






Review

# Plant-Microbe Interaction in Sustainable Agriculture: The Factors That May Influence the Efficacy of PGPM Application

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**Abstract:** The indiscriminate use of chemical fertilizers and pesticides has caused considerable environmental damage over the years. However, the growing demand for food in the coming years and decades requires the use of increasingly productive and efficient agriculture. Several studies carried out in recent years have shown how the application of plant growth-promoting microbes (PGPMs) can be a valid substitute for chemical industry products and represent a valid eco-friendly alternative. However, because of the complexity of interactions created with the numerous biotic and abiotic factors (i.e., environment, soil, interactions between microorganisms, etc.), the different formulations often show variable effects. In this review, we analyze the main factors that influence the effectiveness of PGPM applications and some of the applications that make them a useful tool for agroecological transition.



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## 1. Introduction

The rapid growth of the world population has made it necessary to intensify agricultural production to achieve higher yields of crops and total production in order to ensure food security [1]. On the other hand, agriculture is one of the human activities that significantly contribute to the increase in chemical pollutants because of the excessive use of synthetic chemical fertilizers and pesticides, which cause further environmental damage with potential risks for human health. Among the chemical pollutants resulting from agricultural activity, nitrous oxide (N<sub>2</sub>O), which is produced by the excessive use of nitrogen fertilizers, is one of the main sources of greenhouse gases, which cause global warming. In fact, as much as 74% of the total US N<sub>2</sub>O emissions in 2013 were attributed to agricultural land management [2]. In order to achieve sustainable agriculture, crops need to be endowed with disease resistance; salt, drought, and heavy metal stress tolerance; and improved nutritional value. To reach these objectives, a concrete possibility is offered by using plant growth-promoting microorganisms (PGPMs)—especially bacteria and fungi—which are capable of increasing the plant's capacity to absorb nutrients and its water use efficiency [3] as well as inducing resistance against plant diseases [4]. In fact, numerous studies have demonstrated how plant growth-promoting fungi (PGPF) [5] and plant growth-promoting rhizobacteria (PGPR) isolated from the soil or the plant rhizosphere can effectively be used as biofertilizers, biostimulants, and inducers of resistance against a series of abiotic and biotic stresses [4]. However, the interactions that are created between the microorganisms, the crop, and the environment in the soil, particularly in the rhizosphere, are very complex and interfere with the effectiveness of the application and use of PGPMs. The factors that modulate these interactions can depend not only on the environmental conditions,

such as the temperature and pH of the soil, but also on the genotype and, not least, the microorganisms already present in the soil. This review aims to summarize the factors that can influence the beneficial effects of PGPM application and the considerations necessary to maximize their effectiveness.

## 2. Plant Growth Promoting Fungi (PGPF)

### 2.1. What Are They?

PGPF are a heterogeneous group of non-pathogenic fungi—mostly saprotrophic (i.e., organisms that feed at the expense of decaying organic matter) but in some cases necrotrophic (i.e., organisms that feed at the expense of dead and already largely decomposed organic matter) or biotrophic (organisms that feed at the expense of living organic matter)—that are known for enhancing plant growth by acting on the rhizosphere [5]. They can be subdivided into endophytes that live inside the roots in the inter- and intracellular spaces and exchange metabolites directly with the plant; epiphytes that live free on the surface of the roots; and free-living PGPF, which live freely in the rhizosphere. These fungi are soil-borne and taxonomically belong to the Ascomycetes, Basidiomycetes, and Oomycetes phyla. Among the most isolated genera are *Aspergillus*, *Fusarium*, *Gliocladium*, *Penicillium*, *Phoma*, and *Trichoderma*, the latter being the most isolated genus from different soils. In addition, mycelial isolates of sporeless fungi known as sterile black fungus (SBF), sterile dark fungus (SDF), and sterile red fungus (SRF) are also recognized as PGPF and are often difficult to identify because they lack a formal taxonomic state [6,7]. When we speak of PGPF, we refer to the fungi ectomycorrhiza and ectoendomycorrhiza, which often establish mutualism not necessarily obligated to the host plant. With this clarification, it is possible to distinguish them from the category of the arbuscular mycorrhizal fungi (AMF), usually from the phylum Glomeromycota, which, on the contrary, establish an obligatory mutualism with the host plant for their entire life cycle, producing asexual spores [8].

### 2.2. Promotion of Growth in Plants

It is widely documented that the fungi from the rhizosphere, whether mycorrhiza or saprophytic mycoflora, can positively affect plants by improving their growth and development. The impact of PGPF on plants has positive long- and short term effects on factors such as germination, sprout growth, root growth, photosynthetic efficiency, flowering, and yield [9]. The duration of the biofunctional activities of PGPF in plants is one of the key factors that allow their effective application in the field. They generally show promising effects in the early stages of plant growth but, in several cases, have proved effective even in medium and late ontogenetic stages, thus contributing positively to increase yield [10]. The mechanisms of the continuous positive effects of PGPF on plants have not been fully clarified, but one hypothesis is that fungi establish and continue the colonization of the root system also through the exudates of the plant, which implement their diffusion around and into the rhizosphere [5].

### 2.3. Pattern and Process of Root Colonization

Colonization of the root system is undoubtedly the most important strategy that allows the establishment of an intimate connection to initiate the promotion of growth in plants [11]. This is made possible by the ability of the fungus to survive and proliferate in the long term, despite the presence of indigenous microflora [12]. This ability of fungi is defined as rhizospheric competence and is a necessary condition for efficient PGPF [13]. The ability to reisolate a fungus from the root system as an indirect measure of its colonization ability, and thus of its rhizospheric competence, has been highlighted in several studies. According to Hossain [14], it has been shown that several *Penicillium* strains isolated after 3 weeks in *Arabidopsis thaliana* maintain a high presence rate (>90%). The same was demonstrated for *Aspergillus* in cucumber. Despite the evidence of high reisolation rates, there are studies that show that rhizospheric competence is reached by high rates of root colonization 10 weeks after soil inoculation, such as in the case of *Phoma* spp. on cucumber

plants [15]. There are PGPF—in particular, non-sporulant sterile fungi—that lack the ability to colonize but are still able to promote growth in plants. This evidence suggests that root colonization, in the case of PGPF, is not indispensable for growth promotion [9]. However, PGPF colonization of the root system is not always homogeneous; their density varies in different portions of the root [16,17]. It appears to be higher at the top of the roots than at the middle and basal parts. This could be explained by a rate of radical growth that is higher than the rate of colonization by PGPF [18]. Unlike PGPF, arbuscular mycorrhizal fungi (AMF) colonize the root system in a more homogeneous way, creating shrubs and branched structures that increase the surface area of radical contact with the soil, aggregate with adhesive (glomalin) soil particles, and establish a real network within the soil [19,20]. This type of colonization takes place after the recognition between the plant and the fungus that allows the latter to form the appressorium and penetrate the radical tissue, forming a very intimate connection and establishing the characteristic obligatory mutualism of this category of fungi [21].

#### 2.4. Interaction with the Host and between Microorganisms

A key factor in the use of PGPF is the specificity between the host plant and the PGPF–AMF or among other PGPMs (including bacteria). Preferential interactions are observed among plants and different fungal communities. In fact, numerous studies have shown that one or more well defined fungal species have positive effects on different plant species, but they do not necessarily have the same effect on other species [12,13]. The interaction between saprophytic mycelium and AMF in the rhizosphere may depend on the different intrinsic characteristics of previously tested fungi. The effects on the host plant may be contradictory between species of the same genus as well as between the same species. Generally, the interactions between these groups of microorganisms are synergistic or additive in the promotion of growth in plants and the suppression of different plant diseases. Ad hoc combinations of these fungi can generally increase plant performance and, in particular, stimulate plant protection at different growth stages under different conditions and occupy different or complementary intervention niches [12,16]. The relationship established in the rhizosphere between fungi and growth-promoting bacteria is also highly interesting. Several studies have confirmed that bacteria can easily live and benefit from the fungal hyphae, which can form biofilms from various secretions [19,22,23]. In the same way, mycorrhizal radical exudates also act as substrates for the proliferation of bacteria, transforming into nutrients for the plant [24]. Endosymbiosis is a well-known interaction, especially between bacteria and Basidiomycetes. These symbioses show interesting benefits; in these relationships, different growth-promoting enzymes are generated between bacterial and fungal hyphae in the senescence stage [25].

#### 2.5. Growth-Promoting Mechanisms

The mechanisms by which PGPF modulate plant growth and development can be both direct and indirect. Direct mechanisms are those that involve the production of substances such as antioxidants, enzymes, and volatile organic compounds (VOC) and those in which readily available nutrients are synthesized by the fungus and facilitate the growth of the plant. Indirect mechanisms include the suppression of pathogens and the alleviation of stress (water, salt, high temperatures, and metals) that afflict plants. Usually, PGPF can affect plant growth and development using one or more of these mechanisms [6]. The mechanisms of action of PGPF are highlighted in Table 1.

**Table 1.** Mechanisms of plant-growth promotion by various PGPF (modified from [6]).

Mechanisms	Specific Activities	PGPF Strain	Reference
	Solubilize P by acid phosphatase and alkaline phosphatase	<i>F. verticillioides</i> RK01; <i>Humicola</i> sp. KNU01	[26]

Table 1. Cont.

Mechanisms	Specific Activities	PGPF Strain	Reference
Phosphate solubilization	Solubilize P from rock phosphate and Ca-P by organic acid	<i>A. niger</i> 1B and 6A	[27]
	Solubilize P from tricalcium phosphate (TCP)	<i>A. niger</i> BHUAS01, <i>P. citrinum</i> BHUPC01, <i>T. harzianum</i>	[28]
	Solubilize P by organic acid activities	<i>P. oxalicum</i> NJDL03, <i>A. niger</i> NJDL-12	[29]
	Phytase-mediated improvement in phytate phosphorus	<i>A. niger</i> NCIM	[30]
	Increase HCO <sub>3</sub> and extractable P (23% increase)	<i>P. bilaiae</i> RS7B-SD1	[31]
Mineralization of organic substrate	Increase production of NH <sub>4</sub> -N and NO <sub>2</sub> -N in soil	<i>T. harzianum</i> GT2-1 and GT3-1	[6]
	Increase availability of ammonium nitrogen from barley grain	<i>Phoma</i> sp. GS8-1, GS6-2, GS7-3, GS7-4, GS8-6, GS10-1, GS10-2, Sterile fungus GU21-1	[6]
	Solubilize minerals, such as MnO <sub>2</sub> and metallic zinc	<i>T. harzianum</i> Rifai 1295-22	[32]
	Increase concentrations of Cu, P, Fe, Zn, Mn, and Na in roots; increase concentrations of Zn, P, and Mn in shoot	<i>T. harzianum</i> strain T-203	[33]
	Increase soil organic carbon, N, P, and K content	<i>T. viride</i>	[34]
	Increase availability of macro- and micronutrients and organic carbon	<i>T. harzianum</i> strain Th 37	[35]
Phytohormone and enzyme production	Auxin-related compounds (indole-3- acetic acid, IAA)	<i>T. virens</i> Gv. 29-8	[36]
	Gibberellins (GA1 and GA4) production	<i>A. fumigatus</i> HK-5-2	[37]
	GAs production	<i>Pe. resedanum</i> LK6	[38]
	GAs production	<i>Penicillium</i> sp. Sj-2-2	[39]
	GAs production	<i>Cladosporium</i> sp.MH-6	[40]
	GAs production	<i>Pe. citrinum</i> IR-3-3	[41]
	GAs and IAA production	<i>Chaetomium globosum</i> CAC-1G	[42]
	GAs production	<i>Exophiala</i> sp. LHL08	[43]
	GAs production	<i>Phoma herbarum</i> TK-2-4	[44]
	GAs production	<i>A. fumigatus</i> HK-5-2	[37]
	GAs production	<i>A. fumigatus</i> LH02	[37]
IAA production	<i>T. harzianum</i> T-22	[45]	
Zeatin (Ze), IAA, 1-aminocyclopropane-1-carboxylic acid (ACC)	<i>T. harzianum</i>	[45]	
Volatile organic compounds (VOCs)	Produce abundant classes of VOCs (sesquiterpenes and diterpenes)	<i>F. oxysporum</i> NRRL 26379, NRRL 38335	[46]
	Produce mainly terpenoid-like volatiles, including $\beta$ -caryophyllene	<i>Talaromyces wortmannii</i> FS2	[47]
	Produce 2-methyl-propanol and 3-methyl-butanol	<i>Phoma</i> sp. GS8-3	[48]
	Produce abundant amount of isobutyl alcohol, isopentyl alcohol, and 3-methylbutanal	<i>T. viride</i>	[49]

Table 1. Cont.

Mechanisms	Specific Activities	PGPF Strain	Reference
Amelioration of abiotic stress	Increased tolerance to salt stress	<i>T. harzianum</i> T-22	[50]
	Mitigation of oxidative stress due to NaOCl and cold stress	<i>T. harzianum</i> Rifai strain 1295-22	[6]
	Enhance maize seedling copper stress tolerance	<i>Chaetomium globosum</i>	[42]
	Minimize Cu-induced electrolytic leakage and lipid peroxidation	<i>Pe. funiculosum</i> LHL06	[51]
	Increase tolerance to drought stress	<i>T. atroviride</i> ID20G	[52]
Pathogen suppression	Suppress damping off caused by <i>Pythium irregulare</i> , <i>Pythium</i> sp., <i>P. paroecandrum</i> , <i>P. aphanidermatum</i> , and <i>Rhizoctonia solani</i> AG4	Sterile fungus GSP102, <i>T. harzianum</i> GT3-2, <i>F. equiseti</i> GF19-1, <i>Pe. simplicissimum</i> GP17-2	[6]
	Induced systemic resistance against <i>Colletotrichum graminicola</i>	<i>T. harzianum</i> T22	[53]
	Bacterial wilt disease caused by <i>Ralstonia solanacearum</i>	<i>T. harzianum</i> TriH_JSB27, <i>Phoma multirostrata</i> PhoM_JSB17, <i>T. harzianum</i> TriH_JSB36, <i>Pe. chrysogenum</i> PenC_JSB41	[54]
	Fusarium wilt caused by <i>Fusarium oxysporum</i> f. sp. <i>ciceris</i>	<i>T. harzianum</i> T-75	[55]
	<i>Fusarium graminearum</i>	<i>Sphaerodes mycoparasitica</i>	[56]
	Damping off caused by <i>Rhizoctonia solani</i> AG4	<i>Pe. viridicatum</i> GP15-1	[57]
	Nematodes <i>Pratylenchus goodeyi</i> and <i>Helicotylenchus multicinctus</i>	<i>F. oxysporum</i> V5W2, Eny 7.11o and Emb 2.4o	[58]
	Seedling mortality by <i>Rhizoctonia solani</i>	<i>T. harzianum</i> isolate T-3	[59]

### 2.5.1. Phosphorus Solubilization

Phosphorus is an important component of key macromolecules in living cells. It is necessary for a wide spectrum of functions necessary for the survival and growth of living organisms. Despite the great abundance of this element in agricultural soils, it is mainly found in insoluble forms. This is because phosphorus is complexed with iron, aluminum, or calcium (depending on the type of soil) and becomes insoluble and unavailable for plants. PGPF can play a key role in making insoluble forms of phosphorus soluble in the soil, thus helping to overcome this problem. They produce enzymes that solubilize phosphates (phytase, phosphatase, organic acids) and release soluble phosphorus. According to Radhakrishnan et al. [26,27], the PGPF that produce the most phytase and phosphatase are from the genera *Aspergillus*, *Trichoderma*, *Fusarium*, and *Penicillium*. These fungi have higher solubilization of this element than bacteria, especially in acidic soil conditions. As demonstrated by various studies conducted in this regard, these PGPF provide solubilization of phosphorus through different specific mechanisms [26–30,60]. Another study conducted in Ethiopia on rhizosphere samples of *Brassica integrifolia*, *Vicia faba* L., *Phaseolus vulgaris* L., *Saccharum officinarum* L., and *Lycopersicon esculentum* Mill. showed that the filamentous fungi *Aspergillus niger* and some species of *Penicillium* have the largest percentages of phosphorus solubilization [31].

### 2.5.2. Mineralization of Soil Organic Matter

The process of microbial mineralization of organic matter in soil is crucial for plant growth. Many PGPF, such as *Trichoderma*, encourage plant growth by accelerating the process of soil mineralization [33–36,61,62]. Fungi, in general, have the highest efficiency of substrate assimilation of any type of microbe and are able to break polyaromatic complexes, such as lignin and humic or phenolic acids [63]. In addition, PGPF directly allow the degradation of organic nitrogenous materials through ammonization and nitrification [6]. Fungi

have been found to be the most efficient decomposers among microbes. To demonstrate this, studies conducted on *Metarhizium robertsii* have shown that when it establishes itself as a root endophyte, it is able to translocate nitrogen from dead insects to common bean host plants [62].

### 2.5.3. Phytohormones Production

Phytohormones are implicated in different forms of plant-microbe interactions and thus support the beneficial interactions between plants and PGPF. The most common classes of hormones that are easily found among PGPF are auxins (IAAs) and gibberellins (GAs). IAAs regulate many aspects of the growth in the plant, in particular the radical morphology, by the inhibition of the elongation of the root, which provokes an increase in the production of lateral and adventitious roots. The response of *Arabidopsis* to two *Trichoderma* species (*T. harzianum* and *T. virens*) was evaluated, and the two fungal species were found to promote lateral root proliferation and growth. This was inferred from tests using markers sensitive to auxin produced by *Arabidopsis* [36]. GAs are well known for their role in various plant growth and development processes, including stem elongation, germination, flower development, and flowering time. The production of this hormone class by different *Penicillium* sp. has been ascertained in several studies [63,64]. Another group of hormones through which PGPF promote plant growth are cytokinins, especially zeatin, which stimulates cell division and modifies many of the processes that take place in plants, such as cell distension, flowering, and prevention of senescence. This hormone has been recognized and documented in *Piriformospora indica*, *T. harzianum*, and *Phoma* sp. Numerous studies have demonstrated their effectiveness in producing the abovementioned classes of phytohormones, often in combination with each other [37,41,44,45,53–59,65].

### 2.5.4. ACC Microbial Deaminase

PGPF produces a crucial enzyme: 1-aminocyclopropane-1-carboxylic acid (ACC deaminase), as demonstrated in *T. harzianum* [66]. This enzyme breaks down the ethylene precursor (1-aminocyclopropane-1-carboxylic acid) into ammonia (NH<sub>3</sub>) and butyric acid ( $\alpha$ -ketobutyrate), thereby minimizing the levels of ethylene produced by the plant, which, if they are too high, can lead to senescence [5]. This enzyme is inducible and is encoded by the *AccD* genes of fungi and bacteria [67].

## 3. Plant Growth-Promoting Rhizobacteria (PGPR)

### 3.1. What Are They?

Plant growth-promoting rhizobacteria (PGPR) is a term coined by Kloepper in the 1970s [68] and refers to a set of different groups of soil bacteria, such as *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Azobacter*, *Klebsiella*, *Mesorhizobium*, *Enterobacter*, *Flavobacterium*, *Pseudomonas*, *Rhodococcus*, *Serratia*, *Streptomyces*, *Variovorax*, etc., which are key components of soil-plant systems, in which they are engaged in an intense network of interactions in the rhizosphere, thus affecting plant growth and yield. PGPR promote plant growth and development directly and indirectly by releasing plant growth regulators/phytohormones or other biologically active substances; altering endogenous levels of phytohormones; enhancing the availability and uptake of nutrients through fixation and mobilization; reducing the harmful effects of pathogenic microorganisms on plants; and/or by employing multiple mechanisms of action [69]. They are categorized into two major groups: (1) symbiotic rhizobacteria, which invade the interior/inside of the cell (intracellular PGPR, e.g., nodule bacteria), and (2) free-living rhizobacteria, which exist outside of the plant cells (extracellular PGPR, e.g., *Azotobacter*) [70]. Many benefits can be obtained by plants from PGPR inoculation, and the pathways to reach these benefits are various: nitrogen fixation, phosphate solubilization, siderophores production, phytohormones production, and improving tolerance against abiotic and biotic stresses [71,72].

### 3.2. Mechanisms of Action

According to Kloepper J. W. [68], PGPR-mediated plant growth promotion occurs by the alteration of the whole microbial community in the rhizosphere niche through the production of various substances. Generally, PGPR promote plant growth either directly—by facilitating resource acquisition, such as nitrogen, phosphorus, and essential minerals via biological nitrogen fixation, phosphate solubilization, and iron sequestration by siderophores, respectively, or modulating plant hormone levels, such as auxins, gibberellins (GAs), cytokinins (CK), and nitric oxide (NO)—or indirectly—through rhizosphere competition, induced systemic resistance (ISR), and biosynthesis of stress-related phytohormones, such as jasmonic acid (JA) and cadaverine (Cad), or the ethylene catabolism-related enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase [71]. The mechanisms by which PGPR act are highlighted in Table 2.

**Table 2.** Examples of mechanisms of action of plant growth-promoting rhizobacteria (PGPR).

	Mechanisms	PGPR	Reference
Nitrogen fixation	Symbiotic N <sub>2</sub> fixing	<i>Rhizobium</i> , <i>Bradyrhizobium</i> , <i>Sinorhizobium</i> , <i>Mesorhizobium</i> , <i>Frankia</i> ;	[69,71]
	Non-symbiotic N <sub>2</sub> fixing	<i>Cyanobacteria</i> , <i>Azoarcus</i> , <i>Azotobacter</i> , <i>Acetobacter</i> , <i>Azospirillum</i> , <i>Burkholderia</i> , <i>Diazotrophicus</i> , <i>Enterobacter</i> , <i>Pseudomonas</i> , <i>Gluconacetobacter</i> ;	[72]
Phosphate solubilization	Directly solubilize and mineralize inorganic phosphorus or facilitate the mobility of the organic form	<i>Azotobacter</i> , <i>Bacillus</i> , <i>Beijerinckia</i> , <i>Burkholderia</i> , <i>Enterobacter</i> , <i>Erwinia</i> , <i>Flavobacterium</i> , <i>Microbacterium</i> , <i>Pseudomonas</i> , <i>Rhizobium</i> , <i>Serratia</i>	[73–75]
Siderophores production	Siderophores-producing bacteria isolated from rhizosphere	<i>Bradyrhizobium</i> , <i>Pseudomonas</i> , <i>Rhizobium</i> , <i>Serratia</i> , <i>Streptomyces</i> ;	[65,76,77]
	Positive effects on plants under iron-limiting conditions	<i>Pseudomonas</i> , <i>Rhizobium</i> , <i>Azospirillum</i>	[77,78]
Phytohormones production	Iron sequestration	<i>Alcaligenes</i> , <i>Pseudomonas</i> , <i>Bacillus</i> ;	[73]
	auxins, gibberellins (GA), cytokinins, ethylene and abscisic acid (ABA)	<i>Bacillus</i> , <i>Rhizobium</i> , <i>Pseudomonas</i>	[79]
Tolerance to abiotic stresses	Drought stress	<i>Pseudomonas fluorescens</i> DR11, <i>Enterobacter hormaechei</i> DR16, <i>Pseudomonas migulae</i> DR35, <i>Bacillus subtilis</i> , <i>Achromobacter piechaudii</i> ARV8, <i>Phyllobacterium brassicacearum</i> , <i>Paenibacillus polymyxa</i> , <i>Rhizobium tropici</i> , <i>Azospirillum brasilense</i> ;	[80,81]
	Tolerance to salinity stress	<i>Bacillus pumilus</i> , <i>Exiguobacterium oxidotolerans</i> , <i>Bacillus megaterium</i> , <i>Azospirillum</i> sp., <i>Achromobacter piechaudii</i> , <i>Enterobacter</i> sp. PR14;	[82,83]
Biotic stresses	Various pathogens	<i>Paenibacillus xylanexedens</i> , <i>Bacillus amyloliquefaciens</i> , <i>Streptomyces</i> sp., <i>Ochrobactrum intermedium</i> , <i>Paenibacillus lentimorbus</i> , <i>Pseudomonas</i> spp.;	[84]
	Growth Inhibition of <i>Clavibacter michiganensis</i> subsp. <i>michiganensis</i>	<i>Bacillus licheniformis</i> or <i>Bacillus sonorensis</i> isolates;	[85,86]
	Growth Inhibition of <i>Verticillium dahliae</i>	<i>Bacillus</i> , <i>Pseudomonas</i> , <i>Enterobacter</i> ;	[85,86]
	Disease reduction of <i>Clavibacter michiganensis</i> subsp. <i>michiganensis</i> and <i>Xanthomonas euvesicatoria</i> pv. <i>perforans</i> infections	<i>Pseudomonas</i> spp., <i>Bacillus</i> spp.	[86]

### 3.2.1. Nitrogen Fixation and Related Factors

Nitrogen is one of the dominant rate limiting nutrients in natural systems [71,72]. About 2% of the total dry matter of the plant that enters the food chain is represented by nitrogen [87]. Although nitrogen molecular gas ( $N_2$ ) constitutes about 80% of the atmosphere, plants cannot access it directly; rather, they absorb the fixed nitrogen in the soil in its biologically available form (ammonium and nitrates) through the roots [87]. The molecular  $N_2$  present in the atmosphere is converted into usable forms by plants through the biological fixation of  $N_2$  mediated by PGPR, which transforms nitrogen into ammonia using a complex enzyme system known as nitrogenase [88]. Biological nitrogen fixation occurs, generally at mild temperatures, by nitrogen-fixing microorganisms, which are widely distributed in nature. Nitrogen-fixing microorganisms are generally categorized as (i) symbiotic  $N_2$ -fixing bacteria, including members of the family rhizobiaceae (*Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Mesorhizobium*, and *Frankia*), which form symbioses with leguminous (e.g., *Rhizobia*) [89] and non-leguminous plants (e.g., *Frankia*) [88] and (ii) non-symbiotic (free-living, associative, and endophyte) nitrogen-fixing forms such as *Cyanobacteria*, *Azoarcus*, *Azotobacter*, *Acetobacter*, *Azospirillum*, *Burkholderia*, *Diazotrophicus*, *Enterobacter*, *Pseudomonas*, and *Gluconacetobacter* (*Anabaena*, *Nostoc*) [90]. All nitrogen-fixing organisms are called diazotrophs, and all known ones are prokaryotes. Nitrogen fixing is a widely and paraphyletically distributed ability, both in the bacterial and archaeal domains. The nitrogen fixation capacity in these organisms depends exclusively on the nitrogenase enzyme system, which hydrolyses 16 ATP molecules to fix one  $N_2$  molecule, making it one of the most metabolically expensive processes known in biology [91]. The initiation of the colonization process by PGPR begins with the plant host's molecular communication [72]. During the early colonization stage, soil bacteria release chemical signals, usually flavonoids. These chemical compounds are received by a specific bacteria receptor (NodD) and act as transcriptional activators of other nodulation genes (*nodA*, *nodB*, *nodC*, and *nodFE*) [91].

#### Nitrogen Fixation in Legumes

The nodulation process begins with the interaction between bacteria and root hairs and ends with the formation of root nodules. In these structures, the bacteria are found inside organelles called symbiosomes, where they differentiate into nitrogen-fixing bacteria [90,92]. During the symbiotic relationship, the plant benefits from the nitrogen supply, while the bacteria receive carbon compounds from the plant. This process is generally non-specific, but it is reported that some species of rhizobia induce the formation of nodules on particular legumes. Furthermore, some legumes, such as *Glycine max* and *Phaseolus vulgaris*, can be nodulated by more than one species of rhizobia [92,93]. Some strains of rhizobia are also reported to nodulate in several types of legumes [94,95]. Through in vitro culture methods and, more recently, using metagenomics, it has also been observed that symbiont rhizobes coexist in nodules with other non-nodulating rhizobes and non-rhizobial species [96,97], which can influence the symbiotic process and, therefore, nitrogen fixation [90]. While benefiting from this, legumes consume energy for this process, which is then regulated [98]. The plant has developed several mechanisms to allow the colonization of compatible bacteria and prevent that of incompatible prokaryotes [90]. Furthermore, the plant can sanction the nodules colonized by rhizobia with low nitrogen-fixing capacities [99,100]. Bacteria must overcome both environmental stresses and barriers posed by the plant. Therefore, the rhizobia present adaptations that allow them to survive in certain adverse soil conditions—mechanisms and strategies that facilitate the nodulation of a specific legume [101,102]. Many factors could influence the nodulation and interaction between bacteria and plants and, finally, nitrogen fixation. These factors could be bacterial survival in the rhizosphere, specific recognition for the initiation of the nodulation process, plant defense response, nodule cysteine-rich (NCR) peptides, autoregulation of nodule number, and sanctions for poor nitrogen fixation.



### Bacterial Survival in the Rhizosphere

Near the roots, the biodiversity of soil bacterial communities decreases. Root exudates modulate the composition of the microbial community in the rhizosphere, i.e., the soil influenced by plant roots [103,104]. The persistence of a bacterial population in the rhizosphere depends in part on its chemotaxis toward different components secreted by the roots as well as its ability to use them as substrates [105–108]. The possibility of moving in the soil, and thus the presence of flagella in bacterial species, are characteristics necessary to reach the root and, therefore, influence the nodulation [109]. The composition of microbial communities is also influenced by their microbe–microbe interactions; these can be both competitive and cooperative and help shape the overall community structure in the rhizosphere [110,111]. In these kinds of interactions, the competitive effect may depend on the growth rate; the ability to capture limiting nutrients, such as iron; and the presence of toxic compounds [104,110].

### Specific Recognition for Initiation of the Nodulation Process

Flavonoids and isoflavonoids are found as components of radical exudates [112,113]. A specific flavonoid secreted by the compatible legume activates a transcription factor of the rhizobia called NodD [114–117]. Different species of rhizobia respond to different flavonoids and activate multiple NodD copies and their transcription factors [118]. The different isoforms can play divergent roles; they can therefore be involved in distinct phases during symbiotic infection, or they can be transcribed in different environmental conditions, often in improving the competitiveness of the nodulation or in extending the number of hosts through the perception of different plant signal molecules [118–124].

The NodD gene induces the expression of bacterial genes involved in the synthesis of Nod factors [114], i.e., lipochitin oligosaccharides with different substituents that form a characteristic molecule recognized by specific receptors (LysM receptor-like kinase) on the root of a compatible legume [90]. Once the specific Nod factors are recognized, a cascade of signals starts promoting the physiological, morphological, and molecular changes typical of the nodulation process. Bacteria differentiated into nitrogen-fixing bacteria, once inside the nodule cell, are surrounded by a membrane of plant origin called the peribacterial membrane [125–127].

Two types of nodules have been described: determinate and indeterminate. The determinate nodules have no persistent meristem; they derive from the multiplication of cells in the external cortex and have a round shape, and the bacteria of these nodules differentiate reversibly. The indeterminate nodules, on the other hand, originate from the cells of the inner cortex; they are elongated and have a persistent apical meristem with different areas corresponding to different stages of development [128–130]. Unlike the previous ones, bacterial differentiation is irreversible in indeterminate nodules. Another less widespread nodulation mechanism occurs through a crack-entry infection process of plant tissues [131,132]. At the molecular level, the plant signaling cascade induced by Nod factors induces transcriptional and translational reprogramming involving several transcriptional factors, including micro RNA, enzymes, and phytohormones [133–137]. Another bacterial component involved in the specific recognition process is the exopolysaccharide (EPS) [138]. Differences were observed between different bacterial species, as well as between different strains of the same species, in the structure of their EPS [139,140].

### Plant Defense Response

When attacked by pathogens, plants trigger a first defense response by recognizing molecules as general elicitors known as pathogen/microbial-associated molecular patterns (PAMPs/MAMPs) [141]. The molecules recognized as PAMPs by the plant can be part of various structures, such as flagella, thermo-unstable elongation factor (EF-Tu), different polysaccharides, and different bacterial surface proteins [142–144]. Similar to pathogens, rhizobia exhibiting MAMPs induce a defense response in the plant. However, unlike pathogens, rhizobia flagella are not recognized as MAMPs [145]. PAMPs are recognized

by the plant through specific receptors (kinases similar to the LysM receptor), which then trigger the first defense response, called PAMP-triggered immunity (PTI). Bacteria, via the type three secretion system (T3SS), translocate effector proteins into plant cells, thereby suppressing PTI [146]. On the other hand, the plant can produce proteins that recognize these effectors (or molecules modified by them) and induce a hypersensitivity (HR) response called effector-triggered immunity (ETI) [146]. Despite this, it is reported that through T3SS, bacteria can secrete additional effectors that suppress HR [143,147]. Different rhizobes also present a T3SS [148,149], in addition to the induction of the expression of the nod genes; when NodD is activated by flavonoids, it also upregulates the expression of the transcription factor TtsI, which induces the transcription of T3SS-secreted components and effectors that suppress plant defenses [149,150].

In addition to T3SS, other bacterial protein secretion systems have been described as playing a role in the symbiotic process, such as the type IV and type VI secretion systems (T4SS and T6SS, respectively) [151–153].

#### Nodule Cysteine-Rich (CR) Peptides

Events that define host–rhizobe compatibility also occur in the advanced stages of the nodulation process, i.e., during bacterial differentiation into bacteroides. A diversity of translated peptides is observed in legumes presenting indeterminate nodules. These peptides are known as nodule cysteine-rich (NCR) peptides because of the presence of various cysteine residues [154–156]. Among these peptides, antimicrobial activity has been observed *in vitro* for many of them [157], which, by influencing the permeability of the membrane, can cause cell elongation, DNA duplication, and bacterial cell death. These NCR peptides have evolved from defensins, which support the mechanism of the innate immunity of plants [158]. However, the activity of NCR peptides in the nodule does not always lead to the death of the bacteria but instead induces irreversible terminal bacterial differentiation (the state of nitrogen fixation) by increasing the membrane permeability, polyploidy, larger dimensions, and altering the cellular shape [159]. Thus, the set of interactions between NCR in the nodules, the extent of NCR antibacterial activity, the sensitivity to the rhizobial strain, and the mechanisms that bacteria have developed to tolerate or eliminate these NCR peptides collectively determine the nitrogen-fixing phenotype of the NCR-formed nodule [102].

#### Autoregulation of Nodule Number

In Fabaceae species, there is a systemic mechanism for regulating the number of nodules that allows them to avoid energy waste [160,161]. Autoregulation of nodulation (AON) is a negative feedback system that is mediated by long-distance signals between shoots and roots. The system involves small peptides (12–13 amino acids), which constitute the signal generated when the nodulation process starts at the roots [162].

Negative regulation of CLAVATA/ESR-related (CLE) peptides on nodulation involves specific kinase receptors in the bud [135]. It is hypothesized that CLE peptides travel through the xylem from the roots to the shoot, where they bind to a specific receptor [163]. When CLE peptides are perceived in the sprouts, they induce the biosynthesis of a sprout-derived inhibitor (SDI), which induces further nodule development [164]. The Nod factor-induced signal transduction cascade that will give rise to nodule formation also induces the AON mechanism [162]. Furthermore, Nod factor signaling has been described to induce the expression of other factors that negatively regulate the AON mechanism [165]. This suggests that the regulation of the number of nodules is the result of a delicate balance involving several signaling pathways induced by rhizobia [165]. Specific CLE peptides also participate in the mechanism of inhibition of nodule formation in soils with high levels of nitrates [166].

### Sanction for Poor Nitrogen Fixation

Nodules containing nitrogen-fixing rhizobia have been observed to develop normally, while ineffective or inefficient nitrogen-fixing nodules tend to remain small [90,167,168]. This type of ability that legumes present, which allows them to recognize and limit the presence of ineffective and less effective rhizobia and reduce their suitability with respect to beneficial genotypes, is called sanction [100,169]. This phenomenon is reported in both determined and indeterminate nodules. The plant generally sanctions the ineffective bacteria present in the nodule by inducing a cellular senescence process [170]. This consists of an aging process of the nodule, which is also called a rupture of the nodule organ [171]. Nodules colonized by both effective and ineffective rhizobia may have different sectors containing different bacterial genotypes. Senescence is observed only in cells occupied by ineffective rhizobia [90]. The mechanism by which the lack of nitrogen fixation leads to accelerated senescence is not yet known. Despite the plant's ability to eliminate non-cooperative strains, nodules occupied by less effective rhizobes are observed in nature, probably because of the existence of a variation in the degree of control exerted by different genotypic variants of the host over these rhizobes [172].

### 3.2.2. Phosphate Solubilization

Phosphorus (P) is the second most important limiting nutrient after nitrogen. This nutrient is very abundant in the soil but, unfortunately, not readily available to the plants because of its rapid rate of fixing and complexing with other soil elements, both in the case of inorganic (such as fertilizer) and organic phosphorus [173]. PGPR play an important role in making soil-immobilized phosphorus available to plants by participating in the soil phosphorus cycle [174]. These microorganisms, also called phosphate-solubilizing bacteria (PSB), can directly solubilize and mineralize inorganic phosphorus and facilitate the mobility of the organic form through a biogeochemical cycle for more efficient root uptake [175]. These bacteria belong to different genera, such as *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium*, and *Serratia*, all of which are reported to be the most significant PSB [73]. They can solubilize inorganic sources of P and stimulate plant growth and yield. In several cases, they can also be intimately associated with a large number of agricultural crops, such as potatoes, tomatoes, wheat, and radish [74]. The solubilization of inorganic phosphorus has been documented to occur as a result of the action of low molecular weight organic acids synthesized by the various soil bacteria strains [176]. With regard to organic phosphorus, on the other hand, mineralization occurs following the synthesis of various phosphatases by bacteria, which catalyze the hydrolysis of phosphoric esters [89]. The PGPR *Paenibacillus mucilaginosus* is able to degrade insoluble soil minerals with the release of nutritional ions, such as potassium and phosphorous, and, similar to *P. polymyxa*, *P. mucilaginosus* is also capable of fixing nitrogen [177,178].

### 3.2.3. Siderophore Production

Iron is one of the most widespread minerals on earth, yet it is not readily available to plants [179]. In soils contaminated by heavy metals, plants are often deficient in this element, which is naturally found in the highly insoluble form  $Fe^{3+}$  [180,181]. PGPR may produce siderophores, which are substances characterized by a low molecular weight involved in the chelation process of iron ( $Fe^{3+}$ ) [182]. When iron is limited in the environment, microbial siderophores allow for the reduction of iron to the soluble form  $Fe^{2+}$ , which is then released into the plant cell [65,69,183]. PGPR also enhance plant growth by producing very efficient extracellular siderophores, which allow the control of several plant disease by depriving the pathogens of iron nutrition [104]. In addition to iron, siderophores can also form stable complexes with other metals of environmental concern, such as Al, Cd, Cu, Pb, and Zn [75]. Several studies have documented the isolation of siderophore-producing bacteria from the genera *Alcaligenes*, *Bradyrhizobium*, *Pseudomonas*, *Rhizobium*, *Serratia*, and *Streptomyces* from the rhizosphere [65,76,77]. The positive effects on plants have been documented after the

inoculation of the siderophore-producing bacteria *Pseudomonas*, *Rhizobium*, and *Azospirillum* under iron-limiting conditions [77,78].

#### 3.2.4. Phytohormone Production

Most microorganisms isolated from the rhizosphere of various crops have the ability to synthesize and release growth regulators [184]. In particular, PGPR are able to increase the production of phytohormones and modify the pre-existing pool already available to the plant [71,185]. Among the phytohormones the most secreted by bacterial is IAA (indole-3-acetic acid). It generally affects plants at the level of cell division, extension, differentiation; stimulates germination and increases the rate of xylem and root development; controls the vegetative processes of growth, conveys the responses to light, gravity, and flowering; and influences photosynthesis, pigmentation, and the biosynthesis of different metabolites and the resistance to different stress factors [71]. Generally, the pool of endogenous phytohormones already possessed by the plants can be affected by alterations caused precisely by the pool of phytohormones produced by soil bacteria. Consequently, IAA plays a very important role in rhizobacteria–plant interactions [186]. This production is clearly influenced by environmental stressors that modulate the biosynthesis of these compounds in different bacteria. Such stressors include acid pH, osmotic and matrix stresses, and carbon limiting [71,187]. Moreover, some aerobic sporogenes are capable of producing different phytohormones, such as auxins and gibberellins, and are implicated in the regulation of ethylene production through the synthesis of enzymes, such as ACC-deaminase [188]. In this context, for example, the *Bacillus* strains *B. pumilus* and *B. licheniformis* have been shown to be active, with biostimulating activity through the production of gibberellins [73]. The PGPR *Paenibacillus polymyxa*, formerly known as *Bacillus polymyxa*, can promote plant growth by producing plant hormones, such as IAA, cytokinins, gibberellins, and ethylene, and volatile compounds [188].

### 4. Management of Abiotic and Biotic Stresses

#### 4.1. Abiotic Stresses

Abiotic stresses affect plants in different ways and at different stages of growth, resulting in a yield reduction of many important crops. Light, temperature, water, carbon, and mineral nutrients are the major factors that regulate plant growth, development, and reproduction [178]. Conditions above or below the optimal levels of one or more of these factors limit the growth and the development of plants [189]. In response to extreme levels, plants undergo physiological and morphological modifications to adapt to these abrupt changes [190]. The most dangerous abiotic stresses for plants are drought, salinity, high or low temperatures, and extreme acidic conditions [191,192]. Drought conditions negatively affect the seed germination rate, lead to a loss of integrity of the cell membrane, inhibit photosynthesis, and increase the production of ROS (reactive oxygen species) [193]. Drought and high levels of soil salinity reduce the leaf area, water potential, and stomatal opening and suppress the growth and, in general, the correct development and productivity of the plants [194]. The effect of temperatures depends on the plant species. Generally, high temperatures cause denaturation and aggregation of cellular proteins and lead to plant death, while low temperatures alter metabolic processes through changes in conformation and interaction between proteins and alternative properties of membranes, affecting the enzyme activity [195]. Recent work suggests that crops may have a huge number of previously underestimated factors that are very valid allies in the struggle to overcome abiotic stresses. Agricultural lands contain thousands of different microbial constituents [196,197], and many of these soil microorganisms have been shown to associate preferentially with plant roots [198–200]. These root-associated microbes, as previously mentioned, reside both in and around the roots of plants. However, microbial diversity decreases with proximity to the root system, with more microbes around the proximal area of the root (rhizosphere) and less diversity within the root (endosphere) [201]. As several studies suggest, these changes in the composition of the microbiome occur not only along or within the root tissue

but also in the different stages of growth and development, with significant shifts between members of the previously observed community [202,203]. However, abiotic stresses also impact microbial composition and diversity in the soil [204–206], and as a consequence, the availability of microorganisms that can be recruited from plants, such as PGPMs, depends on the pool of microorganisms available, thus creating a circular feedback loop between the plant and the surrounding microbiome [207]. To date, it is clear how plants, in response to specific abiotic stresses, are able to induce a wide range of molecular, physiological, and biochemical responses [208,209], and it has been hypothesized how these can attract and select specific microbial populations in the root zone [210,211]. Recent work suggests that crops may have a huge number of previously underestimated factors that are very valid allies in the struggle to overcome abiotic stresses [80–82,212,213]. Agricultural lands contain thousands of different microbial constituents [196,197], and many of these soil microorganisms have been shown to associate preferentially with plant roots [83,198,200]. As several studies suggest, these changes in the composition of the microbiome occur not only along or within the root tissue but also in the different stages of growth and development, with significant shifts between members of the previously observed community [198,202]. Abiotic stresses also impact the microbial composition and diversity in the soil [204–206], and as a consequence, the availability of microorganisms, such as PGPMs, that can be recruited by plants depends on the pool of microorganisms available, thus creating a circular feedback loop between the plant and the surrounding microbiome [207]. The microorganisms, apart from the induction of production of phyto-constituents in the plant, produce various mixtures of carbon-based gaseous compounds called volatile organic compounds (VOCs) as part of their metabolism [5,52,214,215]. Another frequently investigated great peculiarity of PGPF concerns the influence on the adaptation of the plant to abiotic stresses, such as salinity, drought, toxicity from heavy metals, extreme temperatures, and oxidative stress [216]. This increase in tolerance to abiotic stress of plants treated with PGPF is explained, in part, by the fact that these possess a high scavenger capacity toward ROS (reactive oxygen species) and recycle oxidized ascorbates and glutathiones (in substance, all secondary metabolites produced by the plant under stressful conditions) [217,218]. In addition, they increase the contents of proline and glycine-betaine, which in turn increase the tolerance to stress, and, in general, induce the synthesis of antioxidants, both enzymatic (peroxidase, catalase, superoxide dismutase, ascorbate peroxidase, glutathione reductase, monodehydroascorbate reductase, dehydroascorbate reductase, glutathione S-transferase, and guaiacol peroxidase) and non-enzymatic (ascorbic acid, reduced glutathione, and oxidized glutathione), which protect the plant from damage [217,218]. Several studies documented that different PGPF species improve the response of crops to abiotic stresses [10,51,52,219,220], similar to what is also widely reported for PGPR [80–83,198,212,213].

#### 4.2. Biotic Stresses

PGPMs are able to suppress or reduce the inoculum and growth of plant pathogens, and thus their invasion, through different mechanisms [5,69]. These mechanisms of action rely mainly on nutrient and space competition, antibiosis systemic resistance induction (ISR), and, limited to PGPF, mycoparasitism [216]. An important PGPF mechanism of action is the production of lytic enzymes, such as proteases, chitinases, and  $\beta$ -1,3 glucanases [56,214,220]. To date, many fungi isolated from the rhizosphere have shown antagonistic activity to pathogen growth [53–55,57,58,221,222], including various PGPF, such as *T. harzianum* [10,223,224]. The production of antibiotics such as gliovirin by *Gliocladium virens* has been demonstrated to limit the growth of *Pythium ultimum* [58]. Kaur et al. [225] reported that non-pathogenic strains of *F. oxysporum* isolated from rhizospheric soil inhibited the growth of pathogenic *Fusarium* strains through competition for nutrients, reduced germination of chlamydospores, and competition to colonize infection sites (roots). Likewise, *Aspergillus fischeri* showed potent antifungal activity against *Botrytis cinerea* [226]. About 90% of the fungal biocontrol agents against pathogenic microorganisms are *Trichoderma* strains [222,227,228]. *Trichoderma* spp. could establish symbiotic relationships

with plants. They are rapid and invasive soil colonizers and, in soils contaminated by pathogens, improve plant growth and biocontrol plant pathogens, including bacteria and nematodes, but above all, phytopathogenic fungi [229]. Amongst the strategies of direct antagonism of *Trichoderma* against fungi mycoparasitism, competition and antibiosis have been reported [230]. The inoculation of different *Trichoderma* species in the rhizosphere has been shown to improve plant defense response against various phytopathogens, such as viruses, bacteria, and fungi, by inducing the activation of different resistance mechanisms, such as induced systemic resistance (ISR), hypersensitive response (HR), and acquired systemic resistance (SAR) [231]. Because of their documented efficacy against plant pathogens, *Trichoderma* spp. have been extensively studied and commercially exploited as biocontrol agents, soil improvers, and biofertilizers [231].

PGPR biocontrol activity could be related to three main mechanisms of action: competition with the pathogens for nutrients and niches; antibiosis; and induction of plant defense responses (ISR) [232]. The production of antimicrobial metabolites, mainly with broad-spectrum activities, has been reported for the biocontrol bacteria belonging to genera *Bacillus*, *Pantoea*, *Pseudomonas*, *Serratia*, *Stenotrophomonas*, *Streptomyces*, and many others [233,234]. Numerous antimicrobial compounds have been described among them: amphisin, 2,4-diacetylphloroglucinol (DAPG), iturin, fengycin, oomycin-A, phenazine, pyoluteorin, pyrrolnitrin, tensin, tropolone, hydrogen cyanide (HCN), and lipopeptides (LPs). These LPs have been reported as strong antibacterial agents mostly active against pathogens, and their mechanism of action is through permeabilization and disruption of the cell membrane. The role of antibiotics in biocontrol was especially investigated in *Bacillus* and *Pseudomonas*, which can produce structurally diverse secondary metabolites that exhibit a wide spectrum of antimicrobial activity [233–235].

## 5. PGPMs and Soil Organic Matter

Soil organic matter (SOM) is associated with soil fertility and plays an important role in nutrient cycling and produces environmental benefits, such as carbon sequestration (C) for climate change mitigation [236]. SOM is present in higher concentrations in the first 20–30 cm of the major soil profiles [237,238]. The practices of intensive agriculture over the millennia have led to an impoverishment of organic matter in the soil, in particular in agricultural soils compared to pastures [239]. The return to a type of conservative agriculture that includes minimal tillage with minimal disturbances to the soil was developed precisely to limit erosion and loss of SOM and increase water retention capacity [240]. In this conservative agriculture, the return to soil crop residues and other forms of fresh organic matter (FOM), such as manure, is proposed in order to restore acceptable levels of SOM. There is a growing focus on the microbial decomposition of the FOM and the incorporation of a portion of the microbial residues within the SOM [241]. Microbial debris is defined by microbial neuromas, including the cell wall and membranes, nucleic acids, extracellular enzymes, metabolites, and extracellular polymeric substances [241]. When microorganisms metabolize C-based substrates, including plant residues, roots, and root exudates, they breathe C as carbon dioxide (CO<sub>2</sub>) and assimilate some of the remaining C in living tissue, referred to as microbial biomass. Upon death and turnover, microbial debris (biomass) is re-metabolized or stored in the SOM [241]. This implies that SOM is derived both from the breakdown of products of plant origin, or more generally of organic origin, and from microbial debris with microbial processes that control the relative contribution of each [242]. It is therefore easy to understand how the soil organic matter cycle is closely linked to the decomposing activity, which mineralizes organic compounds and makes essential nutrients available for plants. It is also reasonable to assume that the abundance, composition, and/or diversity of microorganisms in the soil is important for the functioning of the ecosystem [241]. Different levels of diversity need to be considered, which could be differently influenced or have different effects on microbial decomposition rates. It is necessary to differentiate between species or microbial abundance (total number of individuals of a species or total size of the microbial biomass, respectively), species

richness (total number of species), species uniformity (relative number of species), species identity or composition community (types of species/taxa present), and the diversity of species or ecosystems, which represent the number and frequency of species. For example, changes in microbial abundance have been identified as more important for soil carbon mineralization than differences in the composition of the microbial community [243].

## 6. Soil Properties Influencing Microbial Populations

One of the largest obstacles in researching PGPMs is the inconsistent field results after their application, which can result from inoculation methods and/or abiotic factors, such as soil (nutrients or heavy metal content and pH), water availability, light intensity, and temperatures. In general, PGPMs are used as biofertilizers, increasing the availability of nutrients through nitrogen fixation of atmospheric N and the solubilization of soil minerals, such as phosphorus and potassium. Abiotic conditions can almost radically change the rhizosphere and consequently affect the survival, microbial diversity, and the potential of PGPM inoculants to improve plant health and growth [244–248]. Temperature, water availability, and light intensity can change the composition of the soil, the structure and humidity, the transformations of C and N, metabolic processes, and microbial survival [249]. The fertilizers used and the organic substance present and/or added can significantly modify the pH, thus influencing the availability of nutrients and mineral toxicity, including iron and aluminum. Exposure of the soil surface to sunlight can cause mutations in the DNA of microorganisms or kill them [247–250]. All these factors can lead to more or less beneficial influences in the administration of PGPM inoculants to the soil. Water availability, lack of water (drought), or excess water (flood) can result in very limiting stress for crop production, and PGPMs can improve plant tolerance [251–253]. PGPMs can improve drought stress tolerance [254,255], and this has been shown in several examples, such as *Azotobacter chroococcum* and *Azospirillum brasilense* in *Mentha pulegium* L. [255], and *Pseudomonas* sp. and *Azotobacter* sp. in *Cymbopogon citratus* [256] and *Zea mays* [253]. *Klebsiella variicola* and *Azospirillum* sp. can improve flood stress tolerance through adaptations, such as adventitious root formation resulting from endogenous hormonal adjustments, as reported in *Glycine max* [257] and *Zea mays* [253]. However, water stress can affect Plant-Microbe interactions. Drought increases the temperature of the soil, which can inhibit the multiplication of beneficial microorganisms. Flooding reduces the availability of O<sub>2</sub> in the soil, limiting microorganisms that are not capable of anaerobic respiration [251,252,258]. Furthermore, both stresses (drought and flood) affect the plant by interfering with the production of root exudates [251,253,254,258].

Soil pH is key for the solubility of different metal ions, nutrient availability, and physical properties of the soil [259,260]. In alkaline soils, high pH values affect nutrient availability, causing osmotic stress, nutrient deficiency, and increased production of reactive oxygen species (ROS) [259,261]. In acidic soils, the low pH values and the high concentration of aluminum ions cause toxicity and phosphoric acid complex formation, which make phosphorus unavailable for plants [259,262]. The pH range of 5.5–6.5 is optimal for plant growth and the increase in the production of root exudates for microbes. In general, it can be said that bacteria are favored by a pH close to neutral or slightly alkaline, while fungi are favored by acidic pH conditions [260].

The inoculation of beneficial microorganisms is efficient in improving plant growth and in mitigating adverse stresses caused by extreme temperatures, such as *Pseudomonas putida* in *Triticum* sp. [193] and *Bacillus cereus* in *Solanum lycopersicum* [263]. Regarding low temperatures, however, *Burkholderia* sp. increases tolerance through modifications to the carbohydrate metabolism and increases plant yields in *Vitis vinifera* [264]. Extreme temperatures are recurrent stresses in agriculture and interfere in plant–PGPM interactions by changing the composition of root exudates [193,252,265].

Light can interfere in the plant–microorganism interaction by changing the amount and chemical composition of root exudates [245,266]. The inoculation of beneficial microorganisms can increase plant growth under limited light conditions by increasing shade

tolerance, as seen with *Kaistobacter* sp. and *Pseudomonas* sp. in *Ophiopogon japonicus* and *Lolium perenne* [267]. However, under limited light conditions, it is possible to see an increase in stress for the plant by the microorganisms themselves, such as *Glomus* sp., *Paraglomus* sp., *Rhizophagus* sp., and *Rhizobium* sp. in *Phaseolus lunatus* [268].

## 7. From Microbiome to PGPMs Inoculants

The plant-associated microbiome hosts an innumerable wealth of bacterial taxa, many of which promote tolerance to abiotic and biotic stresses, plant growth, suppress plant diseases, degrade xenobiotic compounds, and positively affect yields [269]. An example of the role of the plant-associated microbiome is an extensive study by [270]; through metagenomic studies and network inference, they showed the trend of fungal infection of *Rhizoctonia solani* in roots of plants of sugar beet seedlings rich in Chitinophagaceae and Flavobacteriaceae in the root endosphere. The study also identified several genes encoding chitinases and other unknown biosynthetic gene clusters that encode for the production of non-ribosomal peptide synthetases (NRPS) and polyketide synthases (PKS). Another study conducted by Ghadamgahi et al. [271] demonstrated that *Pseudomonas aeruginosa* FG106 isolated from the rhizosphere of tomato plants has a clear antagonistic activity against *Alternaria alternata*, *Botrytis cinerea*, *Clavibacter michiganensis* subsp. *michiganensis*, *Phytophthora colocasiae*, *P. infestans*, *Rhizoctonia solani*, and *Xanthomonas euvesicatoria* pv. *perforans*. In addition, *P. aeruginosa* (strain FG106) has been shown to produce proteases and lipases while also inducing high phosphate solubilization, producing siderophores, ammonia, indole acetic acid (IAA), and hydrogen cyanide (HCN) and forming biofilms that promote plant growth and facilitate biocontrol. Through genome mining approaches, genes of this strain related to biocontrol and growth promotion were also found [271].

Extreme environments are of particular interest when it comes to finding a source of useful microorganisms. Inostroza et al. [272] showed, for example, that microbial consortia obtained from the rhizosphere of *Atriplex* sp. grown in soils of an undisturbed arid Chilean ecosystem without any historical anthropogenic disturbance provided growth promotion on wheat seedlings in partially dry soils with poor phosphorus content. This proves how arid ecosystems can be a source of microbial inoculants applicable in agroecosystems poor in nutrients and/or subject to adverse climatic events [272].

The Halophytic environment is also interesting to isolate useful microbes [261]. In an exhaustive study by Christakis et al. [85], a total of 115 endophytic isolates were identified from three crop wild relative (CWR) halophytes: *Cakile maritima*, *Matthiola tricuspidata*, and *Crithmum maritimum*. From this selection, many strains showed antagonistic activity against the plant pathogens *Verticillium dahliae*, *Ralstonia solanacearum*, and *Clavibacter michiganensis* and the human pathogen *Aspergillus fumigatus*. Furthermore, several strains demonstrated growth under increased salinity and plant growth promotion [85].

From the research on the native microbiome, the use of commercially available PGPMs in agricultural ecosystems is adopted mainly because of their compatibility and complementarity with some natural processes concerning the nutrient cycle, the defense of plants from pathogens and parasites, and other related biological processes [273]. The applications of PGPMs in the agro-ecosystem are reported to be mainly positive, bringing partial or total benefits to the entire ecosystem. Different types of relationships are known, some already mentioned in the previous paragraphs of this review. Mutualistic interactions involve the plant providing shelter and/or nutrients for the microbes while, in turn, the microbes promote plant growth and provide biological control against potential pathogens and predators using various strategies [273]. The interactions between plants and microorganisms, as well as between the microorganisms themselves, are complex, and therefore, it is necessary to evaluate whether to apply a single strain or a microbial consortium. One study [274] compared the efficiency of selected single-strain commercial microbial inoculants with proven plant growth-promoting potential versus microbial consortium products under real-life production conditions in large-scale tomato growing systems exposed to diverse environmental challenges. In a protected greenhouse production system, the differ-



ent single-strain fungal and bacterial inoculants and microbial consortia have shown very similar efficacy. A particularly interesting finding was the higher effectiveness of microbial consortia when applied in more difficult environmental conditions, specifically in a tomato production system in the Negev desert in Israel with mineral fertilization at a high pH (7.9), low fertility, and sandy soil. In fact, the treatments with the microbial consortium showed a better acquisition of phosphate (P), greater stimulation of the biomass production of the vegetative shoots, and a higher yield of the final fruits in limiting P conditions. From the same study, consortia inoculation was associated with selective changes in the structure of the rhizosphere bacterial community, especially with regard to Sphingobacteria and Flavobacteria, known protectors of drought stress. In conditions of phosphate deficiency, the diversity of bacterial populations on the root surface (rhizoplane) was reduced, an effect which was canceled by the inoculation of microbial consortia, reflecting the improvement of the P state of the plants. This seems to support the hypothesis that the use of microbial consortia can increase the efficiency and reproducibility of PGPM-assisted strategies for agricultural production, especially in difficult environmental conditions [274]. Another example that confirms how PGPMs application can modify soil microbiome was reported by Baldi et al. [275] in their study conducted on an apricot orchard in Italy, in which two different types of biofertilizers (AMF and *Trichoderma* spp.) were applied and compared with an unfertilized control. The aim of the experiment was to determine if the application of biofertilizers could differently stimulate the native microbiota, in particular by influencing different models of decomposition processes of organic material. Through near-infrared (NIR) spectroscopy and thermogravimetry-differential thermal analysis (TG-DTA), it was possible to detect a significant change in chemical decomposition over time and more rapid degradation of organic matter when *Trichoderma* spp. were applied. Furthermore, by next-generation sequencing, using a metabarcoding approach, differentiated clusters of *Trichoderma* spp. were recorded for degrading litterbags in relation to the final composition of the degraded organic matter by modifying its composition of bacteria and fungi [275].

## 8. Conclusions and Discussion

The continuous increase in the human population will lead to a growing demand for food in the agricultural sector. Several years ago, the Green Revolution managed to increase global agricultural production, saving about a billion people from hunger and malnutrition. However, this has triggered the development and abuse of chemically synthesized chemical fertilizers and pesticides, resulting in an excessive environmental impact, depletion of soil ecosystems, and agrobiodiversity. Numerous studies have shown the impact of PGPMs in terms of biofertilization, biocontrol, and bioremediation, and their positive influence on crop productivity while respecting ecosystems. In this context, PGPMs have the potential not only to be valid substitutes for classic agrochemical industry products in organic farming but also to encourage the transition from conventional agriculture to the integrated, organic, and eco-sustainable management of agro-ecosystems. However, the enormous complexity of ecosystems and their interacting factors leads to inconsistent results of PGPM application on account of the environment, soil, and crops. From the examination of the studies cited in this review, it is clear that preliminary studies are necessary before the application of the PGPMs in order to accurately define the interventions on the basis of the soil conditions, environmental conditions, crops, and cultivated genotypes. The recent and rapid progress in the omics sciences is believed to provide increased knowledge on plant–soil–microorganism interactions and a better understanding of the use of PGPMs. This is an important step in improving crop stability and productivity and overall agro-ecosystem sustainability.

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