P is fixed with Ca^{2+} (Liao et al. 2006). It was shown that low molecular weight exudates like carboxylic acids, sugars, phenolics, and amino acids have a major role in enhancing P acquisition (Carvalhais et al. 2011; Vengavasi et al. 2016, 2017). Two soybean genotypes with contrasting root exudation potential and P uptake efficiency (P-efficient) and (P-inefficient) were grown under natural environment with low and sufficient P availability to assess growth and photosynthetic efficiency and to establish relationship between photo-biochemical processes and root exudation showed that different exudates by roots revealed significant genotypic variation in soybean responses to sufficient and low P availability which indicate the importance of the plant genotype in the plant/microbial interaction for the mutual benefits (Vengavasi and Pandey 2018).

6.2.3 The Contribution of Mycorrhizae and Endophytic Bacteria on Nutrient Acquisition

Vesicular-arbuscular mycorrhizal (VAM) fungi symbioses are an association between obligate biotrophic fungi and more than 80% of land plants and depend on living plant roots for the supply of organic carbon, and they represent the largest component of the soil fungal community (Gosling et al. 2006). VAM and endophytes promote the growth of plants in various ways similar to rhizosphere bacteria (Etesami et al. 2014). The presence of VAM in the rhizosphere or plant roots may change root exudation by the colonized plants, where mycorrhizal plants often grow better than non-VAM plants, in most instances due to higher mineral uptake where colonization has been shown to change the amount and quality of host root exudates (Azaizeh et al. 1995; Marschner 1995). They also play an important role in plant resistance to water and salt stress (Miransari et al. 2008) and acidity and phytotoxic levels of Al in the soil environment (Seguel et al. 2013) and in improving soil structure through the exudation of various compounds (Wu et al. 2008). Some plants colonized with VAM can be more appropriate to uptake heavy metals such as As-contaminated water than soils (Caporale et al. 2014).

Dormant arbuscular mycorrhizal (AM) fungal spores are not only adapted to adverse environments but are also the most effective means of colonization, where the colonization ratio of AM fungi is largely correlated with spore germination which is the precondition of symbiosis with the plants. During the pre-symbiotic phase, many factors (such as a rhizosphere environment, high flavonoid content, presence of soil microorganisms, and plant cell suspension culture) can induce spore germination and promote hyphal growth without the presence of a host plant (Gianinazzi-Pearson et al. 1996; Graham 1982). In addition, root exudates can increase the length and degree of branching of AM fungi hyphae (Tamasloukht et al. 2003) and play an important role in plant-microbe interactions in the rhizosphere zone (Karin et al. 2013). Some studies have shown that root exudates or host extracts can stimulate spore germination; however, others have indicated negative or inconsequential effects (Hepper and Jakobsen 1983; Bécard and Fortin 1988).

In addition, it was found that AM fungal spores can uptake glucose as a carbon source from the environment (Bücking et al. 2008), where the glucose, N sources, and root exudates have great effect on amino acids metabolism in vitro and on spore germination of various AM fungi (Gachomo et al. 2009; Jin and Jiang 2011). The availability of exogenous inorganic N and organic N to the AM fungal spores using only CO_2 for germination generated more than five times more internal free amino acids than those in the absence of exogenous N (Wang et al. 2015b), where the supply of exogenous nitrate to spores with only CO_2 resulted in rise to more than ten times more asparagine than that found without exogenous N supply. The most interesting result was that root exudates were better than glucose at promoting AM spore germination, and exhibited interactions with certain forms of N such as urea and nitrate in the presence of root exudates to increase the spore germination rate and the hyphal length of certain AM fungi (Wang et al. 2015b).

Mineral nutrients such as P or Fe are very reactive and strongly bound to soil particles, where its availability is generally low, especially in calcareous soils, where plant species differ greatly in their capacity to acquire nutrients from soil such as Fe, P or other minerals from calcareous soils, whereas others cannot extract enough nutrients to persist on such soils (Lambers et al. 2008b). Nutrient acquisition from calcareous soils involves rhizosphere processes, such as the exudation of phosphate mobilizing carboxylates (Hinsinger et al. 2001) or the release of Fe-chelating phytosiderophores (Ma et al. 2003; Robin et al. 2008). In order that P is assimilated by plants, the organic P should be converted into inorganic or low molecular weight of organic acids. Phosphatases are enzymes that can hydrolyze phosphate esters and anhydrides including phosphoprotein phosphatases, phosphodiesterases, diadenosine, acid phosphatases, and other types (Zimmermann 2003). Phosphate acquisition from soils with low P concentrations in solution was shown to be enhanced by mycorrhizal symbioses (Richardson et al. 2009). However, even when P acquisition or plant growth are not enhanced in the presence of mycorrhizal fungi, the P taken up by the fungus may represent a major fraction of the total amount of P acquired by the mycorrhizal plants (Smith et al. 2003). Approximately 80% of all higher plant species can form a mycorrhizal symbiosis; of these, the AM association is the most common (Brundrett 2009), especially on relatively young soils (Lambers et al. 2008a). Plants benefit from the fungi because these acquire different nutrients, which are inaccessible because of distance from the plant roots or occurrence as forms that are unavailable and the AM assist the plants to mobilize them from the soil, and the fungi obtain organic compounds produced by the plant (Smith and Read 2008).

The “hyphosphere” represents the soil influenced by the external phase of the mycorrhizal fungus where the release of various compounds and mycorrhizal hyphae can influence microbial activity and nutrient dynamics in the hyphosphere soil, particularly ectomycorrhizal mycelium, which is capable of releasing various hydrolytic enzymes to mobilize nutrients from organic sources (Chalot and Brun 1998), in addition to other compounds (Sun et al. 1999). AM fungi can secrete large amounts of glycoproteins into the soil environment (Rillig et al. 2002, 2003), which may represent a recalcitrant pool of the carbon source in some soils (Rillig et al. 2001). Some of these exuded compounds may subsequently be reabsorbed by the mycorrhizal hyphae just as roots can reabsorb exuded compounds. Microbial activity and composition has been shown to be affected in the hyphosphere of AM fungi (Andrade et al. 1997; Filion et al. 1999; Staddon et al. 2003). Mycorrhizal colonization can influence exudation process in other ways where the ectomycorrhizal colonization increases root longevity (King et al. 2002) while both increased and decreased root longevity has been also reported following AMF colonization (Hodge 2001; Atkinson et al. 2003). The decomposition of the mycorrhizal root is also likely to differ from that of the nonmycorrhizal root because of the different chemistry as a result of the fungus being present in various plant tissues (Langley and Hungate 2003). Thus, rhizodeposition processes from mycorrhizal roots markedly differ from nonmycorrhizal roots (Azaizeh et al. 1995).

The microbes colonizing the rhizosphere also influence plant root exudation process where many studies have shown that the colonization of AM fungi has changed the plant root exudation qualitatively and quantitatively, e.g., increasing secretions of N, phenolics, and gibberellins and reducing secretions of total sugars, potassium ions, phosphorus, and other compounds (Jones et al. 2004). Several studies have shown that different ectomycorrhizal fungi have distinct effects on the amount and the composition of plant root exudates (Fransson and Johansson 2010). The inoculation with ectomycorrhizal fungus and (or) rhizobacteria can alter root exudation quantitatively and qualitatively, where an interesting study has shown that both the abundance and the type of root-associated fungi have influenced plant root exudation rates (Meier et al. 2013).

Nitrogen acquisition can be enhanced greatly by symbiotic N_2 fixation process, which is common in legumes (Vessey et al. 2005), where the symbiotic microorganisms can play a key role in accessing complex organic N; however, in some mycorrhizal systems, saprotrophs play a pivotal role in making N available to the plants. The AM fungi also increase N nutrition by extending the absorption "mycorrhizosphere" zone due to hyphal extensions (Jonsson et al. 2001; Lerat et al. 2003), where the increase in N uptake was related to the stimulation of bacteria growing in the rhizosphere.

Root exudates are considered as one of the mechanisms that explain the ability of AM to suppress or increase different soilborne diseases (Mukerji et al. 2002), where in response to pathogen attack, plants release root exudates, such as oxalic acids, phytoalexins, proteins, and other unknown organic compounds that affect beneficial as well as pathogenic microbes (Steinkellner et al. 2007). The composition of root exudates varies among different plant species and affected by various environmental conditions (Marschner 1995; Tahat et al. 2011). Although it is believed that root exudates play a major role in the infection and colonization of hosts by AM, the actual role or mode of action of exudates was elucidated only in the last few years (Smith and Read 2008). The germination of *Fusarium oxysporum f.* sp. *Lycopersici* as an example was inhibited in the presence of root exudates from the tomato plants (Scheffknecht et al. 2006). Root exudates can have direct defensive traits against various pathogens, where pathogen-activated plant defenses can result in root secretion of various antimicrobial compounds, where it was shown that root-derived antimicrobial metabolites from *Arabidopsis* confer resistance to a variety of *Pseudomonas syringae* pathovars (Bais et al. 2005). In another work, it was shown that transgenic plants which produce antimicrobial proteins can influence rhizosphere microbial communities (Glandorf et al. 1997). The hyphal length of *Glomus mosseae* was greatly affected by the exudates of mycorrhizal plant species, and the growth of *Ralstonia solanacearum* was suppressed due to *G. mosseae* spores germination (Tahat et al. 2010), and exudates from mycorrhizal strawberry plants suppressed the sporulation of *P. fragariae* in in vitro study (Norman and Hooker 2000).

The microbiomes colonizing the roots are critical for plant growth and health due to their influence on biogeochemical cycling and nutrient acquisition, induction of host defense to various pathogens due to the production of plant growth regulators such as hormones and antibiotics (Reinhold-Hurek et al. 2015; Alegria Terrazas et al. 2016). The plant growth-promoting bacteria (PGPB) found in the rhizosphere are capable of enhancing the growth of plants and protecting them from different diseases and abiotic stresses (Grover et al. 2011; Glick 2012). PGPB are good microbes because they colonize roots and supply favorable environmental conditions for growth development and function of the different plant species. It was shown that non-symbiotic endophytic relationships occur within the intercellular spaces of plant tissues, which contain high levels of compounds and inorganic nutrients available for the growth of these microbes (Bacon and Hinton 2006). The success and efficiency of PGPB for agricultural crops are influenced by various factors, and their efficiency in root colonization is closely associated with microbial competition and survival in the soil, as well as cell-to-cell communication via quorum sensing which is considered nowadays as the main factor in this process (Meneses et al. 2011; Alquéres et al. 2013; Beauregard et al. 2013).

6.3 Microbial Tools for Plant Stress Alleviation

Plants are often exposed to different unfavorable influences such as nutrient scarcity, drought, high temperatures, toxic element, etc. In these conditions, they reduce their growth and quality of agricultural products. It is known that more than 80% of soil fertility is due to the microorganisms. The interactions between plants and bacteria can be generalized into three types: positive, negative, and neutral (Whipps 2001). Most of the autochthonous plant-associated rhizobacteria benefit from the interactions, despite they are neutral or positive for the plant. Many rhizospheric bacteria in some conditions could negatively influence the plant development due to pathogenic or parasitic activity or secretion of phytotoxic compounds (Beattie 2006). In opposite, plant growth-promoting rhizobacteria (PGPR) possess tools that help in plant growth and development, even in stress conditions. The bacteria should possess several abilities in order to be characterized as PGPR (Kloepper 1994): (a) they must have the ability to colonize plant root surface; (b) they must be able to grow up, multiply, and compete with other microbial populations; and (c) they must be able to promote plant growth. So, they must be beneficial to the plant. PGPR are often classified according to the place in plant that they occupy as intracellular (iPGPR) or extracellular (ePGPR), depending on the level of association with the root cells. The iPGPR live in the root cells, such as nodules, while the ePGPR are allocated on the surface (rhizoplane) (Gray and Smith 2005; Shilev et al. 2012a). The following bacterial genera, among many others, can be associated to the ePGPR: *Agrobacterium*, *Flavobacterium*, *Micrococcus*, *Azotobacter*, *Cyanobacteria*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Pseudomonas*, *Arthrobacter*, and *Chromobacterium* (Bhattacharyya and Jha 2012; Tilak et al. 2005).

On the other hand, strains such as *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Rhizobium*, part of the family *Rhizobiaceae*, are the iPGPR. Most of rhizobacteria are Gram-negative rods, while Gram-positive ones are less presented. These and other authors reported that numerous communities of actinomycetes are also in the rhizosphere, where display beneficial traits (Bhattacharyya and Jha 2012; Merzaeva and Shirokikh 2006). Plants react to the environmental conditions through the secretion of a number of compounds which influence the plant-microbe interactions, being considered an important instrument for the efficiency of beneficial microorganisms. In addition, soil health is a very important and influences population growth due to several soil characteristics: soil type, nutrients accession, existence of toxic compounds, etc. The results of bacterial promotion on plant growth and development generally are more visible in case of negative conditions to the plants – abiotic (salinity, drought, toxic elements, etc.) or biotic (pathogens) stresses (Glick 2015; Shilev 2013). PGPR may act also as biocontrol agents and indirectly may improve plant development through their activity against phytopathogens. Also, PGPR can directly improve plant growth by facilitating the availability of nutrients or changing the levels of phytohormone (Glick 2005). Consortium of three rhizobacteria significantly increased germination, root and shoot length and fresh and dry weight of wheat plant compared to single inoculation of any rhizobacteria and uninoculated control. It has been suggested that this consortium could be used for the production of an effective bioinoculant for eco-friendly and sustainable production of wheat (Kumar et al. 2018).

6.3.1 Mechanisms that Directly Promote Plant Growth

The direct mechanisms of microbial actions that support plant growth are diverse. They are related to nutrient uptake; nitrogen, phosphorus, potassium, or iron accession to the plants; or the production of phytohormones, siderophores, and exopolysaccharides.

6.3.1.1 Phytohormone Production

Plants produce phytohormones that regulate their own processes in a different way (biochemical, physiological, or morphological) and are important in order to boost the agricultural production (Lugtenberg et al. 2002; Somers et al. 2004). As organic substances their production is strictly regulated by the plant but could be synthesized exogenously by microorganisms or synthetically for use as plant growth regulators. Soil microorganisms are known to produce several compounds that are characterized as phytohormones: auxins, cytokinins, and gibberellins.

Auxin

The auxins are important compounds that regulate several plant processes directly or indirectly (Tanimoto 2005). One of the most studied and important auxin is the indole-3-acetic acid (IAA) that is involved in a plenty of physiological plant processes: induction of plant response (Navarro et al. 2006) and plant development (Gravel et al. 2007), especially root elongation, root hair formation, or lateral root formation, also depending on the IAA levels (Kidd et al. 2009). On the other hand, the production of these phytohormones is widely distributed among rhizospheric bacteria, thus playing an important role in plant-bacterial interactions (Glick 2015). Other researchers informed that majority of isolated rhizobacteria of rice are IAA producers (Souza et al. 2013). Matsukawa and coauthors (2007) suggested that IAA produced by plants and bacteria in rhizosphere acts as a start for *Streptomyces* to increase antibiotic production.

According to Wang and collaborators (2011), bacterial IAA is an important instrument for plant growth promotion, while it directly stimulates plant cell elongation and cell division. In pot experiment with sand/peat substrate under salt-produced stress (100 mM NaCl) was found that *Pseudomonas* inoculants increase the fresh weight of sunflower with more than 10% and accumulate less Na^+ and more K^+, while the strain *Pseudomonas fluorescence* CECT 378 supported up to 66% increment in leaves, 34% in stems, and 16% in roots, and the effect of wild-type strain was more pronounced in shoots with almost 30%. Both strains were found to be IAA and siderophore producers in in vitro experiments (Shilev et al. 2012b). Furthermore, the endogenous IAA in plant tissues and the sensitivity of the plant to IAA are also key factors to determine if the effect of bacterial IAA in plant growth is positive or negative. In plant roots, the level of endogenous IAA may be optimal or suboptimal for supporting plant growth (Pilet and Saugy 1987); therefore, the IAA produced by bacteria could modify the IAA level to optimal or almost optimal, resulting in either PGP or suppression (Kong and Glick 2017). There are different pathways that use L-tryptophan as a precursor of IAA production. Most of the beneficial bacteria synthesize it via indole-3-pyruvate pathway (Lambrecht et al. 2000), while the biosynthesis in plant-beneficial bacteria is inducible (Patten and Glick 1996).

Rhizobacteria are known to possess dual ability – synthesizing and catabolizing IAA (Duca et al. 2014). The same authors suggested that some bacteria stimulate plant growth by metabolizing IAA synthesized by plants when it is detrimentally higher than normal levels. In this way, the degradation of IAA in case of alteration of endogenous plant production could be also a plant growth promotion mechanism. The capacity of catabolizing IAA has been characterized in *Pseudomonas putida* 1290. This strain uses IAA as in the same time a unique source of carbon, nitrogen, and energy. Moreover, the strain 1290 produces IAA in medium with added L-tryptophan. In co-inoculation in radish (*Raphanus sativus* L.) roots, this strain lowered the negative effects of high IAA concentrations produced by the pathogen *P. syringae*. So, this strain can prevent pathogen attack to radish root, but also stimulate their growth (Leveau and Lindow 2005). In addition, the plant-derived IAA is also an attractant that bacteria can use to have a competitive advantage over the bacteria that lack chemotactic capability (Scott et al. 2013).

Cytokinins and Gibberellins

Cytokinins and gibberellins, like IAA, play a crucial role in the regulation of plant growth and development. The cytokinins are involved in protein synthesis, seed germination, cell division, and metabolite transport among others (Salamone et al. 2005; Frugier et al. 2008; Hussain and Hasnain 2011), while the gibberellins participated in cell division, activation of membranes, stimulation of fluorescence, etc. (Tanimoto 2005). Plant growth promotion by bacteria-producing cytokinins (*Rhizobium* spp., *Pantoea agglomerans*, *Paenibacillus polymyxa*, *Rhodospirillum rubrum*, *Bacillus subtilis*, *Azotobacter* spp., *Pseudomonas fluorescens*) and gibberellins (*Bacillus licheniformis*, *Bacillus pumilus*, *Azospirillum* sp.) has been reported by diverse authors (Gutiérrez-Mañero et al. 2001; Pertry and Vereecke 2009). Arkhipova and coauthors (2007) suggested that cytokinin-producing bacteria improve plant growth in moderate drought conditions. On the other hand, Glick (2012) reveals that cytokinin levels produced by PGPR are lower than those from phytopathogens, so that the effect of the cytokinins from the PGPR on plant growth is stimulatory, while the effect of the pathogens is inhibitory.

6.3.1.2 Nitrogen Fixation

Nitrogen is a very important nutrient for the whole living beings, because of its key role in the organic molecules. It is part of DNA, proteins, etc., but its crucial role in physiological and biochemical processes is well known (Krapp 2015). Nitrogen could be a very important obstacle for yield production in deficient soils. That is the reason for the excessive use of agrochemicals in agricultural practices in the last decades. However, most of the fertilization load is not utilized by the plants but conducted to increasing contamination (eutrophication and acidification) and increased financial expenses (Vimal et al. 2017). The magnificent ability of the beneficial bacteria to fix atmospheric N_2 is known, but not very well understood by non-specialists. No other living beings are capable to perform this extraordinary action taking a gaseous molecule, converting it in mineral compound, and finally releasing it to the others (plants, microorganisms, etc.).

The soil nitrogen fixation is due to two kinds of microorganisms – symbiotic and free-living – which contribution to the global nitrogen load is of about 180×10^6 tons per year, divided into 80–20% between both groups (Graham 1988). As was discussed earlier, organic inputs in rhizosphere from the roots alter microbial biodiversity, thus increasing also N uptake. In any case, N_2 fixation is very "expensive" from the point of view of energy consumption, because to reduce 1 mole of elemental N_2 microorganisms spend 16 moles of adenosine triphosphate (ATP). Symbiotic N_2 fixation is a process exclusively driven by bacteria, as they are the unique organisms capable to take the elemental nitrogen possessing the enzyme nitrogenase and reducing it to ammonia in the root nodules (Kidd et al. 2009). Genes that encode N_2 fixation ability are present in both free-living and symbiotic bacteria. They are involved in activation of iron-proteins and in the biosynthesis of cofactor of iron and molybdenum and donation of electrons. These genes are found in clusters of 20–25 kb with 7 operons encoding of about 20 proteins. The symbiotic N_2-fixing bacteria are considered as iPGPR spread in genera *Rhizobium*, *Mesorhizobium*, *Azorhizobium*, *Bradyrhizobium*, etc., belonging to the *Rhizobiaceae* family, although some authors do not recognize them as PGPR except when the association is with non-legumes (Dobbelaere et al. 2003). The most famous association is with Fabaceae plant species (pea, alfalfa, garden peas, soybeans, etc.). Also, *Frankia* species and some endophytes are considered iPGPR too. On the other hand, the non-symbiotic N_2-fixing bacteria include *Azotobacter*, *Azospirillum*, *Pseudomonas*, *Agrobacterium*, *Erwinia*, *Bacillus*, and *Burkholderia*, among others (Gray and Smith 2005). Because of high energy requirements and relatively low metabolic activity, the productivity of ePGPR in N_2 fixation is limited. According to good agricultural practices, N mineral fertilization is between 150 and 250 kg/ha/year, depending on the crop, state of development, etc. Compared to the productivity of ePGPR, which is around 5-15-20 kg/ha/year (Dobbelaere et al. 2003), it is evident that a combination of tools (more growth-promoting capabilities) is needed for the characterization of that strain as beneficial and continues further with the exploration of possibilities for formulation as biofertilizer.

6.3.1.3 Phosphate Solubilization

Phosphorus is a very important nutrient for the plant and is also required by plants for normal development, in appropriate amounts for optimal growth. Generally, in soil, it exists in two forms, as organic and inorganic phosphates. Microorganisms are capable to convert the insoluble phosphates (organic or inorganic) into accessible to the plant forms, thus increasing the crop yield (Igual et al. 2001; Rodriguez et al. 2006). According to Goldstein (1994), the amount of soluble phosphorus in the soil is commonly quite low, usually at levels of 1 ppm or less. Plants can absorb different forms of phosphorus but the major part is absorbed in the forms of HPO_4^{-2} or $H_2PO_4^{-1}$. The fixation or precipitation of phosphorus in the soil is strongly dependent on the pH and the soil types. Some authors describe the release of soluble phosphorus by microorganisms (Ohtake et al. 1996; McGrath et al. 1998; Rodriguez and Fraga 1999).

Phosphorus plays an important role in almost all metabolic processes, including energy conversion, signal transduction, respiration, molecular biosynthesis, and photosynthesis (Anand et al. 2016). However, 95–99% of the phosphorus is present in insoluble, immobilized, or precipitated forms; therefore, it is difficult for plants to absorb it. Organic acids of low molecular weight synthesized by different soil bacteria solubilize inorganic phosphorus (Sharma et al. 2013b). Phosphate-solubilizing PGPR involves the genera *Arthrobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Microbacterium*, *Pseudomonas*, *Erwinia*, *Rhizobium*, *Mesorhizobium*, *Flavobacterium*, *Rhodococcus*, and *Serratia*; they have been found to enhance plant growth and yield (Oteino et al. 2015). These data are presented by Gouda et al. (2018).

A large number of microorganisms, such as *Pseudomonas* spp., *Agrobacterium* spp. and *Bacillus circulans*, exhibit the ability to assist in the absorption of inorganic phosphorus by solubilization and mineralization (Babalola and Glick 2012). Others involve strains like *Azotobacter*, *Bacillus*, *Burkholderia*, *Erwinia*, *Rhizobium*, *Bradyrhizobium*, *Sinomonas* and *Thiobacillus*, even *Salmonella* and *Serratia* (Postma et al., 2010; Kumar et al., 2014; Zhao et al., 2014). Various types of molds and yeasts, which function in a similar way, include the strains *Alternaria*, *Arthrobotrys*, *Aspergillus*, *Cephalosporium*, *Cladosporium*, *Cunninghamella*, *Fusarium*, *Glomus*, *Micromonospora*, *Myrothecium*, *Oidiodendron*, *Paecilomyces*, *Penicillium*, *Phoma*, *Pichia fermentans*, *Populospora*, *Pythium*, *Rhizoctonia*, *Rhizopus*, *Saccharomyces*, *Schizosaccharomyces*, *Sclerotium*, *Torula*, and *Trichoderma* between many others (Srinivasan et al. 2012; Alori et al. 2017; Sharma et al. 2013a). Different bacterial strains have the capability to dissolve bioinavailable phosphate (mineral phosphate) compounds (Rodriguez and Fraga 1999; Rodriguez et al. 2006). Strains of genera *Rhizobium*, *Pseudomonas*, *Bacillus*, among others, are very effective solving phosphates (Illmer and Schinner 1992; Halder and Chakrabarty 1993; Rodriguez and Fraga 1999; Banerjee et al. 2006). Biosynthesis of different organic acids is involved in phosphate solubilization by bacteria (Rodriguez and Fraga 1999). Also, organic acid biosynthesized with microbial origin plays a role in phosphate-dissolving (2-ketogluconic acid). This compound is found to be produced by *Rhizobium leguminosarum*, *Rh. meliloti*, *Bacillus firmus*, and other soil bacteria (Kidd et al. 2009). Other microorganisms (*Bacillus licheniformis* and *B. amyloliquefaciens*) were proven to excrete lactic, isovaleric, isobutene, and acetic acids (Hayat et al. 2010).

The activity of different phosphatases in rhizosphere indicates that phosphatase activity is significant in the rhizosphere mainly at pH below 7. Many acidic phosphatases are synthesized by bacteria of genera *Rhizobium*, *Pseudomonas*, *Bacillus*, etc. (Chen et al. 2006). There is other information regarding the dissolution of phosphates by *Rhizobium* (Halder et al. 1990) and by the non-symbiotic nitrogen-fixing *Azotobacter*. The efficacy of the *Mesorhizobium* strain has been shown to improve the growth and absorption of phosphorus in chickpea and barley plants without the addition of phosphates. The most common mechanism used by microorganisms to dissolve tricalcium phosphates is acidification of the near environment releasing organic acids (Rodríguez and Fraga 1999). Gene manipulations of these bacteria have been used to improve plant yield (Rodríguez et al. 2006). Although some of the bacterial (such as *Pseudomonads* and *Bacillus*) and fungal strains (*Aspergillus* and *Penicillium*) have been identified as PSMs, their relative performance under in-situ conditions is not reliable, so there is a need for genetically modified strains which have more pronounced qualities (Ingle and Padole 2017).

A significant number of microorganisms – phytase producers of various taxonomic groups – bacteria, yeasts, and molds, have been found to synthesize enzymes with certain biochemical properties and catalytic capacity, which depend primarily on the producer and the medium conditions. Plants and the other autotrophic organisms are always the first link in the food chain (primary producers), after which the various species of the animal kingdom may continue it. Finally, the microorganisms end the food chain with demineralization of the final products. Phosphate groups give this molecule a high-negative charge and therefore a strong binding ability that reduces the nutrient bioavailability of amino acids and minerals such as Ca^{2+}, Zn^{2+}, and Fe^{2}+ (Haros et al. 2001). Many essential metal ions (Ca^{2}+, Zn^{2}+, Fe^{2}+) are associated with IP_6 and form precipitates under neutral or slightly alkaline conditions. The stability of the complexes formed between IP_6 and the metal ions at low pH values is in the following order $Zn^{2}+ > Cu^{2}+ > Co^{2}+ > Mn^{2}+ > Ca^{2}+$, whereas at pH 7.4 the order is $Cu^{2}+ > Zn^{2}+ > Ni^{2}+ > Co^{2}+ > Mn^{2}+ > Fe^{2}+ > Ca^{2}+$. These complexes are insoluble and this is the main reason why the bioavailability of minerals in high phytic acid diets is reduced. The simultaneous presence of two different types of cations increases the amount of IP_6-metal complex precipitates (Simpson and Wise 1990).

Microorganisms of various taxonomic groups – bacteria, yeasts, and molds – produce phytases (Dvorakova 1998; Vohra and Satyanarayana 2003; Vats and Banerjee 2004). Phytase-synthesizing microorganisms were isolated from a significant number of sources, including soil, fermented food/raw materials, contaminated water, gastrointestinal fluids of ruminants, and plant roots. In almost all mold producers, enzymes are excreted in the culture medium, and for this reason, they most often affect the absorption of phosphorus from plants. Both intracellular and extracellular production has been reported for the bacteria. Recently, data on yeast phytase producers indicated exclusively intracellular activity, but lately enzyme secreting strains were also cited (Lambrechts et al. 1992; Nakamura et al. 2000). Volfova et al. (1994) isolated several *Aspergillus niger* strains that produced phytases, the most active being *A. niger 89* and *A. niger 92*. Both strains synthesize the enzyme during active cell growth and simultaneously produce organic acids that lower the pH of the medium and thus contribute to the chemical degradation of phytates. In the case of solid-phase cultivation of producers from the *Aspergillus*, *Mucor*, and *Rhizopus* genera, phytases were also synthesized, the cultivation of *Aspergillus ficuum* in wheat bran medium being the most effective (Fujita et al. 2000). Many enzymes are released in the soil, such as cellulases, hemicellulases, amylases, pectinases, and fungal protein, which increase the absorption and the biologic value of nutrients absorbed by plants from the soil (Bogar and Srakers 2003).

Pandey et al. (2001) investigate strains of *Schwanniomyces castellii*, *Schw. occidentalis*, *Hansenula polymorpha*, *Arxula adeninivorans*, *Rhodotorula gracilis*, and others. An increase in the amount of phytase is often observed in the study of soils with low phosphate content. This is reported for *Candida tropicalis* and *Yarrowia lipolytica* (Hirimuthugoda et al. 2007). It has been found that certain yeast species secrete the enzyme in the soil: *Schwanniomyces castellii* (Segueilha et al. 1992), *Arxula adeninivorans* (Sano et al. 1999), *Pichia spartinae*, and *P. rhodanensis* (Nakamura et al. 2000). Lambrechts et al. (1992) examined 21 yeast strains of 10 species and selected 5 of them – *Candida tropicalis CBS 5696*, *Torulopsis candida CBS 940*, *Debaryomyces castelli CBS 2923*, *Kluyveromyces fragilis U1*, and *Schwanniomyces castellii CBA 2863* – which grow well in a medium with sodium phytate as the sole carbon source. *Schwanniomyces castellii* has a higher phytase potential than other phytase-producing yeasts. Its ability to degrade phytate in some natural raw materials – wheat bran and cottonseed meal has been studied by Segueilha et al. (1993).

Candida krusei WZ-001 was isolated from soil from Dalian Province in China (Quan 2002). The phytase isolated from *Pichia anomala* is characterized by high pH and thermostability and broad substrate specificity, indicating that this strain can develop in different soil types (Vohra and Satyanarayama 2002). Sano and co-workers (1999) reported a very high extracellular activity is characteristic of strains of the species *Arxula adeninivorans*.

In *Schw. castellii* the phytase production decreases when the content of organic or inorganic phosphate increases (Pandey et al. 2001).

Pavlova et al. (2008) isolated yeasts from samples of soils, roots, mosses from the Bulgarian base on the Livingston Peninsula in Antarctica for the first time. They identified them as representatives of different genera and species and examined them for the production of extracellular and cell-associated phytases in environments containing calcium phytate. They cite the strain *Cryptococcus laurentii* AL27 as the most promising one.

Several types of bacteria, such as *Lactobacillus amylovorus*, *Escherichia coli*, *Bacillus subtilis*, *B. amyloliquefaciens*, *Klebsiella* spp., and others, have been studied for phytase biosynthesis (Pandey et al. 2001). The ability to produce indolylacetic acid and to mineralize organic phosphorus by phytase are characteristic of some rhizobacteria. These properties were recorded in *Bacillus sp.* and *Paenibacillus sp.* (Acuca et al. 2011). Phytase activity was also detected in *B. amyloliquefaciens* DS11 (Kim et al. 1999). Several researchers (Shimizu 1992; Griener et al. 1993; Kim et al. 1998) investigated bacterial strains of *Bacillus* spp. and *E. coli*, isolated from soil near the roots of legumes. Yoon et al. (1996) consider that with the exception of strains *Enterobacter* spp. and *B. subtilis*, the phytases of the other bacteria are intracellular. *B. subtilis* strains grow very well on scalded soybeans that are rich in phytates, without other nutritional supplements, indicating that the strains can be beneficial for the uptake of organic phosphorus by plants. During their cultivation, the phytase activity reached a maximum on the 5th day (Shimizu 1992).

6.3.1.4 Siderophore Production

Bacterial activities could conduct to an improvement of plant nutrient uptake, which also results in higher growth and development even in stressful conditions. One of the very important elements is the iron. It takes part in various microbial enzymes, so its importance is proven. In any case, the iron in the aerobic environment exists mainly as Fe^{3+} forming insoluble complexes hydroxides and oxyhydroxides, unavailable to microorganisms and plants. To "solve" this problem bacteria have developed an efficient strategy to make the complexes available. In an iron-deficient environment, they synthesize low molecular weight compounds (<1000 Da) named siderophores (Neilands 1983). These molecules have affinity to metal ions forming complexes, although the siderophores act as solubilizing agents for much more ions from minerals or less soluble organic compounds, such as Al, Cd, Pb, Cu, Zn, etc. (Schalk et al. 2011). According to Boukhalfa and Crumbliss (2002), more than 500 different siderophores are identified. Despite this, metal binding side of the siderophores are α-hydroxycarboxylic acid, catechol, or hydroxamic acid moieties sites and thus can be classified as hydroxycarboxylate-, catecholate-, or hydroxamate-type siderophores (Raymond and Denz 2004). Many siderophores are polypeptides and are synthesized by the non-ribosomal peptide synthetase multienzyme family, which is also responsible for the synthesis of most of microbial peptide antibiotics.

In addition, many of the hydroxamate and α-hydroxy acid-containing siderophores are not polypeptides. They are produced by dicarboxylic acid and either diamine or amino alcohol building molecules linked by amide or ester. Such siderophores are constructed by the non-ribosomal peptide synthetase – independent siderophore pathway, which is widely utilized in bacteria (Rajkumar et al. 2010). The structure and biosynthesis of siderophores are studied in the last years by different authors (Miethke and Marahiel (2007); Barry and Challis (2009). According to Jalal and van der Helm (1991) and Madigan and coauthors (1997), the siderophores form complexes with Fe^{3+} 1:1, which is taken up by the bacterial plasma membrane, reducing Fe^{3+} to Fe^{2+} after liberating the ion in cell plasma. This mechanism of iron uptake in bacteria is described by Krewulak and Vogel (2008). Although the siderophores are produced by pathogens and free-living and symbiotic nitrogen-fixing bacteria, they are most common in PGPR. The beneficial bacteria possess many abilities that improve plant development even in unfavorable conditions where advantage given by siderophores is more evident. However, the function of siderophores is bound to the metal ion uptake improving the Fe nutrition, especially in an extreme environment as scarcity of nutrition or metal contamination. On the other hand, the siderophore production may alter positively the synthesis of IAA, thus increasing overall effect of beneficial bacteria (Dimkpa et al. 2008).

Costa and collaborators (2014) analyzing PGPR data found that 64% of the isolates and 100% of all bacterial genus presented siderophore production. Plants often capture Fe^{3+}-siderophore bacterial complexes utilizing them and do not suffer depletion mediation by bacterial siderophores (Dimkpa et al. 2009). In addition, Pahari and Mishra (2017) reported that siderophore producing isolates significantly increase the growth parameters like root length, shoot length, and biomass of okra (*Abelmoschus esculentus* L.) but also showed antagonistic effect against different phytopathogens including *Rhizoctonia solani* (ITCC-186) and *Fusarium oxysporum* (ITCC-578). According to Berendsen and coauthors (2015), siderophores are one of the key factors stimulating induced systematic resistance in plants against phytopathogens. *Azospirillum brasilense* produces siderophores that expressed in vitro activity against *Colletotrichum acutatum* (anthracnose producing microbe). Inoculated plants of strawberry with the same bacterial population were able to decrease their disease symptoms (Tortora et al. 2011). Pattan et al. (2017) discussed that isolated siderophore showed the antagonists effects against human pathogenic *Pseudomonas aeruginosa* and on phytopathogenic fungi. In maize research, Szilagyi-Zecchin and collaborators (2014) found that endophytic strains from *Bacillus* sp. express various PGP characteristics, including siderophore production, and these were efficient against the growth of *Fusarium verticillioides*, *Colletotrichum graminicola*, *Bipolaris maydis*, and *Cercospora zeae-maydis* fungi.

6.3.1.5 Exopolysaccharide Production

Exopolysaccharide (EPS) production is very important for certain abilities of beneficial microorganisms. They could be defined as high molecular weight compounds of intracellular, structural, and extracellular EPSs found in bacteria, algae, and plants. They display a wide spectrum of variety and are from importance in biofilm formation, root colonization, formation of shielding from desiccation, and stress protection, among others (Gupta et al. 2015; Qurashi and Sabri 2012; Tewari and Arora 2014). EPSs produced by *P. putida* strain GAP-p45 alleviate salt produce stress to sunflower seedlings (Sandhya et al. 2009). According to Parada and co-workers (2006), EPSs are very important for the beneficial bacteria in their interactions with the plant using them as signal molecules and providing defense response of infection. Many of the EPS-producing beneficial microorganisms play a vital role in soil fertility and agricultural sustainability (*Rhizobium* sp., *Azotobacter vinelandii*, *Bacillus drentensis*, *Enterobacter cloacae*, *Agrobacterium* sp., *Xanthomonas* sp.).

6.3.2 Indirect Mechanisms

Indirect mechanisms are those through which the PGPR suppress or prevent negative effects on plants provoked mostly by abiotic or biotic stresses.

6.3.2.1 Antibiosis

The use of microbial antagonism against phytopathogens in agriculture is not a new approach. Biocontrol uses beneficial (non-pathogenic) microorganisms that suppress the development of unwanted, harmful microorganisms and thus is one of the most studied biocontrol issues in the last years (Ulloa-Ogaz et al. 2015). According to Ramadan and co-workers (2016), most of the *Pseudomonas* strains produce antifungal antibiotics (phenazines, phenazine-1-carboxylic acid, phenazine-1-carboxamide, pyrrolnitrin, pyoluteorin, 2,4diacetylphloroglucinol, rhamnolipids, oomycin A, cepaciamide A, ecomycins, viscosinamide, etc.), bactericines (andazomycin), and so on (Ramadan et al. 2016). In addition, *Bacillus* sp. also produces a wide range of antagonistic substances with ribosomal or non-ribosomal origin (subtilosin A, subtilintas A, sublancin; chlorotetain bacilysin, mycobacillin, rhizocticins, difficidin, etc.) (Wang et al. 2015a). Bacterial antibiosis is recorded in different investigations with *Bacillus* inoculating alfalfa seedlings, *Pseudomonas* in wheat, etc. (Vejan et al. 2016; Gupta et al. 2015).

6.3.2.2 Induced Systematic Resistance

Induced systematic resistance (ISR) is a specific physiological state of enhanced defensive capability as a response to determined stressors. Beneficial microbes could induce such resistance in different ways activating the mechanisms through several signals (bacterial components), such as cyclic lipopeptides; siderophores; lipopolysaccharides; 2,4-diacetylphloroglucinol; volatiles, like 2,3-butanediol and acetoin; and homoserine lactones (Berendsen et al. 2015). In this way, plants are “immunized” against a broad spectrum of pathogens; thus, future attacks are repelled. *Bacillus* and *Pseudomonas* species were found to improve plant defense against phytopathogens in many plants through ISR. On the other hand, *Xanthomonas campestris* (black rot) in cabbage was suppressed by biocontrol agent *Paenibacillus*, inducing systematic resistance (Ghazalibigla et al. 2016). Although the ecological niches of ePGPM and iPGPM are different, they use similar mechanisms to suppress phytopathogens and promote plant growth (Shilev 2013). The effect of combined population of PGPR was studied in chilli, showing ISR and growth promotion in greenhouse condition. The authors (Audipudi et al. 2016) concluded that the combined application is more appropriate to be used because of the combination of several different mechanisms presented in distinct microbial populations. Studying the potential of *Pseudomonas aeruginosa* PM12 in the induction of ISR against *Fusarium* in tomato plants, Fatima and Anjum (2017) found strong antifungal effect of 3-hydroxy-5-methoxy benzene methanol of bacterial extracts after GC-MS analysis. Thus, the compound showed intensive remodulation in defense-related pathways against *Fusarium oxysporum*. In conclusion, the application of beneficial microorganisms as biocontrol agents against soilborne pathogens could be an advantage in integrated pest management.

6.3.2.3 Enzyme Production

Ethylene is a very important regulator of plant growth and development, especially in the case of stresses (Gamalero and Glick 2012; Hao et al. 2007). According to Swain (1974), ethylene is associated with the environmental stress, and then plant increases the internal concentration of the phytohormone. These factors are mainly of abiotic origin, such as water stress, salinity, toxic metals, extreme temperature, etc. As a response to the abiotic stress, plants inhibit their growth increasing root endogenous ethylene production. Thus, plant roots have limited growth that reflects to whole plant in reduction of plant biomass. In such conditions, different mechanisms are known that reduce the concentration of ethylene in plants. One of them involves the activity of the bacterial enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Glick et al. 1998). A model of lowering ethylene concentration in plants by beneficial soil bacteria that possess the enzyme ACC deaminase is proposed. ACC deaminase-containing beneficial bacteria can facilitate plant growth and development through the conversion of the immediate ethylene precursor ACC into α-ketobutyrate and ammonia, thus reducing the levels of plant ethylene and improving plant growth in an unfavorable abiotic environment (Glick 2012; Gamalero and Glick 2012; Nascimento et al. 2018). In this case, beneficial bacteria utilize ACC as a sole nitrogen source. Stress induces ACC oxidase in the plant so that there is an increased flux resulting in a first increase of ethylene that induces the transcription of protective genes in the plant. In that moment, bacterial ACC deaminase is activated by the increased concentration of ACC as a result from the function of ACC plant synthesis so that the level of next ethylene peak is decreased tremendously till 90%. Because oxidase has a greater affinity for ACC than does ACC deaminase, when ACC deaminase-producing bacteria are present, plant ethylene levels are dependent upon the ratio of ACC oxidase to ACC deaminase (Glick et al. 1998). This approach is very often applied in phytoremediation strategies dealing with toxic metals. Plant-beneficial bacteria that possess ACC deaminase association improve the growth of the plant, as well as their metal tolerance (Rodriguez et al. 2008).

Pseudomonas sp. and *Acinetobacter* sp. possess ACC deaminase and produce IAA in salt stress environment in the rhizosphere of barley and oats, thus promoting plant growth (Chang et al. 2014). Iqbal and collaborators (2012) observed improved growth characteristics of lentil, such as number of nodules, weights, etc., but also nitrogen content in grains. All these were related to the lowered ethylene production through the plant growth-promoting *Pseudomonas* sp. strains possessing ACC deaminase activity. In other study, Ahmad and collaborators (2013) reported about growth enhancement and quality improvement of mung beans when *Rhizobium* and *Pseudomonas* strains were inoculated under salt stress conditions. In addition, Shaharoona and co-authors (2006) reported that in the same crop, the co-inoculation of *Bradyrhizobium* and of ACC deaminase presenting strain resulted in the stimulation of nodulation. Similarly, Ali and co-workers (2014) found that tomato plants treated previously with the endophytic *P. migulae* and *P. fluorescens* showed ACC deaminase activity and presented improved growth under high salinity stress compared with plants treated previously with an ACC deaminase-deficient mutant and control.

Finally, bacterial ACC deaminase activity can be divided into two sections, based on the level of enzymatic activity (Glick 2010): high ACC deaminase-expressing microorganisms and low ACC deaminase-expressing microorganisms. The first ones are situated near to the plant surfaces and include plenty of microorganisms from rhizosphere, phyllosphere and also endophytes. In contrary, low ACC deaminase-expressing microbes only adhere to specific plants or are only present in determinate tissues. These microorganisms do not lower the whole level of ethylene produced by the plant, but they could prevent a certain increase in ethylene levels. This kind of beneficial microorganisms includes most of the *Rhizobium* sp. (Glick 2005). Also, genus diversity of beneficial bacteria exhibiting ACC deaminase activity had been identified in a wide spectrum of genera such as *Pseudomonas*, *Achromobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Acinetobacter*, *Ralstonia*, *Agrobacterium*, *Enterobacter*, *Alcaligenes*, *Serratia*, *Rhizobium*, etc. (Kang et al. 2010; Onofre-Lemus et al. 2009).

6.3.2.4 VOCs

Biocontrol strains may produce volatile organic compounds (VOCs) that possess antagonistic activity against phytopathogenic fungi, bacteria, or nematodes. In a biocontrol study, the VOCs of *P. fluorescens* WR-1 not only showed a concentration-dependent bacteriostatic effect on the growth of *R. solanacearum* but also could inhibit its virulence habilities. The VOCs can spread over a long distance and bacteriostatic environment persists around the plant rhizosphere compared to the antibiotics, which can be effective only if biocontrol agents colonize plant roots effectively (Raza et al. 2016). On the other hand, the interaction between VOCs of *Bacillus subtilis* and *Ralstonia solanacearum* and plant results in growth promotion and induced systemic resistance against the bacterial wild pathogen *R. solanacearum* (Tahir et al. 2017).

6.4 Production and Formulation of Bacterial Biofertilizers

A biofertilizer could be defined as the formulated product containing one or more microorganisms that enhance the nutrient status (and the growth and yield) of plants by either replacing soil nutrients or by making nutrients more available to plants or by increasing plant access to nutrients (Malusa and Vassilev 2014). The oldest, officially recognized invention on plant-beneficial microorganisms appeared in 1896 (Nobbe and Hiltner 1896). However, the application of plant-beneficial microorganisms started in the 1950s when seeds were coated with bacterial cultures to promote plant growth and development (Brown 1974). Now, the production and commercialization of plant-beneficial microorganisms is one of the most active fields of the biotech industry. The market of plant growth promoters is estimated at 946.6 million of dollars in 2015, but this value will increase with 14.08% till the end of 2022. Due to the increasing human population the need for agro-chemical products will raise, which will simultaneously increase the need of biofertilizers (Markets and markets 2016).

In general, the main steps of a biostimulant production follow a scheme, which includes up to eight key experimental groups of studies (Fig. 6.2).

Selection of plant-beneficial bacterial strains is normally carried out using criteria-specific properties including plant growth-promoting or antimicrobial metabolites, competing with other (local) soil microorganisms for nutrients, and demonstrating sufficient level of genetic stability and resistance toward various abiotic and biotic factors (Herrmann and Lesueur 2013). Selection is generally oriented to two main groups of plant-beneficial activities: fixation of nitrogen by mutualistic endosymbionts, such as *Rhizobium,* and mutualistic, rhizospheric plant growth promoters. It should be noted, however, that biofertilizers are normally characterized by multifunctional properties, which affect all aspects of nutrition and growth, various stresses, and interactions with other organisms in the soil-plant systems (Berg et al. 2014; Vacheron et al. 2013; Vassileva et al. 2010). For example, nitrogen-fixing bacteria, in addition to their main function, may manifest other properties typical for bacteria stimulating plant growth and development such as biosynthesis of phytohormones, siderophores, amino acids, polysaccharides, etc., thus increasing the overall benefits to plants (Pathak and Kumar 2016).

The selected bacteria should be easily cultivated, preserving their metabolic functions. Soil microorganisms, including bacteria, are living in the soil – a complex medium creating specific environment for each living organism. Many bacteria were isolated from soil and characterized and their plant-beneficial properties described (Jacoby et al. 2017). However, all these studies are carried out in an

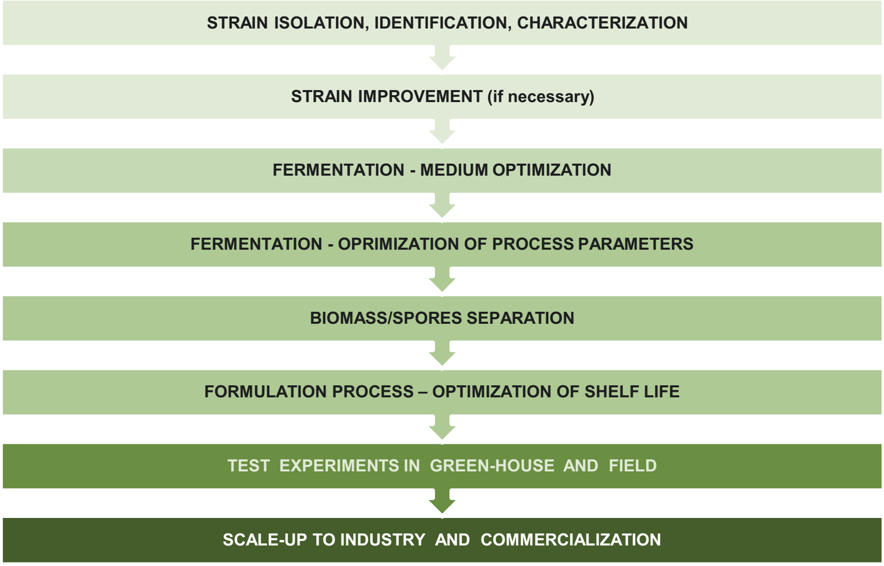

Fig. 6.2 Main steps in biofertilizer/biocontrol development and production. (Modified from Vassilev and Mendes 2018)

artificial, synthetic medium incapable of mimicking the endogenous abiotic and biotic conditions required for microbial growth, and many bacteria are categorized as uncultivable in such conditions (Pham and Kim 2012).

In the production of biofertilizers for commercial use, a high-quality biomass and/or spores of the target inoculum is required that further must retain high viability during the formulation process, storage, transportation, and after application to seed or in soil. The biomass or spore production is carried out in fermenters in conditions of liquid submerged or solid-state fermentation (SSF) processes based on inexpensive media (Malusa et al. 2012; Vassilev et al. 2015; Vassilev and Mendes 2018). Extensive studies are needed to optimize medium composition, process parameters, and transfer the laboratory technology to large-scale production. According to the type of the process, fermentations depend on the inoculum age and size, medium composition, concentration of the medium constituents and their ratio, water activity, the level of dissolved oxygen/aeration, addition of precursors, humidity, temperature, initial pH and its maintenance (if necessary), and time of harvest. The liquid submerged bacterial fermentation is well studied and described. In submerged cultures, bacteria and fungi may produce biomass and spores. This process depends on the microorganism, its nutritional medium or fermentation process (McCoy et al. 1988). During the last 20 years, the SSF has attracted more attention in the biotechnology industry although in general, the biofertilizer production process in SSF is more suitable in small-scale conditions. SSF has been defined as the bioprocess carried out in the absence, or near-absence, of free water; however, the substrate must possess enough moisture to support the growth and metabolic activity of the microorganism (Costa et al. 2018). SSF is a process, which includes a unique solid, liquid, and gaseous phase interactions, thus ensuring advantageous microbial growth and metabolic activity. This eco-friendly process, which is normally based on solid agro-industrial wastes used as a substrate or cell-carrier, is particularly characterized by lower energy and water needs, lack of contaminants, and high metabolic target activity (Thomas et al. 2013). To use submerged fermentation or SSF is a question of economic choice and also depends on the bacterial properties and specificity of the formulation procedure.

While the cultivation processes and optimization of fermentation parameters for bacterial growth and biomass/spore production are well studied, formulation procedures are far from the market and farmers' requirements (Lesueur et al. 2016). Biofertilizer, produced as a result of solid-state fermentation, in fact is a ready-to-use commercial product, thus avoiding the formulation step of the overall production process (Mendes et al. 2015). The final product of the fermentation, containing mineralized agro-industrial waste, bacterial biomass, and all released metabolites are simply dried ground and introduced into sterile bags. The problem with the SSF-based formulation is that the products are bulky, thus requiring extra space for processing and storage. For this reason, the liquid-state fermentation is preferred to obtain large quantities of biomass often in shorter time (Jambhulkar et al. 2016). In conditions of submerged fermentation, bacteria can be separated from fermentation broth and further concentrated and formulated. Alternatively, both biomass and medium can be formulated to form granules, pellets, wettable powders, or liquids. It is widely accepted that the fermentation process for the production of abundant and dense biomass/spores is the most decisive part of the overall production of a final biofertilizer commercial product (Bashan et al. 2014).

Four groups of biofertilizer formulates are commercialized depending on the carrier material: soil-related materials, plant derivates, inert carriers, lyophilized and oil dried bacteria, liquid carriers, and capsule-based carriers (Bashan 1998).

The carrier is the inoculant portion that ensures the effective release of the bacterial cells. Carrier diversity is enormous including water, vermiculite, perlite, calcium sulfate, calcium phosphate, coal, biochar, mineral soil, vegetable oil, corn cob, natural and artificial polysaccharides, etc. (Bashan 1998). The carrier characteristics include to be easily available and inexpensive and chemically stable; to be nontoxic, thus ensuring a friendly environment for the microorganism; to maintain sufficient humidity; to be capable of delivering of metabolically active cells in the soil; to be easy to process; and to ensure cell viability after determined periods of storage. Here, we will describe the most widespread and the most innovative carriers and formulations.

Peat is the solid carrier of choice for biofertilizer formulation, but it is not easily available and is expensive (Stephens and Rask 2000). However, this carrier material is well known, and farmers are familiar with its application. It is important to note that peat, with its high surface area and high water-holding capacity ensures bacterial metabolic activity and cell multiplication continues during the storage period.

Another solid carrier is biochar produced by pyrolysis of biomass under limited oxygen availability. Biochar can derive from plant biomass or animal bones and due to the specific porous structure and properties is an excellent carrier for soil microorganisms (Hale et al. 2014; Warren et al. 2009). Biochar enhances the soil physical and biochemical properties, and particularly animal biochar serves as a high-quality P source (Vassilev et al. 2013).

Talc, a metamorphic mineral composed of hydrated magnesium silicate, is frequently used as a formulation agent. It easily permits bio-preparations of more than one plant-beneficial microorganism (Shanmugam et al. 2011; Sahu et al. 2013). It is interesting to mention that talc formulations can be used directly and as a suspension to the seeds or as a spray. Talc is also used as filler, adding bulkiness to formulations based on costly polysaccharides used in immobilized-cell-based technologies (Sahu and Brahmaprakash 2016).

Liquid formulations, based on aqueous medium containing all components necessary for microbial growth, are now gaining popularity for different types of plant-beneficial microorganisms. Current liquid biofertilizer formulations are easy to handle and adapted for existing seeding equipment or directly in soil (Herrmann and Lesueur 2013). They can be produced in conditions of liquid submerged fermentations, processed aseptically, and maintained metabolically active before use (Mahanty et al. 2017). This kind of formulations is cost-effective, as they do not need solid carrier material and normally contain high bacterial concentrations thus allowing the application of a lower quantity compared to carrier-based biofertilizers. Liquid biofertilizers can be enriched with cell protectant and additives to improve inoculant performance during storage and in soil (Sahu and Brahmaprakash 2016). However, liquid formulated biofertilizers are very sensitive when applied on seeds and need addition of high molecular weight polymers to improve their survival (Singleton et al. 2002; Vassilev et al. 2017a). Liquids with biofertilizing properties could be produced without cells and/or using immobilized cells – a technique, which allows for more effective, multifunctional products (Mendes et al. 2017; Vassilev et al. 2017b).

During the last 20 years, application of immobilization methods in the field of biofertilizer and biocontrol production was observed (Bashan 1998; Vassilev et al. 2001, 2005; Malusa et al. 2012). Immobilization methods make use of non-toxic polymeric natural compounds such as alginate, agar, agarose, polyacrylamide gel, pectin, chitosan, etc. (Bashan et al. 2014; Vassilev et al. 2015). Compared to free cell systems, immobilization of plant-beneficial microorganisms offers advantages including enhanced metabolic activity and stability, better fermentation control, and low risk of contamination (Vassilev et al. 2007). In case of applications in disturbed soils or soil-plant systems, formulated plant-beneficial microorganisms encapsulated in natural gel carriers ensure very efficient barrier against biotic and abiotic stresses (Cassidy et al. 1996; Vassileva et al. 1999; Vassilev et al. 2012). In addition, results show a strong positive effect of such kind of formulations on both maintenance of viability/metabolic activity during storage and upon introduction into soil and delivery of these active cells, thus ensuring higher rhizosphere microbial enrichment compared to the direct introduction of the respective free microbial forms (Vassileva et al. 1999). To immobilize bacterial cells, processes such as spray drying, interfacial polymerization, and gelation are widely studied. However, novel techniques are continuously developed to improve the viability and resistance of cells during drying procedures and storage (Vassilev et al. 2015).

The tendencies in the field of production and formulation of biofertilizers for the nearest future are well determined (Vassilev et al. 2015; Bashan et al. 2014). Briefly, co-cultivation (fermentation) processes, addition of medium constituents with both nutrient and protective properties, development of large-scale SSF processes, liquid cell-free biofertilizers, economically acceptable immobilization techniques, and inclusion of fillers and additives in the immobilization matrixes are among the most acceptable and easy to develop scientific procedures in biofertilizer production and formulation. The most important is to create smart systems based on a multifaceted technological approach gathering achievements from various scientific fields.

6.5 Conclusion

The interactions between plants and microbes in the rhizosphere are complex where the root exudation is the key point in this interaction. There are too many papers demonstrating that interactions in rhizosphere are mediated directly or indirectly by root exudates. However, recently the sequencing technology allows investigating the interactions at the community level. Furthermore, studies analyze the interactions at functional level identifying the signals involved in interactions among different species which is the key point in the utilization of these processes for the benefits of the crops and sustainability of the plant species. Root exudates are crucial and fundamental signals in plant, fungal, and microbe communications in the soil. They are some kind of messengers that intermediate communication between all partners in the rhizosphere. Thus, the rhizosphere with all beauty presented above, is extremely complex, with continuously changing characteristics. What is important is that *we know that we don't know sufficient*, but we have to reach more deeply in the research of interactions between the microbes, the plants, the other soil organisms, and the abiotic environment.

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