Chapter 2
Microorganisms Used as Growth Regulators in Modern Agriculture

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Abstract Biofertilizers and biological products are increasingly being used to enlarge the productivity of crops. Of these, microbes known as Plant Growth-Promoting Microorganisms (PGPM) are the most valuable as biofertilizers, having the capacity to directly impact the growth and development of plants. Plant Growth-Promoting Fungi (PGPF) and Plant Growth-Promoting Bacteria (PGPB) help crops to face biotic and abiotic stresses by enhancing the defense system and several other parameters related to plant growth. This chapter is focused on explaining the function and positive influence of the PGPF and PGPB on several crops, and also to provide a general view of the application of microorganisms in modern agriculture.

Keywords Agriculture · Plant growth-promoting microorganism · Plant growth-promoting bacteria · Plant growth-promoting fungi · Growth regulator

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2.1 Introduction

Nowadays, agriculture continues to use numerous chemicals (fertilizers and pesticides) to ensure the growth and development of plants. Many of these products have been related to the degradation and pollution of soils, water, and even crops themselves (Jiménez et al. 2011).

The excessive application of synthetic pesticides is the direct cause of the resistance of several organisms, and therefore, the loss of their effectiveness. Chemical control also produces decrease in populations of natural enemies, resurgence of pests with resistance against pesticides, and outbreaks of secondary pests (Pacheco et al. 2019).

One way to increase the efficiency of agronomic systems in the long term is through the application of microbial inoculants, which represent a new technology that can be considered as clean, aligned with the principles of sustainable agriculture, against the irrational increase in the use of pesticides and fertilizers (Naiman et al. 2009). An alternative to increase root growth in plants is by incorporating microorganisms that contribute to the implantation, production, and development of crops. Other factors include soil exploration, access to water and limiting nutrients for crops, reduction of processes for mobile nutrients loss, attenuating periods of moderate water stress and maintaining active growth rates of the crop, and improving its photosynthetic capacity (Díaz-Zorita and Fernández 2008).

Biofertilizers and biological products are increasingly being used to boost crop productivity, being the microbes that stimulate plant development, known as PGPM (Plant Growth-Promoting Microorganisms), most valuable as biofertilizers, having the capacity to directly increase the growth and development of crops (Bashan et al. 2014; Varma et al. 2012; Giri et al. 2019).

An example of PGPM are the Plant Growth-Promoting Bacteria (PGPB) which have been studied not only regarding their impact on the plant, but also relating to the mechanisms they use to promote growth and interact with the plant (Sgroy et al. 2009; Prasad et al. 2015). Some of the characteristics sought for the selection of bacteria with PGPB potential are: ability to solubilize inorganic phosphorus (genus *Paenibacillus*, genus *Enterobacter*), biological fixation of atmospheric nitrogen (species of *Rhizobium, Azotobacter, Bacillus, Clostridium*, and *Klebsiella*), production of plant growth inducers such as auxins, mineralization of organic phosphorus, ACC deaminase activity, production of siderophores (*Azotobacter vinelandii, Bacillus megaterium, Bacillus subtilis, Pantoea allii* and *Rhizobium radiobacter*), hydrocyanic acid and salicylic acid, among others (Glick et al. 2007; Sgroy et al. 2009).

Another group of PGPM are the Plant Growth-Promoting Fungi (PGPF). These microorganisms are gaining importance in organic agriculture because they are soil-borne filamentous fungi which are innocuous to plants, and yet they are of great importance. These fungi act by colonizing the root of plants for development, improvement, protection, and growth (Hyakumachi 1994). Some examples of

PGPF are species of *Aspergillus*, *Trichoderma*, *Penicillium*, and several other endophytes (Mishra et al. 2015).

The PGPF remove or suppress pests in the rhizosphere area through the production of plant hormones and hydrolytic enzymes, and also through mineral solubilization (P, N, and Fe). Some other functions include stimulation of systemic resistance, competition for saprophytic colonization, and mycoparasitism (Lewis and Papavizas 1991).

All the above information demonstrates the importance of knowing the microbiota regardless of the function it performs in the plant (plant growth promoter, nitrogen fixer, or phosphate solubilizer), with the aim of maximizing the beneficial effects of biofertilization and biostimulation, to promote more sustainable agricultural production, and satisfy the rising demand for food with the required quality. In this way, using microorganisms able to promote plant growth is a great alternative for biofertilization. The aim of this chapter is to provide information on fungi and bacteria used as growth regulators in modern agriculture describing the species most commonly employed and their function in plant growth.

2.2 Microorganisms in Modern Agriculture

Microorganisms appeared on Earth 4 billion years ago. The conquest of the terrestrial surface emerged with the green algae, which evolution turned them into the first plants, an event that occurred about 3.5 billion years later. Afterwards, agriculture began in the Neolithic, about 10,000 years ago. These facts show that microbes have occupied the soil long before other organisms, and that the cultivation of agricultural species has always been associated with them. Nonetheless, only 300 years ago, we have known about the existence of microorganisms, and even less time has elapsed since they began to be considered important and even vital in various processes, including agriculture.

The discovery of the presence of microbes in soil, water, the plant rhizosphere, plant surface, and even inside plant tissues has motivated their in-depth study, in search of relationships and influences that enhance agricultural production. In recent decades, awareness of the contamination of agroecosystems by fertilizers and pesticides has opened up new avenues for taking advantage of the beneficial microorganisms that promote growth, to substitute or reduce the amount of those products used in agriculture.

Research on the relationships between plants and microorganisms, including many PGPBs and various genera of PGPF, have led to the discovery of two large groups of mechanisms (direct and indirect) in which this stimulation manifests itself, which will be reviewed below.

2.2.1 Direct Mechanisms

2.2.1.1 Biological Nitrogen Fixation and Supply of Other Nutrients

In soils low in nitrogen, the presence of bacteria of the genus *Rhizobium* in symbiosis with various legumes favors the growth of these plants. *Rhizobium* fixes atmospheric nitrogen in the form of ammonia, assimilated by the plant. The symbiosis begins with the emission of radical, exudates with a flavonoid structure that attracts microorganisms, and these respond by activating genes that synthesize nodulation factors (Oldroyd 2013). The plant-microbe association is genetically regulated by miRNA (Hoang et al. 2020) at various points of the symbiosis (Varma et al. 2020).

The miRNAs are small RNA fragments capable of controlling the expression of numerous and diverse genes through repression of translation or degradation of mRNA. The first miRNA was discovered in the nematode *Caenorhabditis elegans* (Lee et al. 1993). The regulation by miRNA in legumes occurs during the mutual recognition between the plant and the microbe, in the formation and growth of the nodules and the modulation of the synthesis and degradation of enzymes, reactive oxygen species (ROS), auxins, and cytokinins during the symbiotic process (Subramanian et al. 2008; Tóth and Stacey 2015; Wang et al. 2015; Yan et al. 2016; Tsikou et al. 2018).

Although the best-known nitrogen (N) fixation process is done by *Rhizobium*, another no less important N fixation is done by the actinobacteria *Frankia* in woody species (Van Nguyen and Pawlowski 2017). In this symbiosis, nodules develop on lateral roots, and the microorganism protects the nitrogenase enzyme complex from oxidation. Other bacterial genera also capable of fixing nitrogen include *Azotobacter* (Jnawali et al. 2015), *Azospirillum* (Fukami et al. 2018), *Bacillus* (Kuan et al. 2016; Yousuf et al. 2017), *Paenibacillus* (Shi et al. 2016), and others. Apparently, the expression of genes involved in N fixation is regulated by the presence of elements and substances such as oxygen and ammonia in the medium, as in *Paenibacillus* (Shi et al. 2016; Do Carmo et al. 2020).

Phosphorous and potassium, in addition to nitrogen, are macroelements consumed in large quantities by plants, and consequently are present in many synthetic chemical fertilizers. Phosphorus is an element commonly found in soils in an insoluble form, which cannot be assimilated by the plant. However, bacteria of the genera *Enterobacter, Pseudomonas, Rhizobium, and Bacillus* and fungi of the genera *Aspergillus, Penicillium*, and arbuscular mycorrhizae act as phosphorus mobilizers or solubilizers (Adhya et al. 2015; Alori et al. 2017; Satyaprakash et al. 2017). The solubilization pathway of phosphorus from phosphate compounds by bacteria such as *Pantoea* sp. is the acidification of the medium by the production of gluconic acid, which is transformed to 2-ketogluconic acid, solubilizer of phosphate (Castagno et al. 2011).

Potassium is the cation most absorbed by plants, but its availability in soils has decreased due to erosion and leaching (Sindhu et al. 2016). *A. tumefaciens* and *R. pusense* are rhizosphere bacteria that exhibit high levels of potassium solubilization (Meena et al. 2015) but a large variety of bacterial genera, as well as the fungi *P. frequentans* and *C. cladosporioides*, perform this metabolic activity (Sindhu et al. 2016). These microbes obtain potassium from the solubilization of minerals such as mica and feldspar, through methods like the production of organic acids, exchange reactions, and chelation (Etesami et al. 2017).

Even though iron is one of the most abundant elements in the earth's crust, its ferric form (Fe^{3+}) is not assimilable by plants. Instead, bacteria produce small organic molecules (siderophores) that can bind to this ion. Crowley (2006) showed that siderophores of microbial origin are the main source of iron for plants. In addition to the production of siderophores by *E. coli, Streptomyces* sp., and *Pseudomonas* sp. (Saha et al. 2015), its synthesis has also been demonstrated in the fungi *Trichoderma harzianum, Penicillium citrinum, Aspergillus niger* (Yadav et al. 2011), and *Trichoderma asperellum* (Qi and Zhao 2013). Zinc, mycorrhizal fungi (Gadd 2007), and some species of *Acinetobacter, Gluconacetobacter, Pseudomonas,* and mainly *Bacillus* solubilize this element from insoluble compounds (Sharma et al. 2012).

2.2.1.2 Production of ACC Deaminase

In higher plants, excess ethylene can cause defoliation, wilting, rot, and death events. ACC (1-aminocyclopropane-1-carboxylate) is a precursor of ethylene, and one way to avoid the excessive increase of ethylene is its deamination by the enzyme ACC deaminase of rhizospheric microorganisms, synthesizing NH_3 that can be used by plants. In general, the activity of this enzyme is present in most microorganisms that live with plants, especially in environments considered stressful (Timmusk et al. 2011). In the contact among plants and numerous bacteria known to stimulate plant development, such as *Burkholderia, Pseudomonas,* and *Rhizobium*, and fungi like *Trichoderma asperellum*, the activity of microbial ACC deaminase plays an important role (Nascimento et al. 2014).

The high ACC-deaminase activity exhibited by PGPB participates in the reduction of ethylene levels that occur under conditions of flood stress, heavy metals, drought, and salinity. Maxton et al. (2017) found that *Burkholderiacepacia* showed the highest ACC-deaminase activity of three bacterial species tested, and also it induced the highest growth promotion in pepper (*Capsicum annuum* L.) under water and saline stress. The bacterium *Leclercia adecarboxylata* is ubiquitous, and previously considered to belong to the genus *Escherichia* until its reclassification (Tamura et al. 1986). Recently, its ability to reduce saline stress in tomato (*Solanum lycopersicum* L.), which seems to be associated with its high ACC-deaminase activity (Kang et al. 2019) has been demonstrated. Two bacterial lines isolated from the rhizosphere of garlic plants (*Allium sativum* L.), identified as *Aneurinibacillus aneurinilyticus* and *Paenibacillus* sp., were the only ones among six that showed ACC-deaminase activity, and also the only ones capable of promoting *in vitro* growth of *Phaseolus vulgaris* plants under conditions of water and saline stress (Gupta and Pandey 2019).

The presence of ACC-deaminase activity in pathogenic microbes suggests that in these cases it could help the microorganism to overcome the plant defense responses to infection, which involve the ACC metabolic pathway (Singh et al. 2015). However, the use in agriculture of microorganisms with high ACC-deaminase activity is an option to increase tolerance to abiotic stress with more sustainable agricultural practices (Orozco et al. 2020).

2.2.1.3 Synthesis and Modulation of Phytohormones

In one way or another, all the effects of PGPB and PGPF are linked to phytohormones, either through the synthesis of these compounds or through the modulation of pathways such as salicylic acid in systemic acquired resistance (Heil 2001) and ethylene and jasmonic acid in induced systemic resistance (Ongena et al. 2005; Bisen et al. 2016).

The synthesis of indoleacetic acid (IAA) by PPGB is a pathway by which bacteria stimulate the growth of lateral roots and root hairs (Jeyanthi and Kanimozhi 2018). The softening of the cell walls leads to cell growth and to an increase in the effective surface producing exudates useful for bacteria (Glick 2012a, b). Auxin synthesis by PGPB has been demonstrated in *Pseudomonas* (Egamberdiyeva 2007), *Azotobacter* (Jnawali et al. 2015), *Bacillus* (Kuan et al. 2016), *Azospirillum* (Fukami et al. 2018), and other genera. The stimulation of root growth by the fungi *Trichoderma harzianum* (Harman et al. 2004a) and *Trichoderma virens* (Contreras-Cornejo et al. 2009), as well as by other genera (*Penicillium, Aspergillus, Fusarium, Talaromyces* and *Mortierella*) (Murali et al. 2021) is mediated by auxin synthesis.

Cytokinins not only promote cell division and shoot growth, in which the microorganisms that synthesize them can cooperate with plants (Wang et al. 2018; Swarnalakshmi et al. 2020); their influence in plant-pathogen relationships have also been shown (Saleem Akhtar et al. 2020). Gibberellins, mainly synthesized by different genera of fungi, play a role in stem elongation and root colonization (Hossain et al. 2017a). However, the nature of the effects of both phytohormones remains to be clarified, since they have been proven to be produced by both beneficial and pathogenic microorganisms.

The modulation of hormone synthesis involved in acquired and induced systemic resistance (jasmonic acid, ethylene, and salicylic acid) can also be exerted by *Trichoderma* sp. (Houssien et al. 2010; Tucci et al. 2011; Nawrocka et al. 2018).

2.2.2 Indirect Mechanisms

2.2.2.1 Natural Enemy Suppressants

A great amount of fungi and bacteria synthesize substances that function as antagonists of plant pathogenic microorganisms. By reducing the chances of infection, they indirectly favor plant growth and development (Patil et al. 2021).

Abundant information exists on the pathogen-suppressive effects of the genera *Pseudomonas, Burkholderia,* and *Bacillus* (bacteria) and *Gliocladium* and *Trichoderma* (fungi). The genus *Burkholderia* contains a great amount of species that produce antibiotic substances of various types (Depoorter et al. 2016). The pyrrolnitrin synthesized by *Burkholderia* and *Pseudomonas* is known to be a broad-spectrum antibiotic, capable of acting against various genera of pathogenic microbes such as *Verticillium, Botrytis, Rhizoctonia*, and *Sclerotinia* (Raaijmakers and Mazzola 2012). The *Burkholderia tropica* line MTo431 synthesizes almost 20 volatile substances, several of them derived from toluene and terpenoids, capable of inhibiting to a greater or lesser extent the growth of the fungi *F. culmorum, F. oxysporum, S. rolffsi,* and *C. gloeosporioides*, pathogens of various plant species (Tenorio et al. 2013).

The 2,4-diacetylphloroglucinol produced by *Pseudomonas fluorescens* is recognized as an antibiotic against several species of pathogenic fungi, including *Gaeumannomyces graminis* var. *tritici* (Mazzola et al. 2004). However, it has also been found that other isolates of this same bacterium are capable of inhibiting the growth of this fungus through the production of hydrogen cyanide (HCN) and siderophores (Warren et al. 2016). The growth suppression of *Phytophthora infestans* in potato, mediated by *Pseudomonas protegens*, is also stronger in lines that synthesize HCN (Hunziker et al. 2014). *Pseudomonas chlororaphis* synthesizes other antibiotics such as pyrrolnitrin, diacetylphloroglucinol, rhizoxine, phenazines and their derivatives (Arrebola et al. 2019).

For its use as a biocontroller, *Bacillus* sp. has the advantages that it grows in numerous types of soil, it is easily cultivable under laboratory conditions, and several of its species produce antibiotics. Zwittermicin A is an antibiotic synthesized by *Baccillus cereus* (Savini 2016) and that acts on oomycetes such as *Phytophthora* (Singh et al. 2017). Iturin A produced by *Bacillus subtilis* is an effective antifungal against *Rhizoctonia solani* in tomato (Zohora et al. 2016). *Bacillus thuringiensis* synthesizes thuricin-17, a small peptide with biocidal or growth-retarding effects on many prokaryotes (Nazari and Smith 2020). In general, *Paenibacillus* and *Bacillus* species elaborate a whole variety of protein and peptide structures that have a deleterious action on other microbes (Olishevska et al. 2019; Miljaković et al. 2020).

Fungi of the genus *Trichoderma* are abundant in the rhizosphere and are capable of parasitizing other fungi and producing lethal effects on numerous microorganisms (Harman et al. 2004b). In recent years, documented reviews have been published on their ecology, mode of action, and use as biocontrollers of pathogens (Contreras et al. 2016; Ghazanfar et al. 2018; Singh et al. 2018; Al-Ani and Mohammed 2020).

The metabolites produced by *Trichoderma* sp. are very diverse, and include antibiotics, siderophores, and hydrolytic enzymes; they are effective against pathogens such as *Sclerotium rolfsii* (Evidente et al. 2003), *Gaeumannomyces graminis, Pythium ultimum, Rhizoctonia solani* (Vinale et al. 2006), *Botrytis allii, Colletotrichum lini, Fusarium caeruleum* (Reino et al. 2008), and *Phytophthora citrophthora* (Druzhinina et al. 2011), among others.

Gliocladium sp. is a genus of fungi that, due to its morphology and coexistence in the habitat, is often confused with *Hypocrea, Penicillium, Verticillium,* and *Trichod*erma, to the extent that some of its species have undergone reclassification (Castillo et al. 2016). The genus produces gliotoxin and gliovirin, antifungals against *R. solani* and *P. ultimum*, respectively (Keswani et al. 2017). *Gliocladium catenulatum* is effective against *Botrytis cinerea* (Van Delm et al. 2015); *Gliocladium virens* controls *Verticillium dhaliae, Curvularia lunata* (Rizk et al. 2017); *Gliocladium fimbriatum* reduces *Fusarium* infection by 48% (Fitrianingsih et al. 2019).

Although the antimicrobial effects of all these microorganisms are recognized, their massive application should be done with discretion, since some species of these genera are pathogens of plants, animals, and man, such as *Pseudomonas aeruginosa, Bacillus cereus, Bacillus anthracis* and *Burkholderia cepacia*, and they live in the same habitat of beneficial microorganisms.

2.2.2.2 Induced Resistance

During their evolution, plants developed ways of recognizing the pathogens that attack them and defending themselves against those attacks. In addition, research on the interaction of crops with abiotic and biotic stresses has shown that there is another type of resistance, which depends on the contact of the plant with pathogenic or beneficial microorganisms. This has been called induced resistance (Carvalho et al. 2010).

Induced resistance phenomena could be classified into two large groups: systemic acquired resistance (SAR) and systemic induced resistance (SIR) (Peteira 2020). SAR is nonspecific and occurs as a result of attack by a pathogen; it is regulated through the salicylic acid pathway and pathogenesis-related proteins (PRP) participate in it (Heil 2001). PRPs are not involved in SIR, but it is controlled by ethylene and jasmonic acid. In addition, pathogens do not participate in this regulation, but growth-promoting bacteria (Ongena et al. 2005) and non-pathogenic growth-promoting fungi do participate (Bisen et al. 2016). Although the molecular signals, genes, and products involved are different, both mechanisms have a common result: the resistance of plants to stress (Peteira 2020).

Systemic induced resistance is particularly interesting, because despite involving harmless bacteria, it can increase resistance to pathogens and tolerance to abiotic stresses. Among the PGPB, the genera *Bacillus* and *Paenibacillus* have been the most studied. Inoculation with *Bacillus subtilis* decreased cucumber susceptibility to *Colletotrichum lagenarium* and of tomato to *Pythium aphanidermatum* (Ongena et al. 2005). In peanuts, the presence of *Paenibacillus polymyxa* in the rhizosphere contributed to the control of crown rot disease caused by *Apergillus niger* (Haggag 2007). *Bacillus cereus* induces resistance against *Pseudomonas syringae*, a pathogen of various crops (Nie et al. 2017). The synthesis of elicitors by the resistance-inducing microorganism plays a determining role in the process. Mutants of *Bacillus amyloliquefaciens* exhibiting deficiencies in the production of extracellular compounds are also deficient in the ability to induce resistance to *Pseudomonas syringae* and *Botrytis cinerea* in *Arabidopsis* (Wu et al. 2018a, b).

Not only bacteria are capable of causing SIR; fungi of the genera *Trichoderma, Penicillium, Phoma, Aspergillus, Fusarium,* and *Piriformospora* also induce this phenomenon (Hossain et al. 2017a). Undoubtedly, the best known and most used in agriculture is *Trichoderma* sp. (Yoshioka et al. 2012; Singh et al. 2014; Saxena et al. 2015; Bisen et al. 2016), but abundant examples exist of the effects of the remaining genera. Resistance to cucumber mosaic virus can be induced by *Penicillium simplicissimum* (Elsharkawy et al. 2012) and by *Phoma* sp. (Elsharkawy 2018). Two *Aspergillus* species increase the synthesis levels of defensive metabolites against various pathogens in corn (Mahapatra et al. 2014), while *Aspergillus terreus* induces resistance to *Pseudomonas syringae* in tomato (Yoo et al. 2018).

The defense spectrum provided by SIR can also include herbivorous insects (Rashid and Chung 2017) and abiotic stress. The increase in tolerance to salinity caused by NaCl due to the effects of *A. tumefaciens*, *Bacillus* sp., and *Pseudomonas* sp. has been reported (Gayathri et al. 2010; Rashid et al. 2012; Kumar et al. 2016).

2.2.2.3 Bioremediation

Bioremediation is a biological process of decontamination of soils and water, which is carried out by taking advantage of the natural properties of bacteria, fungi, algae, and other organisms, so it is essentially a biotechnological procedure. These organisms convert waste and hazardous materials into less or nonhazardous substances (Singh et al. 2019) thereby reducing pollution of the ecosystem.

The pollutants most approached from science and practical application are pesticides, polycyclic aromatic hydrocarbons (PAH), and heavy metals (HM). Liu et al. (2017) reviewed the bacteria and fungi capable of reducing the presence of these contaminants and include genera well known to farmers, such as the bacteria *Bacillus, Pseudomonas,* and *Enterobacter*; and the fungi *Fusarium, Pleurotus, and Trichoderma*.

In bioremediation, bacteria, particularly PGPB, can act in two ways: a direct and an indirect (Kaur 2021). The first one includes mechanisms that allow bacteria to degrade pollutants (chelation, use of hydrolytic enzymes, biotransformation) and the second one relates to supporting plants that are capable of assimilating pollutants (particularly MH) in the process called phytoremediation (Sarkar et al. 2022; Prasad 2022; Sonowal et al. 2022). This collaboration mainly increases the bioavailability of these elements so they are absorbed by plants, and stimulating crops development through the production of phytohormones, with which crops increases its phytoremediation potential.

The enzymatic mechanisms used by fungi to degrade contaminants have been reviewed by several authors, and they include the activity of hydrolytic enzymes (such as lipases, cellulases, xylanases), the reduction of heavy metals to less toxic forms, their metabolic assimilation or immobilization in soil, among others (Deshmukh et al. 2016; Singh et al. 2019; Pérez and Héctor 2021).

2.2.3 The Microbiome Approach

Although the mechanisms of plant growth stimulation by microorganisms are separately observed for their study, as well as the effects that one or another microbe can exert, this phenomenon is much more complex. Many studies show that the rhizosphere is an ecosystem itself, in which a great diversity of microorganisms interrelates with the roots of plants. These relationships are established through communication mechanisms through the segregation of chemical substances by the participating organisms (Mhlongo et al. 2018). Plants are capable of regulating which microorganisms live in the microbiome through radical exudates and, instead, certain microbial species have evolved to live in that environment (Jacoby et al. 2017).

Researchers have understood this, and that is why studies have been developed in which several microorganisms or substances synthesized by them are combined, seeking to enhance effects such as the acquisition of mineral elements from the soil. The combined inoculation of *Rhizobium leguminosarum* + arbuscular mycorrhizae (*Glomus mosseae*) increases N_2-fixation several times compared to the inoculation of these microorganisms separately (Meng et al. 2015). The co-inoculation of *Rhizobium* with the PGPB *Bacillus aryabhattai* and *Azotobacter vinelandii*, particularly with the latter, increases nitrogen fixation in *Trifolium repens* (Matse et al. 2020). The PGPB *Bacillus velezensis* increases the nodulation and N fixation produced by *Bradyrhizobium diazoefficiens* in soybeans (Sibponkrung et al. 2020).

Microbial and microbe interactions with plants are also important in defense against pathogens. One bacterium (*Streptomyces griseorubens*) and two fungi (*Gliocladium virens* and *Trichoderma harzianum*) cooperate with each other to control *Fusarium oxysporum* f. sp. *capsici*, *in vitro* and *in vivo* (Suryaminarsih et al. 2015). In alfalfa, the combination of the effects of the bacterium *Sinorhizobium medicae* and the mycorrhizal fungus *Funneliformis mosseae* reduces the severity of leaf spot caused by *Phomamedicaginis* (Gao et al. 2018). Co-inoculation of *Streptomyces atrovirens* and *Trichoderma lixii* is effective for the control of *Rhizoctonia solani* in infected soils (Solanki et al. 2019). The effects of the phytopathogenic fungus *Phytophthora capsici* on *Sechium edule* (Jacq.) Sw. are reduced by combined inoculation with *Rhizophagus intraradices* and *Azospirillum brasilense* (Aguirre et al. 2021).

Knowledge has also been achieved on the effect of the microbiome in reducing abiotic stress in plants. Inoculation with *Bradyrhizobium japonicum* combined with the addition of thuricin-17, produced by *B. thuringiensis*, protects soybeans from water stress (Prudent et al. 2015). Chickpea is more resistant to salinity after triple inoculation with *Rhizobium*, the endophytic bacterium *Stenotrophomonas maltophilia*, and arbuscular mycorrhizal fungi (Abd-Alla et al. 2019). The phytoremediation capacity of cadmium of *Sulla coronaria* is increased by co-inoculation with *Rhizobium sullae* and *Pseudomonas* sp. (Chiboub et al. 2020). By jointly inoculating *Rhizobium* and arbuscular mycorrhizae, the natural population of bacteria of the genera *Proteobacteria, Actinobacteria, Acidobacteria,* and *Chloroflexi* is increased, with which alfalfa plants take up more nutrients from the soil and better resist cadmium stress (Wang et al. 2021).

A very recent study by Sauer et al. (2021) in two medicinal plants illustrates the difficulty of relationships that could happen in the rhizosphere of plants: in the microbiome of *Hamamelis virginiana* L., 141 genera of fungi and 1,131 species of bacteria were identified, and in that of *Achillea millefolium* L., 161 genera of fungi and 1,168 bacterial species were observed. With such microbial populations, it is evident that the relationships between them and with the plant are very complex, and that very detailed studies are needed to effectively take advantage of the mechanisms governing these interactions.

2.2.3.1 Fungi Used as Growth Regulators in Modern Agriculture

The use of PGPF in today's agriculture is becoming increasingly common because its use reduces the application of chemicals such as pesticides and fertilizers, and with this the accumulation of chemical residues in vegetable and fruits are diminished. Up to now, only a few studies have informed on PGPF because researchers pay more attention to their use for induction of resistance and plant development improvement by triggering induced systemic resistance (ISR) in crops (Fig. 2.1) (Zhang et al. 2018; Sindhu et al. 2018; Hossain et al. 2017b).

Some of the species that have been used as PGPF in agriculture as mentioned above are *Aspergillus*, *Trichoderma*, *Penicillium*, and also mycorrhizas.

2.2.3.2 *Aspergillus* spp. as PGPF

The genus *Aspergillus* includes several endophytic fungi that are applied in many treatments and forms because they represent beneficial effects to crops growth promotion and protection. Some of the beneficial effects of *Aspergillus* spp. according to Hung and Lee (2016) are:

- Extracellular production of phytases [phytate is a phosphorylated derivative of myo-inositol important in the storage and retrieval of inositol, ions, and

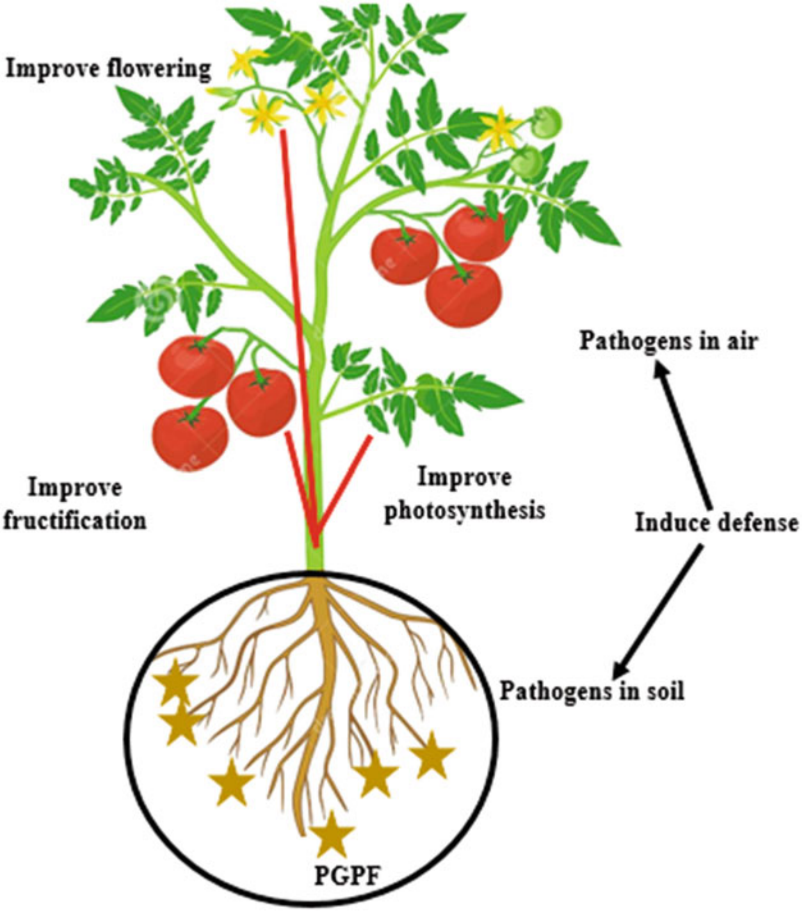

Fig. 2.1 Stimulation of several physiological processes (flowering, fructification, growth) in tomato plant by Plant Growth-Promoting Fungi (PGPF)

phosphorus during plant germination and development (Raboy 2003)] during soil pretreatment

- Induction of growth promotion through the production of gibberellins, auxins, and other phytohormone-like compounds and secondary metabolites
- Reduce stress experienced by the plant

Aspergillus ochraceus Wilhelm (1877) was reported by Badawy et al. (2021) as providing salt stress tolerance (200 g L^{-1}), for which barley plants (*Hordeum vulgare* L.) were irrigated with seawater at 15% and 30% and inoculated with the fungus. Because of this, morphological parameters such as sugars, proteins, pigments, and yield characteristics increased, while the contents of hydrogen, proline, malondialdehyde, and peroxide besides the activities of antioxidant enzymes decreased. Another experiment addressing salt stress was done by Ali et al. (2021)

with plants of *Vigna radiate* (L.) R. Wilczek inoculated with *A. awamori* with the aim to evaluate ionic status of the plant, biochemical indices, seedling growth, antioxidant enzymes, and endogenous IAA.The main results showed that growing plants inoculated with 150 mM NaCl displayed growth promotion and increase of IAA contents.

Khushdil et al. (2019) inoculated plants of *Pennisetum glaucum* L. with *A. terreus* and they were grown under salt stress conditions, finding that under 100 mM salt stress, the plants significantly improved ($P = 0.05$) chlorophyll, relative water content, phenol, flavonoid, and soluble sugar because the fungus produced higher amounts of indole acetic acid (IAA).

Syamsia et al. (2021) studied the effect of six isolates of endophytic fungi on growth of the plant *Cucumis sativus* L. A combination of fungi isolates F6, F8, F9, and F12 induced an increase in cucumber plants height, whereas the isolate F8 improved the fresh weight of the plants and the isolate F4 improved root growth. The isolates were identified using molecular methods and it was found to be closely related to *Aspergillus foetidus, Daldinia eschscholtzii, Penicillium allahabadense, Sarocladium oryzae,* and *Rhizoctonia oryzae*.

Soybean (*Glycine max* L.) and sunflower (*Helianthus annuus* L.) seedlings were inoculated with *A. flavus* to analyze the plant response to thermic stress. Crops were grown in a thermal chamber with temperatures of 25 °C and 40 °C. Plants inoculated with the fungus exposed to high-temperature stress showed low levels of proline, abscisic acid (ABA), and high levels ascorbic acid oxidase, flavonoids, and phenols catalase. Also, an increase in dry weight, root-shoot length, and chlorophyll was registered in the inoculated plants. The results of this study suggested that *A. flavus* could be used in crops growth promotion under heat stress conditions (Hamayun et al. 2019).

Hamayun et al. (2020) identified the species *Aspergillus violaceofuscus* that also is useful under heat stress conditions. This species had higher quantities of secondary metabolites that increased biomass, plant height, and total chlorophyll content of *H. annuus* and *G. max* seedlings under heat stress. Conversely, the plants associated to *A. violaceofuscus* showed small levels of abscisic acid, proline, reactive oxygen species, ascorbic acid oxidase, catalase, and a general improvement of the nutritional value.

The inoculation of *Aspergillus ustus* on plants of *Arabidopsis thaliana* (L.), Heynh. and *Solanum tuberosum* L. induces changes in developmental stage and promotes growth mainly in roots (roots-induced root hair and lateral root numbers and also increased root and shoot growth). Authors also confirmed that *A. ustus* synthesizes gibberellins and auxins in liquid cultures (Salas-Marina et al. 2011).

2.2.3.3 *Trichoderma* spp. *as PGPF*

Trichoderma is a genus of opportunistic symbiont fungi that proliferates in the rhizosphere of plants. Species of this genus can produce elicitors that activate plant defense against various pathogens, as well as induce the synthesis of plant

Fig. 2.2 Experiment with tomato plants (*Solanum licopersicum* L.) at Facultad de Ciencias Agrícolas y Forestales of Universidad Autónoma de Chihuahua where (**a**) Tomato without *Trichoderma* spp. in a greenhouse, small fruits; (**b**) Tomato with *Trichoderma* spp. in a greenhouse, larger fruits (Source: Crescencio Urias Gracia and Melisa Magaña González)

growth-promoting substances and help phosphorus solubilization (Hohmann et al. 2011).

Species of *Trichoderma* predominate in agricultural soils or in forests (terrestrial ecosystems) with a low nutritional requirement and a temperature range of 25–30 °C for their growth (Sandle 2014). Also, they have a great adaptability to ecological conditions, for which they develop several substrates, which facilitates their massive production for use in agriculture (Ramos et al. 2008; Zeilinger et al. 2016).

Various species of this genus can promote crops development and growth (Fig. 2.2), due to the fact that they can be endophytically related or associated with the rhizosphere of crops. Further, they produce auxins and gibberellins, as well as organic acids (fumaric, citric, and gluconic) that influence the reduction of the pH in soil and can promote the solubilization of magnesium, phosphates, manganese, and iron; nutrients that are essential for plant functioning (Sharma et al. 2017).

Secondary metabolites produced by *Trichoderma* species function as plant growth regulators. As an example, a strain of *T. harzianum* (SQR-T037) released harzianolide, a growth inducer in tomato seedling in soil or in hydroponic system at very low concentrations (0.1 ppm and 1 ppm). Also, this metabolite can improve root development (Cai et al. 2013). Others species such as *T. atroviride* and *T. virens* can produce some auxin-related substances like IAA, a plant hormone that have many functions including induction of plant growth, root development, among others (Contreras-Cornejo et al. 2014).

The inoculation of the fungus *Trichoderma* sp. on plants such as *Arabidopsis* (Contreras-Cornejo et al. 2014) can have various effects such as increase in root tip, and shoots and root may have high iron levels (Yedidia et al. 2001). These results showed that the transport of this nutrient improved in plants, and also harzianic acid may control plant growth because of its Fe(III)-binding activity (Vinale et al. 2013).

One of the best roles of *Trichoderma* spp. is the development of roots, probably due to the control or production of hormones that can regulate this activity, for example harzianic acid, auxin, and harzionalide (Contreras-Cornejo et al. 2009; Vinale et al. 2013; Cai et al. 2013). Further, plants of cucumber (*C. sativus*) inoculated with *T. harzianum* considerably improved the root area on the 28th day, and also increased the concentrations of several nutrients like copper (Cu), phosphorus (P), zinc (Zn), iron (Fe), sodium (Na), and manganese (Mn) (Yedidia et al. 2001).

Chagas et al. (2019) studied the efficiency of *Trichoderma asperellum* (UFT 201 strain) as a plant growth promoter in soybean (*G. max*) by analyzing the possibility to synthesize IAA and to solubilize phosphate under greenhouse conditions. This study found that the production of IAA was higher (26.7%) in plants inoculated with *T. asperellum* UFT compared to the positive control. Also, soybean plants inoculated with the fungus showed higher biomass than controls. The inoculation of soybean plants with *T. asperellum* UFT 201 showed the high efficiency of this *Trichoderma* strain as a growth promoter.

In *Capsicum chinense* (Jacq.) var. ‘Chichen Itza’ the efficiency of *Trichoderma* spp. for the promotion of vegetative growth was analyzed and plants treated with *Trichoderma sp*. by foliar application at 28 days after germination had a biomass (dry = 0.13 g and plant^{-1} fresh = 0.8 g plant^{-1}), higher stem diameter (2.6 mm), aerial height (11 cm), and root volume (dry = 0.04 g plant^{-1}and fresh = 0.13 g plant^{-1}), compared to the treatments evaluated (co-application of both a chemical fungicide (Captan®) and a commercial product (Tri-HB®: *Bacillus subtilis* and *Trichoderma harzianum*) (Larios et al. 2019).

Halifu et al. (2019) compared two species of *Trichoderma* spp. (*T. harzianum* E15 and *T. virens* ZT05) according to their effect on fungal community and plant growth rhizosphere soil nutrients of *Pinus sylvestris* var. mongolica annual seedlings. The results showed differences between the control and the two species studied. Parameters such as root structure index, seedling biomass, soil enzyme activity, and soil nutrients were considerably higher compared to the control

($p < 0.05$). For *T. harzianum* E15 treatment, the seedling total biomass, ground diameter and height were higher than that of *T. virens* ZT05 treatment. Regarding the results of enzyme activity and rhizosphere soil nutrient content, treatment with *T. virens* ZT05 showed higher values than those of *T. harzianum* E15.

Nuangmek et al. (2021) described morphological and phylogenetically a new species named *Trichoderma phayaoense*. The fungus promoted growth in the plant *Cucumis melo* L. by increasing plant shoot, root dry weight, and height. Also, *T. phayaoense* had positive effect on fruit quality by increasing its diameter, circumference, weight, and total soluble solid of fruit. Further, it is important to point out that *T. phayaoense* tolerated a frequently applied fungicide (metalaxyl) in recommended dosages for field applications.

2.2.3.4 *Penicillium* spp. as PGPF

The genus *Penicillium* was first described by Link in 1809. Thom, in 1910, considered *P. expansum* as the type species of the genus. The species included in the genus *Penicillium* are ubiquitous, widely distributed throughout the world, and considered saprophytic. Many of them live in the soil or in decaying organic matter (Pitt 1981).

The species of *Penicillium* could be identified with high frequency (Domsch et al. 1993), but, very little information is available about the influence of these fungi in plant growth or interactions between species of the genus *Penicillium* and other soil fungi.

Ismail et al. (2021) performed a field study on *Phaseolus vulgaris* L. inoculated with fungal (*Penicillium commune* PF3 and *Alternaria sorghi* PF2) and endophytic bacterial (*Brevibacillusagri* and PB5, *Bacillus thuringiensis* PB2) strains compared to two hormones that were exogenously applied (benzyl adenine [BA] and IAA). The biochemical characteristics of the plants and their growth were evaluated. The plants inoculated with endophytic bacterial and fungal strains showed higher photosynthetic pigments, antioxidant enzyme activity, plant biomass, endogenous hormones, carbohydrate and protein contents, and yield, compared to plants with exogenous application of hormones (BA and IAA).

Surya and Yuwati (2020) inoculated *Penicillium citrinum* on Gerunggang (*Cratoxylon glaucum*) seedlings, and they found that only the height of the plants changed significantly, whereas leaf number and growth of plant diameter were not affected. To understand these responses, authors inoculated other plants with different application methods and dosage but the responses after 5 months were the same in plant growth parameters (leaf number, dry weight of plants, height, diameter, soil P content, and chlorophyll content). On the other hand, *Penicillium* spp. (*Penicillium neoechinulatum* or *Penicillium viridicatum*) isolated from zoysiagrass rhizospheres stimulated disease resistance and growth in cucumber plants (*Cucumis sativus* L.) (Hossain et al. 2014).

Species of *Penicillum* have also been reported as phosphate-solubilizing microorganisms. For this function, *Penicillium oxalicum* I1 is able to induce growth in maize plants (*Zea mays* L.) (Gong et al. 2014).

Nasim et al. (2012) reported several isolates of *Penicillium* that had a positive influence on growth of tomato plants (*S. licopersicum*) as follows:

- The nine isolates tested (*P. simplicissimum, P. citrinum, P. oxalicum, P. verrucosum var. cyclopium, Penicillium sp., P. billii, P. granulatum, P. expansum* and *P. implicatum*) significantly improved seed germination.
- Growth promotion increased up to 90% by the application of cultural extracts of *P. billi* and *P. expensum.*
- *P. oxlalicam* and *P. implicatum* expressively increased root development in tomato seedling.
- *P. granulatum, P. implicatum,* and *P. verrucosum* enhanced shoot length.
- *P. implicatum* improved root length and shoot in tomato seedlings.
- On seedling growth *P. citrinum* and *P. simplicissimium* were less effective.

Mushtaq et al. (2012) investigated the effect of several species of *Penicillium* (*Penicillium citrinum, Penicillium expansum, Penicillium oxalicum, Penicillium implicatum, Penicillium verrucosum, Penicillium simplicissimum* and *Penicillium bilaii*) in tomato plants (S. *licopersicum*), and they improved seed germination, plants' shoot and root system. On the other hand, *Penicillium chrysogenum* interrupted the dormancy of opuntia (*Opuntia streptacantha* Lem.) seeds (Delgado-Sánchez et al. 2011).

Salinity is one of the main stressors affecting plant growth. In this sense, one strain of *Penicillium citrinum*, KACC43900, was reported by Khan et al. (2009) as growth promoter in *Ixeris repens*. The strain was isolated from the same plant and this was the first report on the reduction of salinity stress in plants using *P. citrinum* KACC43900 (Khan et al. 2009). Another *Penicillium* species that reduced the negative effect of salinity stress in plants was *P. resedanum* LK6 specifically in *Capsicum annuum* L. from where it was isolated. Also, when this strain (LK6) was inoculated in *C. annuum* plants together with gibberellic acid treatment, an increase of several physiological parameters of plant growth was observed, such as shoot length, biomass, photosynthesis rate, and chlorophyll content (Khan et al. 2015).

2.2.3.5 Mycorrhizas as PGPF

Mycorrhizas constitute the most common synergy between microorganisms and plants called mycorrhizal symbiosis. According to Bonfante and Genre (2010), mycorrhizas (Arbuscular Mycorrhizal Fungi (AMF) endomycorrhiza, arbuscular mycorrhiza (AM)) are endophytic fungi belonging to the *Glomeromycota* genera that can colonize over 90% of higher plant families for symbiotic relationships (Prasad et al. 2017).

AMF improve the nutrient in plants and water uptake by spreading the root and so the absorbing zone and plants provide them carbohydrates to finish their life cycle. In turn, the AMF reduce in plants the negative effect of abiotic stresses like salinity, drought, heavy metals, and high temperatures (Kumar et al. 2017). The mechanisms by which AMF are adapted to these stresses are commonly related to increased gene regulation, hydromineral nutrition, production of osmolytes, synthesis of antioxidants, phytohormones, and ion selectivity. Additionally, they improve ecosystem stability and enhance bacterial communities, the quality of soil aggregation, and plant structure (El-Sawah et al. 2021).

Mycorrhizas could mitigate the stress caused by drought in plants because AMF can increase the area of plants for water absorption due to the symbiosis with roots of crops through AMF hyphae which allow them access to distant soil regions where water is retained by soil pores (Augé 2001). Several studies show the mitigation of drought stress by AMF due to the increase of nutrient contents and the efficient use of water in important agricultural crops such as tomato (*S. lycopersicum*) (Subramanian et al. 2006), *Allium cepa* L. (Nelsen and Safir 1982), *Triticum aestivum* L. (Allen and Boosalis 1983), *Trifolium repens* L. (Ortiz et al. 2015), *Lactuca sativa* L. (Ruiz-Lozano et al. 2015), and other crops.

Mycorrhizas can also mitigate the stress produced by salinity in plants, since plants inoculated with AMF have better capacity to absorb water and take nutrients, improving the ionic homeostasis (Khanam 2008; Munns and Tester 2008), inducing the accumulation of osmoregulators like sugars and proline (Yamato et al. 2008), and reducing the uptake of Cl^- and Na^+ (Li et al. 2020a, b). Also, crops inoculated with AMF and exposed to salinity show a reduction in oxidative damage and enhanced stomatal conductance (Estrada et al. 2013; Pedranzani et al. 2015). Some examples are:

- *F. mosseae* inoculated on tomato plants (*S. lycopersicum*) exposed to saline water increased fruit fresh production, shoot contents of potassium (K), iron (Fe), zinc (Zn), phosphorous (P), copper (Cu), and plant biomass (Al-Karaki 2006);
- *F. mosseae* colonizing tomato plants (*S. lycopersicum*) roots diminished the concentration of sodium (Na) and increased several enzymes activity related to oxidative stress in plants [ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT)] (Latef and Chaoxing 2011).
- AMF inoculation on wheat plants (*Triticum aestivum* L.) significantly reduced the oxidative damage (Talaat and Shawky 2014). Also, authors reported an increase in carbon and nitrogen metabolism.
- Plants of *Z. mays* under saline conditions were inoculated separately with three native AMF [*Claroideoglomus etunicatum* (Becker and Gerdemann 1977), *Rhizophagus intraradices* (Schenck and Smith 1982), and *Septoglomus constrictum* (Trappe 1977)] resulting in increased content of K and proline in shoots as well as plant biomass (Estrada et al. 2013).

In several important crops, the influence of AMF on plant physiological parameters and growth have been studied. Example of such crops include *Withania somnifera* (L.) Dunal (Parihar and Bora 2018), *Phaseolus vulgaris* L. (Ibijbijen et al. 1996), *Solanum lycopersicum* L. (Bona et al. 2016; Gamalero et al. 2004), *Cucurbita maxima* Duchesne (Al-Hmoud and Al-Momany 2017), *Sorghum bicolor* (L.) Moench (Nakmee et al. 2016; Kim et al. 2017), and others. In these species, AMF enhanced the uptake of important nutrients such as phosphorus and nitrogen (Jansa et al. 2019; Song et al. 2020), and growth parameters such as yield, quality, and nutritional value (Bona et al. 2016), root architecture (Gamalero et al. 2004), and root system morphology (Berta et al. 1995).

AMF were used by El-Sawah et al. (2021) as biofertilizers in guar (*Cyamopsis tetragonoloba* L.) to improve nutrients, soil microbial activity, and also the crop seed quality, growth, and yield. AMF were applied individually or in combination with *Bacillus subtilis* (Ehrenberg 1835) Cohn 1872 and *Bradyrhizobium sp*. Results showed a great increase in plant growth (plant dry weight, shoot length, root length, nutrient uptake, number of branches, chlorophyll content, and leaf area index (LAI)), as well as an increase in seed yield and improvement of fat, total protein, starch, and carbohydrate contents in seeds. In addition, the use of the biofertilizer improved the microbial activity of the soil. This research demonstrated that the use of biofertilizers with the correct doses can diminish the use of chemical fertilizers in about 25%.

Arbuscular Mycorrhiza (AM) as PGPF together with *Azotobacter* and *Pseudomonas sp*. as PGPB were used in *Capsicum frutescens* L, crop growing on infertile lateritic soil (deficient in nitrogen and phosphorous) and the results after the use of these three microorganisms together indicated an increased in growth (leaf area, leaf number, height, number of flowers, and root collar diameter), productivity (number of fruits, final dry and fresh yield), root colonization, and spore count of AM (Kulla et al. 2021).

Five species of AMF (*G. versiforme, Diversispora spurca*, *Acaulospora scrobiculata*, *G. mosseae*, and *Glomus etunicatum*) were used to determine their effect on leaf gas exchange, plant growth, root nutrient contents, and root morphology of walnut (*Juglans regia* L. Liaohe 1) seedlings. After 3 months, AMF colonized roots in 47.0% to 76.4%. Also, plants that were inoculated with *G. etunicatum*, *G. mosseae*, and *D. spurca* had greater projected area, volume, and root length. Four AMF (*D. spurca, G. etunicatum*, *G. mosseae,* and *A. scrobiculata*) improved transpiration rate, stomatal conductivity, and leaf photosynthesis rate, whereas leaf temperature and intercellular CO_2 concentrations were reduced (Huang et al. 2020).

2.2.4 Bacteria Used as Growth Regulators in Modern Agriculture

2.2.4.1 The Rhizosphere and the Interaction of Beneficial Microorganisms

Among terrestrial ecosystems, the soil is one of the richest habitats in microbial taxa. More than 80% of the biological functions of this ecosystem are carried out by algae, bacteria, fungi, and nematodes. The classification of organisms, by their body size, are divided into microflora (<0.02 mm); microfauna (0.02–0.2 mm); mesofauna (0.2–10 mm); macrofauna (10–20 mm); and megafauna (>20 mm) (Wolters 2001; Wardle 2002). The rhizosphere is defined as the zone of soil that is located just in narrow zone of the plant roots, and is directly influenced by the root exudates with a high content of amino acids, sugars, carbohydrates, secondary metabolites, and organic acids that favor growth of microbial populations. The rhizosphere is divided into (1) endorizosphere, which corresponds to the endodermis, the root cortex and the apoplastic space between cells; (2) rhizoplane (root surface); (3) ectorizosphere, an area that extends from the rhizoplane to outside the area of the rhizosphere. Microbial groups found in the rhizosphere interfere with nutrient cycling, protect the plant from attack by pathogens, or act as plant parasites (Philippot et al. 2013; Ahkami et al. 2017; Vives-Peris et al. 2020).

The growth, health, and development of plants is influenced by the interactions that occur between microorganisms that inhabit the rhizosphere. Mycorrhizal fungi and plant growth-promoting bacteria (PGPB) play a key role in sustainable agriculture by reducing the use of chemical fertilizers and pesticides, solubilizing nutritional resources, and producing antagonistic compounds of potential phytopathogens (Genre et al. 2020; Phour et al. 2020; Trivedi et al. 2020; Molina-Romero et al. 2021). Mycorrhizae are fungi that, in combination with plant roots, externally or internally, form networks that capture nutrients and water from the soil (Varma et al. 2012). Ectomycorrhizae are mainly associated with trees and shrubs; while endomycorrhizae can be arbuscular (related to a great variety of taxa), ericoides (restricted to the order of Ericales plants), and orchids (associated with the Orchidaceae family). Some bacteria have the ability to modulate mycorrhizal symbiosis with the plant; as is the case of various species of the genus *Pseudomonas* that have the ability to help the mycorrhizal process, and are called mycorrhizal helper bacteria (Rigamonte et al. 2010; Xing et al. 2018; Genre et al. 2020). These synergistic interactions between both microorganisms can be useful to improve the growth and tolerance of plants in stressful environments (Moreira et al. 2016).

2.2.4.2 Plant Growth-Promoting Bacteria (PGPB)

PGPBs are bacteria that inhabit the rhizosphere, from where they take glutamine, betaine, and trehalose sugars to improve their growth. PGPBs are divided into two groups: extracellular (ePGPB) and intracellular (iPGPB). The ePGPBs colonize the root surface or intercellular space of the cortex; while the iPGPBs produce special cells inside the roots called nodules and develop within these structures. Both groups of bacteria stimulate plant growth (Barber 1995; Yadav 2010). The genera *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Erwinia*, *Micrococcus*, *Pseudomonas,* and *Serratia* integrate the ePGPBs (Adesemoye and Egamberdieva 2013); iPGPBs include *Allorhizobium*, Azorhizobium, *Bradyrhizobium*, *Frankia*, *Mesorhizobium,* Ochrobactrum, *Rhizobium,* and *Sinorhizobium* (Quiza et al. 2015; Hakim et al. 2021; Stone et al. 2000). Plant growth, promoted by these bacterial groups, is carried out through indirect or direct mechanisms. The first is achieved by increasing nitrogen fixation, phosphate solubilization, the availability of iron and other essential nutrients, and improving regulation of the levels of phytohormones (abscisic acid, auxins, cytokinins, ethylene, and gibberellins) and siderophores (Gouda et al. 2018; Kalam et al. 2020; Rastegari et al. 2020; Singh et al. 2020). On the other hand, the indirect mechanism includes the increase of the enzymatic

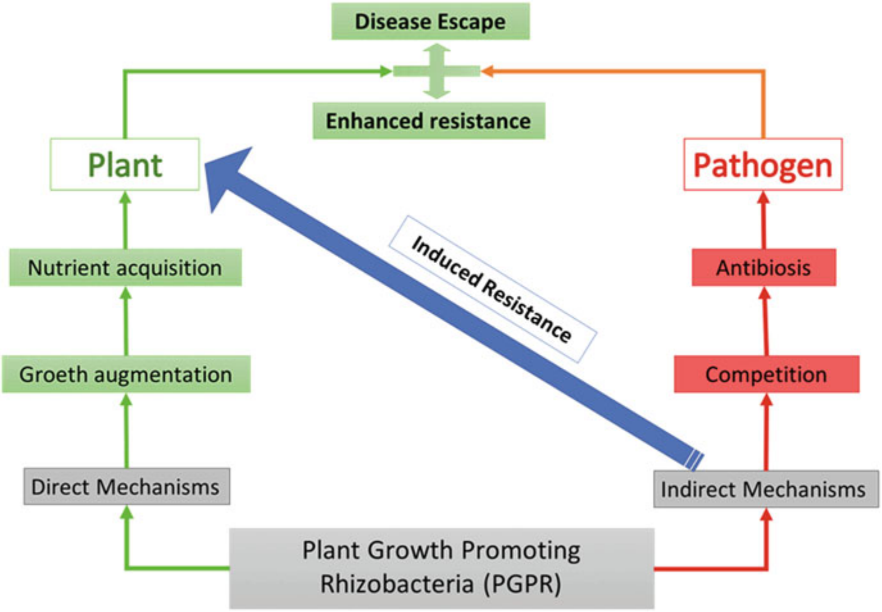

Fig. 2.3 Mechanisms of action of plant growth-promoting bacteria (modified from Basu et al. 2021)

activity related to the defense of the plant such as proteases, β-1,3-glucanases, and chitinases, the reduction of ethylene (endogenous associated with stress), and the induced systemic resistance suppressing the development of root and foliar phytopathogens (Fig. 2.3) (Beneduzi et al. 2012; Glick 2014; Kour et al. 2020; Meena et al. 2020; Rana et al. 2020). PGPBs that exhibit both direct and indirect mechanisms have advantages in being more competent bioinoculants (Hernández et al. 2015).

2.2.4.3 PGPB and Biotic and Abiotic Stress

PGPBs have the ability to convert infertile soils to fertile by mineralizing organic pollutants, and are used in soil bioremediation (Dessaux et al. 2016; Bibi et al. 2018). In addition, they confer a better adaptation of plants to various biotic factors such as diseases caused by plant pathogens (bacteria, fungi, insects, nematodes, viruses, among others) and abiotics that include drought, soil salinity, floods, extreme temperatures, and heavy metal contamination (Table 2.1) (Santoyo et al. 2017; Gimenez et al. 2018; Gamalero and Glick 2020). Various studies have mentioned that the inoculation of plants with PGPB consortia has a synergistic effect on their development by producing various defense compounds and reducing abiotic and biotic stress. The co-inoculation of *Bacillus megaterium* and *Paenibacillus*

Table 2.1 Benefits of inoculating plant growth-promoting bacteria (PGPB)

Bacterium	Benefits/type of stress	Hosts	References
Alcaligenes feacalis RZS2, *Bacillus* spp., *B. cereus*, *Enterobacter* sp. RZS5 *Ochrobactrum* sp., *Pseudomonas* spp., *P. fluorescens*, *P. aeruginosa* RZS3	Bioremediation by pollutants and heavy metals/abiotic	*Withania somnifera*, *Arachis hypogaea*, *Zea mays, Oryza sativa*	Pandey et al. (2013), Sayyed et al. (2015), Das and Kumar (2016), Khan et al. (2016), Patel et al. (2016), Kalam et al. (2017)
Paenibacillus polymyxa, Pantoea sp. S32	Increased nutrient absorption/ abiotic	*Capsicum chinense, Oryza sativa*	Pii et al. (2015), Castillo-Aguilar et al. (2017), Chen and Liu (2019)
Bacillus subtilis, *Rhizobium* spp., *B. cereus*	Improved soil fertility/abiotic	*Vigna radiata, Populus* sp.	Ahmad et al. (2011), Islam et al. (2016), Jang et al. (2017)
Achromobacter piechaudii, *Azospirillum* sp., *Bacillus megaterium, B. pumilus*, *Eneterobacter* sp. PR14, *Exiguobacterium oxidotolerans*	Tolerance to salinity/abiotic	*Bacopa monnieri*, *Eleusine coracana*, *Lactuca sativa*, *Oryza sativa* cv. *Sahbhagi*, *Solanum lycopersicum*, *Sorghum bicolor*, *Zeamays*	Mayak et al. (2004), Marulanda et al. (2010), Bharti et al. (2013), Fasciglione et al. (2015), Sagar et al. (2020)
Achromobacter piechaudii ARV8, Azospirillum brasilense, Bacillus subtilis, Enterobacter hormaechei DR16, Paenibacillus polymyxa, Pseudomonas fluorescens DR11, P. migulae DR35, Phyllobacterium brassicacearum, Rhizobium tropici	Drought tolerance/abiotic	*Setaria itálica*, *Zea mays*, *Phaseolus vulgaris*, *Arabidopsis thaliana*, *Solanum lycopersicum* cv. F144, *Capsicum annuum* cv. Maor, *Triticum aestivum*	Figueiredo et al. (2008), Yang et al. (2009), Bresson et al. (2013), Timmusk et al. (2014), Niu et al. (2018), De Lima et al. (2019)
Bacillus amyloliquefaciens, *Ochrobacttrum intermedium*, *Paenibacillus lentimorbus*, *P. xylanexedens*, *Pseudomonas* spp., *Streptomyces* sp.	Biocontrol/ biotic	*Oryzasativa*, *Pinus taeda*, *Solanum lycopersicum*, *Triticum aestivum*	De Vasconcellos and Cardoso (2009), Khan et al. (2012), Gowtham et al. (2016), Ilyas et al. (2020), Srivastava et al. (2016), Reshma et al. (2018)
Rhizobium etli, Bacillus cereus, Serratia marcescens,		*Heterodera avenae*, *H. glycines*, *Meloidogyne* spp.	Reitz et al. (2000), Hamid et al. (2003), Siddiqui et al. (2005),

(continued)

Table 2.1 (continued)

Bacterium	Benefits/type of stress	Hosts	References
B. coagulans, B. licheniformis, B. pumilus, B. megaterium, B. subtilis, B. pumilus L1, *Pseudomonas aeruginosa, B. thuringiensis, P. stutzeri, P. fluorescens* CHA0		*M. incognita*, *M. arenaria*, *M. graminícola*, *M. javanica* *Bursaphelenchus xylophilus*, *Helicotylenchus multicinctus*, *Rotylenchulus reniformis*, *Radopholus similis*	Mohammed et al. (2008), Almaghrabi et al. (2013), Rahul et al. (2014), Khan et al. (2016), Fatima and Anjum (2017), Lastochkina et al. (2017), Basyony and Abo-Zaid (2018), Mostafa et al. (2018), Xiang et al. (2018), Ahmed (2019), El-Nagdi et al. (2019), Forghani and Hajihassani (2020), Jiang et al. (2020), Mazzuchelli et al. (2020)
Arthrobacter protophormiae, *Dietzia natronolimnaea, B. subtilis, Azospirillum lipoferum*, *Bacillus* sp.	Production of phytohormones	*Triticum aestivum, Solanum lycopersicum*, *Oryza sativa*	Barnawal et al. (2017), Tahir et al. (2017), Kalam et al. (2020), Cassán et al. (2001)
Azotobacter chroococcum, *Bacillus subtilis*, *B.pumilus*, *Exiguobacterium oxidotolerans*, *Pseudomonas putida*	Modulation of secondary metabolites	*Bacopa monnieri*, *Ocimum basilicum*	Banchio et al. (2009), Ordookhani et al. (2011)
Azospirillum lipoferum, *Bacillus subtilis*, *Brevundimonas diminuta*, *Pseudomonas fluorescens*, *P.putida*, *Providencia* sp., *Serratia marcences*	Improved seed germination	*Triticum aestivum*, *Zeamays*	Nezarat and Gholami (2009), Rana et al. (2011), Almaghrabi et al. (2014)

polymyxa, in combination with *Rhizobium*, has shown an improved plant biomass of *Phaseolus vulgaris* compared to the individual inoculation of *Rhizobium* (Korir et al. 2017). Likewise, the application of *Pseudomonas* and *Rhizobium* increased the biomass and the yield of *Vigna radiata* (Ahmad et al. 2012).

2.2.4.4 PGPB as Biological Control Agents for Pathogens

Biocontrol is a promising strategy to control plant pathogens and is an ecological alternative to chemical pesticides and fertilizers. In recent years, the application of PGPB as biocontrol agents for plant pathogens has been implemented in the world. This strategy provides a safe, economical, durable, and environmentally friendly alternative (Table 2.1) (Etesami 2019; Prasad et al. 2019). Bacteria of the genus *Bacillus* belong to the phyla Firmicutes, family Bacillaceae, and are gram positive. This group is characterized by forming rod-shaped endospores, which gives them the ability to adapt to adverse conditions in a wide variety of habitats (Ducrest et al. 2019; Kuebutornye et al. 2019; Liu et al. 2019; Li et al. 2020a, b). *Bacillus* spp., like PGPB, have been documented to confer numerous advantages in the agricultural sector (Radhakrishnan et al. 2017). In disease management, this bacterial genus controls the proliferation of phytopathogens by suppressing plant immunity or induced systemic resistance (Glick 2012a, b; Shafi et al. 2017). Likewise, it improves the immunity of plants by producing antimicrobial metabolites (directly) and antioxidant enzymes (indirectly) (Belbahri et al. 2017; Rais et al. 2017; Sarwar et al. 2018; Wu et al. 2018a, b).

The *Pseudomonas* group are found in the phyla Proteobacteria, family Pseudomonadaceae, and are Gram-negative, rod-shaped bacteria. *Pseudomonas* spp. is ubiquitous in agricultural soils and has many characteristics that promote plant growth. For this reason, they have been used on a large scale for biotechnological applications as biological control agents (*P. putida* and *P. fluorescens*) (Anayo et al. 2016; David et al. 2018; Kandaswamy et al. 2019). Some species of the genus *Pseudomonas* are pathogenic to plant (*P. syringae*) (Morris et al. 2008) and human (*P. aeruginosa*) (Diggle and Whiteley 2020). Bacteria of the genus *Enterobacter* belong to the phyla Proteobacteria, family Enterobacteriaceae. They are Gram-negative, rod-shaped, and do not form spores. Reports show that *Pseudomonas* sp. and *Bacillus* sp. are used in the management of nematode parasites of plants such as *Heterodera*, *Meloidogyne*, and *Rotylenchulus* (Siddiqui and Mahmood 1999; Kokalis-Burelle et al. 2002; Siddiqui et al. 2005).

The genus *Enterobacter* has potential as PGPB in agricultural systems (Jha et al. 2011), and even when the mechanisms for improving the yield and growth of plants due to *Enterobacter* spp. are not fully understood, it is inferred that they work by facilitating the absorption of certain nutrients from the soil, synthesizing particular compounds for plants, and reducing or preventing plant diseases through antagonism or growth-promoting activities (Kumar et al. 2020). The genus *Streptomyces*is is included in the row Actinobacteria, class Actinomycetes, family Streptomycetaceae. They are gram-positive, filamentous bacteria. Most *Streptomyces* species are efficient colonizers of the rhizosphere and rhizoplane. They can also act as endophytes that colonize the internal tissues of host plants (Sousa and Olivares 2016). This group has a high potential for biocontrol due to the production of antibiotics, volatile compounds, secondary metabolites (Som et al. 2017; Quinn et al. 2020), and production of extracellular enzymes (Gherbawy et al. 2012; Mukhtar et al. 2017).

The species of this bacterial genus grow as a mycelium of branched hyphae and reproduce in the form of mold sending aerial branches that become chains of spores (Chater 2006). *Streptomyces* spp. act as PGPB in plant development (Viaene et al. 2016; Vurukonda et al. 2018).

2.2.4.5 Use of PGPB as Biofertilizers

During the last decades, the increasing use of fertilizers to improve crop yield has caused environmental pollution and deteriorated the biological and physicochemical characteristics of agricultural soils throughout the world. The use of PGPB as biofertilizers is of utmost importance to reduce the application of agrochemicals in crop production (Yang and Fang 2015; Bishnoi 2018; Dong et al. 2019; Anli et al. 2020). A biofertilizer is defined as a product that contains live or inactive microorganisms that, when applied to the soil, seeds, or plant surface, individually or in combination, colonizes the rhizosphere or the interior of it, and promotes their growth and performance, by increasing the availability of primary nutrients and secreting growth-promoting substances (Vessey 2003; Dineshkumar et al. 2018). Biofertilizers can fix N_2 from the atmosphere, solubilize the nutrients required by plants (phosphate, potassium, and zinc), and also secrete hormones and substances that promote plant growth (Table 2.1) (Borkar 2015; Kumar et al. 2018).

Due to the indirect and direct effects caused by PGPBs in plants, several microbial taxa have been commercialized as efficient biofertilizers (Table 2.2). However, these bacteria are affected by various factors such as the biological and physicochemical characteristics of the soil, crop rotation, natural selection, and the use of organic and chemical fertilizers. Mahajan and Gupta (2009) mentioned that some important measures must be carried out for the efficacy of the biofertilizer to be successful: (1) it is essential that its concentration contains at least 10^7 viable cells per gram of inoculum when supplied in the field and that it comes from a reputable manufacturer; (2) it should only be applied to the crops specified in the product, since biofertilizers are highly specific; (3) all the remainder must be applied in the field so that the microorganisms of the inoculum begin to interact with other microbiota in the rhizosphere and begin their colonization; (4) the biofertilizer must be stored in shaded and cool places, at temperatures between 25 and 28 °C; (5) the contact of the biofertilizer with synthetic agrochemicals should be avoided; and (6) about 200 g of biofertilizer can be effectively used to treat 10 kg of seeds.

2.3 Conclusions

Plant growth-promoting microorganisms are increasingly being used in agriculture to reduce the application of chemicals and thus restore soils and reduce pollution of water and crops. The use of PGPF allows plants to produce bioactive substances, like plant hormones; decomposing organic matter through mineral solubilization;

Table 2.2 Plant growth-promoting bacteria used as commercial biofertilizers

Bacteria	Trade name	References
Azospirillum sp.	Nitrofix®	García-Fraile et al. (2015, 2017)
Azospirillum sp.	Rhizosum Aqua	García-Fraile et al. (2015, 2017)
Azospirillum spp.	Bio-N	Aloo et al. (2020), Uribe et al. (2010)
Azospirillum sp.	Ajay Azospirillum	Aloo et al. (2020)
A. brasilense	Azofer®	García-Fraile et al. (2017)
A. brasilense	Zadspirillum	Aloo et al. (2020)
A. brasilense B-4485	Azotobacterin®	García-Fraile et al. (2015, 2017)
A. brasilense, Azotobacter vinelandii, Bacllius megaterium	BactoFil® A10	Aloo et al. (2020)
Azospirillum sp., *Rhizobium* sp., *Acetobacter* sp., *Azotobacter* sp.	Symbion N	Macik et al. (2020)
Azospirillumbrasilense, *A. lipoferum*	Azo-N	Adeleke et al. (2019)
Azospirillumbrasilense, A. *lipoferum*, *Azotobacter chroococcum*	Azo-N Plus	Adeleke et al. (2019)
Azorhizobium sp., *Azoarcus* sp., *Azospirillum* sp.	TwinN®	Adeleke et al. (2019)
Azorhizobium spp., *Azoarcus* spp., *Azospirillum* spp.	TripleN®	Dal Cortivo et al. (2020)
Azotobacter chroococcum	Dimargon®	Uribe et al. (2010)
Azotobacter vinelandii, *Rhizophagus irregularis*	Rhizosum N®	García-Fraile et al. (2017), Dal Cortivo et al. (2020)
Azotobacter chroococcum, *Bacillus megaterium*	Phylazonit M	Macik et al. (2020)
Azotobacter chroococcum, *Azospirillum brasilense*, *Bacillus megaterium*	Azoter	Artyszak and Gozdowski (2020)
Azotobacter chroococcum, A. *vinelandii*, *Acetobacterdiazotrophicus*, *Azospirillum lipoferum*, *Rhizobium japonicum*	AgrilifeNitrofix	Mehnaz (2016)
B. subtilis, *Bradyrhizobium japonicum*	Nodulator® PRO	García-Fraile et al. (2017)
Bradyrhizobium japonicum	Nodulator®	García-Fraile et al. (2017)
B. japonicum	BactoFil®Soya	Mustafa et al. (2019)
B. japonicum	Nodulest 10	Mehnaz (2016)
B. japonicum	Rizo-Liq Top	Adeleke et al. (2019)
B. japonicum	BiAgro 10®	Uribe et al. (2010)
Bradyrhizobium spp.	Nodumax	Adeleke et al. (2019), Aloo et al. (2020)
Bradyrhizobium sp., *Mesorhizobium ciceri*, *Rhizobium* spp.	Rizo-Liq	Adeleke et al. (2019), Aloo et al. (2020)
Delftia acidovorans, *Bradyrhizobium* sp.	Bioboost®	García-Fraile et al. (2015, 2017)
Paenibacillus polymyxa	Custom N2	García-Fraile et al. (2017)

(continued)

Table 2.2 (continued)

Bacteria	Trade name	References
Pseudomonas fluorescens/putida, *Klebsiella pneumoniae*, *Citrobacter freundii*	BioGro®	Uribe et al. (2010)
Rhizobia	Nitragin Gold®	García-Fraile et al. (2017)
Rhizobia	Cell-Tech®	García-Fraile et al. (2017)
Rhizobia	Mamezo®	García-Fraile et al. (2015, 2017)
Rhizobia	Biofix	Adeleke et al. (2019), Aloo et al. (2020)
Rhizobia, *Penicillium bilaii*	TagTeam®	García-Fraile et al. (2017)
Rhizobium etli	Rhizofer®	García-Fraile et al. (2017)
Rhizobium sp.	Nitrasec	Aloo et al. (2020)
Rhizobium sp., *Bradyrhizobium japonicum*	Legume Fix	Adeleke et al. (2019), Aloo et al. (2020)
Bacillus megaterium	Bio Phos®	Mehnaz (2016), Macik et al. (2020)
B. megaterium	Symbion vam Plus	Aloo et al. (2020)
B. megaterium var. *phosphaticum*	Phosphobacterin	Mahajan and Gupta (2009)
Bacillus mucilaginosus, *B. subtilis*	CBF	Uribe et al. (2010)
Bacillus spp., *Glomus intraradices*	CataPult	Mehnaz (2016)
Bacillus megaterium, *Frateuria aurantia*, *Rhizophagus irregularis*	Rhizosum PK®	García-Fraile et al. (2017), Dal Cortivo et al. (2020)
Pseudomonas fluorescens	Fosforina®	Uribe et al. (2010)
Pseudomonas striata, *Bacillus polymyxa*, *B. megaterium*	P Sol B	Mehnaz (2016), Macik et al. (2020)
Azotobacter chroococcum, *P. fluorescens*	Bio Gold	Mehnaz (2016), Macik et al. (2020)
PGPB consortia	EVL Coating®	García-Fraile et al. (2015)
PGPB consortia	Bioativo	Aloo et al. (2020)
Pseudomonas azotoformans	Amase®	Mehnaz (2016), Mustafa et al. (2019)
Frateuria aurantia	Rhizosum K	García-Fraile et al. (2015, 2017)
F. aurantia	K Sol B	Mehnaz (2016)
PGPR consortia	Biozink®	García-Fraile et al. (2017)
Thiobacillus thiooxidans	Zn Sol B	Mehnaz (2016)

increasing plant defenses against biotic and abiotic stresses; improving photosynthetic processes through the increase of total chlorophyll content; increasing IAA contents, root-shoot length, plants' dry and fresh weight, nutrient uptake, and many other beneficial effects.

The PGPB are increasingly being used in sustainable agriculture with the aim of reducing the use of chemical products and also generating stability to the plant in presence of unfavorable conditions of abiotic and biotic origin. Using these bacteria allows a more natural way to cope with agricultural challenges. Moreover, these bacteria must be highly competent, environmentally friendly and compatible with other organisms in the rhizosphere. These features may allow the plant to produce bioactive substances and increase its defenses against extreme conditions and pest attacks. These biostimulant microorganisms are emerging as an innovative solution to the current crop-production crisis.

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