

Review

# Plant Growth Stimulation by Microbial Consortia

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**Abstract:** Plant-associated microorganisms play an important role in agricultural production. Although various studies have shown that single microorganisms can exert beneficial effects on plants, it is increasingly evident that when a microbial consortium—two or more interacting microorganisms—is involved, additive or synergistic results can be expected. This occurs, in part, due to the fact that multiple species can perform a variety of tasks in an ecosystem like the rhizosphere. Therefore, the beneficial mechanisms of plant growth stimulation (i.e., enhanced nutrient availability, phytohormone modulation, biocontrol, biotic and abiotic stress tolerance) exerted by different microbial players within the rhizosphere, such as plant-growth-promoting bacteria (PGPB) and fungi (such as *Trichoderma* and *Mycorrhizae*), are reviewed. In addition, their interaction and beneficial activity are highlighted when they act as part of a consortium, mainly as mixtures of different species of PGPB, PGPB–*Mycorrhizae*, and PGPB–*Trichoderma*, under normal and diverse stress conditions. Finally, we propose the expansion of the use of different microbial consortia, as well as an increase in research on different mixtures of microorganisms that facilitate the best and most consistent results in the field.

**Keywords:** biotic and abiotic stress; sustainable agriculture; plant-growth-promoting bacteria; plant microbiome



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## 1. Introduction

Today, there is a need to produce enough food for the more than 7 billion people on the planet, and it is expected that by the year 2050, the global population will reach ~9.5 billion [1]. Moreover, in 2020, it was estimated that ~900 million people were malnourished. For decades, the indiscriminate use of agrochemicals (mainly chemical fertilizers and pesticides) in agriculture to increase production and/or decrease the constant threat of infections caused by plant pathogens has led to a loss of plant health. Unfortunately, the ways in which the production of the various agricultural systems has increased in the vast majority of countries is not sustainable [2]. Agricultural soils, directly or indirectly, are continuously losing their quality and physical properties (soil texture, permeability, porosity, and drainage), as well as their chemical (imbalance of nutritive elements) and biological (beneficial organisms) health [3]. In the case of the soil microbiota, some authors have shown that pesticides can decrease their abundance and diversity, leading to an impairment of their functioning in agro-systems [2–4]. Pesticides also negatively impact other beneficial organisms in agriculture, such as pollinating insects, which are important in improving the production of several crops [5,6]. In certain regions of the world, attempts have been made to reduce or eliminate the use of potentially deleterious agrochemicals,

mainly due to their risk to human health, but in many developing countries, they continue to be used without any type of regulation [7].

There is a pressing need for approaches that facilitate food production without the excessive use of agrochemicals and for the use of genetically improved crops, including selection of plant varieties that are resistant to pests and various adverse environmental conditions [8]. Much of this may be achieved by the genetic modification of plants [9,10] and/or the application of plant-growth-promoting microorganisms [11–15]. In some cases, using a mixture of two or more compatible microorganisms of different species (or strains) can facilitate beneficial additive or synergistic results, since the lack of activities in one added microbe can be found through the action of the other [16]. Here, it is important to define these two concepts in the context of this work. An additive effect is the sum of activities, while synergy refers to an effect that goes beyond the sum of individual actions, since there is a stimulation of one action (or microorganism) by another.

These new “plant microbiome engineering” approaches, consisting of adding effective bioinoculants, induce new structured biological networks in diverse soil types. This promotes the recovery of functional, beneficial microbial groups that are positively linked to soil fertility and replenishes the natural microbiome, which has been reduced by crop domestication practices. The addition of microbial consortia, therefore, can restructure and stimulate plant-growth-promoting mechanisms in both optimal conditions and under different types of biotic and abiotic stress [17]. Here, the strategy of designing microbial consortia between bacteria, *Trichoderma*, and/or arbuscular mycorrhizae fungi to stimulate plant growth is reviewed; this is a strategy that is expected to significantly increase agricultural productivity.

## 2. Plant-Growth-Promoting Microorganisms

Plant-growth-promoting microorganism (PGPM) is a term that applies to all microorganisms (e.g., bacteria, actinomycetes, fungi, and algae) that have a beneficial effect on plant growth through the action of either direct or indirect mechanisms (e.g., mineral nutrition, ethylene reduction, disease suppression) [18]. PGPMs have a significant role in sustainable agriculture. They increase the production of various crops, improve soil fertility, promote diversity and interaction with other beneficial microorganisms, inhibit the growth and infective action of potential pathogens, and generally maintain the sustainability of the systems [18,19].

Most studies of PGPMs are based on interactions of single microorganisms with plants, evaluating different parameters of growth and plant health, such as length or weight of the plant or its individual tissues, chlorophyll content, or the nutritional content of its tissues or fruits [18,20–22]. This has led to a better understanding of plant–microbe interactions, but leaves aside the “real” factor of these interactions in the environment, where a multiplicity of microbial species can exist. For example, one gram of soil typically contains a wide range of organisms, including bacteria ( $\sim 9 \times 10^7$  cells per g), actinomycetes ( $\sim 4 \times 10^6$  cells per g), fungi ( $\sim 2 \times 10^5$  cells per g), algae ( $3 \times 10^4$  cells per g), protozoa ( $\sim 5 \times 10^3$  animals per g), and nematodes ( $\sim 3 \times 10^1$  animals per g) [23]. From this diversity of organisms, several species can occupy different niches and multiple interactions can take place. The plant influences the interactions in the rhizosphere, since, through the exudation of compounds (e.g., sugars, amino acids, and organic acids), new battles for nutrient acquisition, colonization of spaces, and survival are generated. It has been suggested that, due to the plethora of interactions that can occur when single species are inoculated in the field, positive and consistent results in terms of facilitating plant growth are not always achieved [24]. However, more consistent positive results may be obtained by inoculating plants with microbial consortia containing two or more beneficial microorganisms [25,26].

Following seed germination, plants continuously interact with microorganisms that reside both below and aboveground. These interactions are dynamic and change depending on the microbial structure that is formed during the different stages of plant growth and development [27,28]. In part, this dynamic is due to the volatile compounds emitted by the

aerial parts of the plant as well as root exudates that are secreted into the soil, attracting and structuring a particular rhizospheric microbiome [28]. Other abiotic factors can also influence the interactions that occur between the soil microbiome and plants, including temperature, water availability, pH, and the availability of nutrients [29]. Under natural conditions, where the environment is continuously changing, plants communicate with multiple microbial species, and in turn, these microbes communicate with each other to give rise to networks that can have beneficial (or harmful) repercussions for plant growth, thus shaping a plant microbiome [30,31].

Various studies have suggested that microbial consortia can generally perform tasks better than individual strains. This includes metabolizing complex compounds, carrying out reactions with two or more steps, degrading plant polymers such as cellulose, and remaining stable in a fluctuating environment. Some of these activities are not resident in a single microorganism; therefore, the use of microbial consortia is necessary [32].

The first commercialized bioinoculants included single biological agents [33], such as rhizobial bacteria, which can form nodules on the roots of legume plants and therein fix atmospheric nitrogen, facilitating plant growth and development. Unfortunately, the effectiveness of this type of bioinoculant is limited in that it can only benefit legumes.

In some instances, legumes, such as *Phaseolus vulgaris* (bean), are co-cultivated with non-legumes, such as *Cucurbita pepo* (zucchini) or *Zea mays* (maize). In these instances, the application of a bacterial consortium, such as *Rhizobium* plus *Pseudomonas* or *Bacillus*, or a bacterial-fungal consortium, such as *Rhizobium* plus *Trichoderma* or a mycorrhizae strain, could benefit the three above-mentioned vegetable crops. This increase in plant growth might occur through provision of a better supply of assimilable nutrients (such as P, Fe, and N) [34,35].

Bioinoculants based on microbial consortia may include bacteria of different species, while others may include both beneficial bacteria and fungi. The application of different PGPM species with diverse mechanisms of action should provide a wide spectrum of benefits for the plant, including direct stimulation of its growth and health, as well as increases in production. In addition, a decrease in diseases caused by pathogens would be expected [36,37].

### 3. Bacterial Consortia

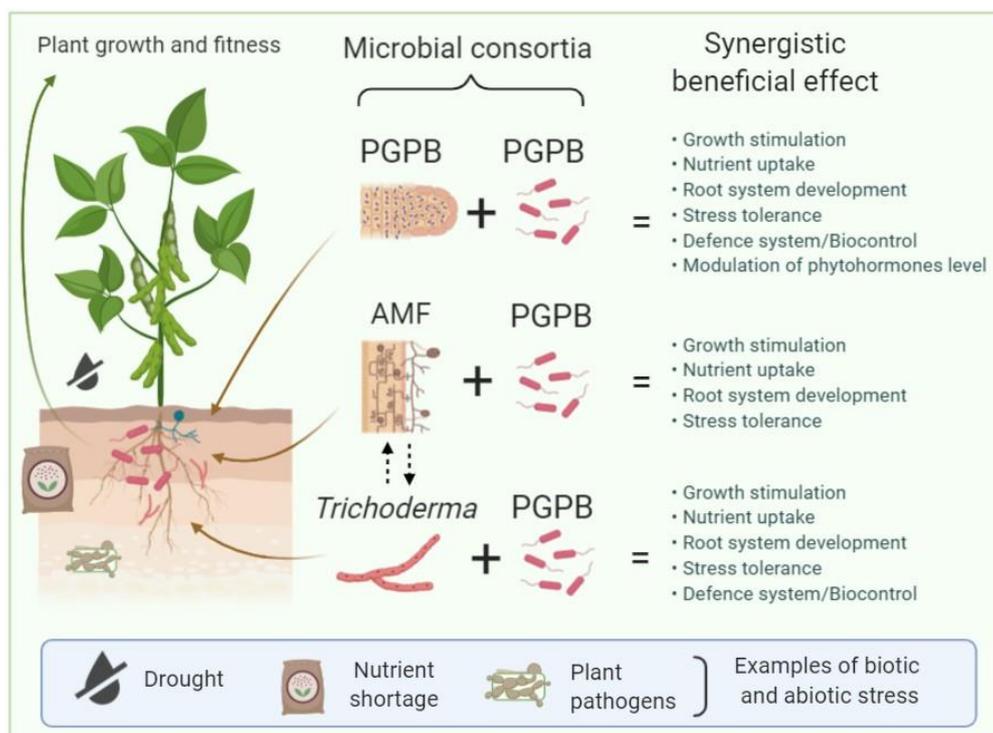
Currently, synthetic fertilizers are applied to crops on a large scale to meet the growing global food demand, leading to high health, economic, and environmental costs [38]. A well-studied and sustainable alternative for improving plant growth and soil fertility is the application of plant-growth-promoting bacteria (PGPB), which possess functional traits that regulate the growth, development, and productivity of crops. These growth-promoting effects are due to the improvement of the availability and biosynthesis of several limiting macro- and micronutrients, as well as crop protection against stressful environmental conditions [15,39].

In recent years, the impact of numerous PGPB strains on plants has been well explored, leading to the commercialization of a large number of microbial inoculants [40,41]. To enhance the beneficial functions displayed by these bacteria, the design of bacterial consortia has gained interest as a suitable strategy for sustainable food production. A bacterial consortium generally constitutes two or more compatible bacteria of different species in a synergistic or additive interaction [42–44]. In some cases, a mixture of different strains of the same species can exhibit enhanced activities and also be considered a consortium. Bacterial consortia have been reported to improve beneficial traits in plants in comparison to individual strains due to the coverage of a diverse set of plant growth promotion and biological control mechanisms [45]. The use of these consortia is a feasible strategy for ameliorating drought [46], salinity [47], nutrient uptake [48], pests, and phytopathogenic infections [49] of agricultural crops. In addition, some bacterial consortia can fix nitrogen, transform some unavailable nutrients into an assimilable form, produce phytohormones,

and chelate iron, which is important in maintaining soil quality and health; these can also reduce the negative effects of some conventional non-sustainable agricultural practices [50].

There are two types of bacterial consortia known—simple and complex. The differences are the fermentation strategy or protocol (production of a large population of bacteria to be later formulated into an inoculant), where strains are grown individually or in combination with other species/strains in a suitable medium for all PGPB species [51]. This is an important stage, since a higher number of species generally results in a higher number of interactions among the strains, therefore generating differences in metabolite secretions. On the other hand, the success of bacterial consortia under field conditions is dependent on the type and function of strains used, where some aspects require special attention, including adaptation to adverse climatic conditions, survival, and persistence in the soil after inoculation [50,52].

The selection of these strains is dependent upon the source of the strain isolation, since consortium members need to proliferate in the environmental conditions (soil type, climate, and host) where they will be applied. In addition, it is important to note that, when two or more strains are part of a bacterial consortium, each strain not only competes functionally with the others for plant growth promotion, but also complements the others for soil and/or plant establishment [53–55]. Figure 1 summarizes the different types of microbial consortia discussed in this manuscript.



**Figure 1.** Microbial consortia. Rhizosphere microorganisms like plant-growth-promoting bacteria (PGPB), arbuscular mycorrhizal fungi (AMF), and fungi from the genus *Trichoderma* spp. can establish beneficial interactions with plants, promoting plant growth and development, increasing the plant defense system against pathogens, promoting nutrient uptake, and enhancing tolerance to different environmental stresses. Rhizosphere microorganisms can influence one another, and the resulting consortia of PGPB + PGPB (e.g., a nitrogen-fixing bacterium such as *Rhizobium* spp. and *Pseudomonas fluorescens*), AMF + PGPB, and *Trichoderma* + PGPB may have synergetic effects on plant growth and fitness, providing the plant with enhanced benefits to overcome biotic and abiotic stress. Dashed arrows indicate beneficial interactions between AMF and *Trichoderma*.

#### 4. Bacteria–Bacteria Interactions

There is a great diversity of bacteria that are part of the plant microbiota and that have traits that promote the growth and development of plants in both optimal and stress environments [56,57]. A key factor influencing the beneficial effects of bacterial consortia is the interaction between their members to guarantee a stable long-term co-existence [58].

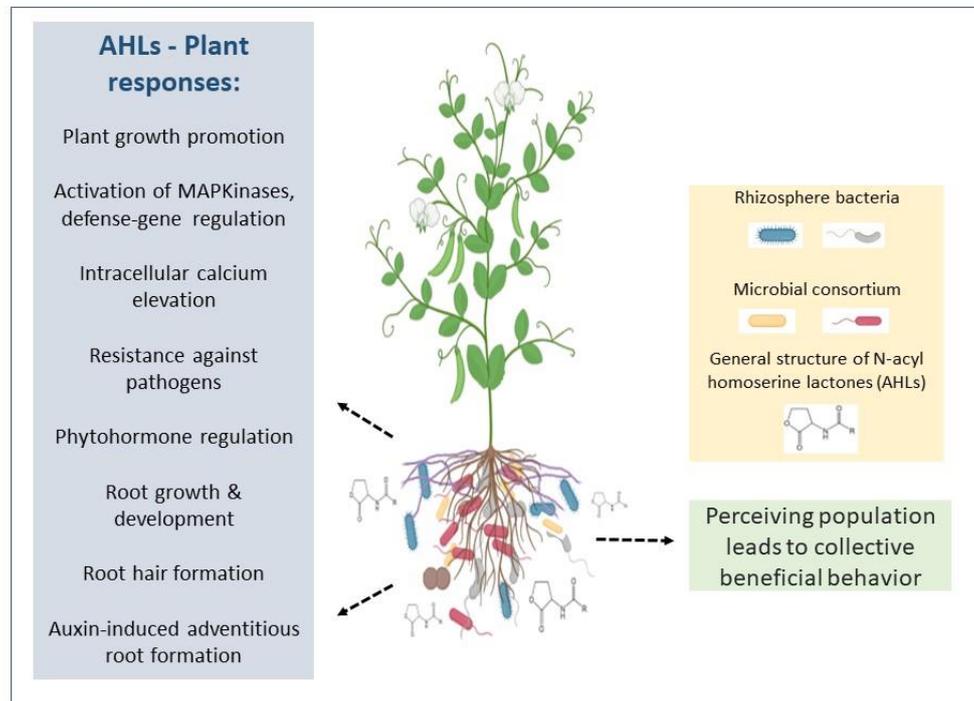
Bacterial interactions within a consortium can be classified into three types based on the effects they have on each other: (i) stimulatory or positive, (ii) inhibitory or negative, or (iii) neutral [58]. Positive interactions generally create a network to support individual members through cross-feeding, where one bacterium utilizes the metabolic products produced by another consortium member. Mutualism, proto-cooperation, and commensalism are examples of positive associations. In mutualism, each of the members need the others to survive since they mutually exchange required substances or mutually remove toxins [59]. In proto-cooperation, the interaction between species is beneficial to the growth rate of both populations, but is not required for either to persist [58]. Commensalism is a positive one-way interaction, in which one member benefits while the other is unaffected [60].

Negative interactions lead to the suppression of bacterial members in a consortium, destroying the community structure and its functioning [60]; they include amensalism, predation, parasitism, and competition. Amensalism is a type of unidirectional interaction where the growth of one of the members is affected by the production of toxic compounds by its partner [59]. Predation and parasitism describe interactions where the growth of one species depends on consuming another species so that the population dynamics often show continuous oscillations. Competition occurs when members of a consortium need the same resource, be it nutrients, water, or even space; therefore, the faster-growing species dominates over time [59,60]. In neutral interactions, members of the consortium do not influence or affect one another. Neutralism occurs when two species consume different substances (nutritional divergence) and neither produces compounds inhibitory to other members of the consortium [58].

In agriculture, consortia members should positively interact, where mutualistic growth is desirable for stable performance over prolonged cultivation to obtain the expected positive effect when applied to a crop [61,62]. In this regard, bacterial communication is only superficially understood at the present time. This communication relies on the production, detection, and response to extracellular signaling molecules that regulate and shape the bacterial population in the consortium, where only compatible microbes are involved in altering the plant defense response affecting overall plant health and growth [63]. Consortium communication is highly dependent on molecular signals; among them, quorum sensing plays a significant role in bacterial compatibility in consortium formulations [61]. Among several signal molecules, the acyl homoserine lactone (AHL) signal molecules are the most well known in bacteria [63]. Pure AHLs have shown induction of intracellular  $Ca^{2+}$  levels and primary root growth [61,64], while AHLs produced by PGPB, such as *Serratia liquefaciens* and *S. phymuthica*, have stimulated root development and total plant biomass; other bacteria, like *Sinorhizobium fredii* and *Pantoea ananatis*, stimulated the formation of biofilm in the roots of *Oryza sativa* (rice) and *Phaseolus vulgaris* (bean) plants [65]. Other species of nitrogen-fixing bacteria, such as *Sinorhizobium meliloti*, producers of AHLs, promoted nodulation in *Medicago truncatula* [62,66] (Figure 2).

Quorum sensing allows bacteria to switch between two distinct gene expression programs: (i) one at low cell density for individual and asocial behavior, and (ii) another at high cell density for social and group behaviors, which are preferential for consortia [67]. Williams et al. [68] indicated that the response to fluctuations in cell number in quorum-sensing systems occurs as follows. Low-molecular-weight molecules called auto-inducers are synthesized intracellularly; then, these molecules are passively released or actively secreted outside of cells. As the number of cells in a population increases, the extracellular concentration of auto-inducers increases. Finally, the auto-inducers are accumulated above the minimum threshold level required for detection, and the cognate receptors bind the auto-inducers and trigger signal transduction cascades that result in population-wide

changes in gene expression. Thus, quorum sensing enables cells in a population to function in unison and, in so doing, they carry out behavior as a collective, not altering the desired effects of compatible PGPB in consortia [69,70].



**Figure 2.** Plant responses to N-acyl homoserine lactones (AHLs) produced by plant-growth-promoting bacteria in the rhizosphere. Single members of a bacterial consortium could interact/communicate to perceive certain population densities and respond as a collective to induce several plant-beneficial activities, such as stimulation of root hair formation, root growth and development, and general plant growth and self-defense mechanisms.

Other important signaling compounds reported in bacterial consortia are volatile organic compounds (VOCs), which are implicated in both bacteria–bacteria and plant–bacteria communication [71]. These compounds include terpenoids, alkanes, alkenes, ketones, sulfur-containing compounds, and alcohols that act as low-molecular-weight (<300 Da), low-boiling-point, high-vapor-pressure, and lipophilic signal molecules [72]. These properties facilitate evaporation and diffusion through gas- and water-filled pores in soil and rhizosphere environments [73]. VOCs produced by bacteria can have positive effects on the growth of other nearby or distant bacteria, modifying their behavior and modulating bacterial resistance to antibiotics. Bacterial VOCs can also have direct antagonistic effects against other bacteria; for this reason, many species of *Pseudomonas* and *Bacillus* that produce VOCs with antibacterial activity are used as biocontrol agents against plant pathogens [74,75]. Furthermore, VOCs influence gene expression involved in hormonal signaling, defensive pathways, and microbial stress tolerance, virulence, and biofilm formation [76].

The success of bacterial interaction in a consortium depends on (i) a proper description of the consortium, the taxonomic affiliation of the strains, and identification protocols, (ii) a detailed explanation of how the consortium was made, (iii) a full statement of sensitive parameters, such as soil physicochemical parameters, and the exact dosage applied, and (iv) appropriate living populations of each species co-existing, which impacts the inoculated consortium’s success [51,77].

## 5. Plant Growth Stimulation by PGPB Consortia Under Non-Stress Conditions

There are several studies in which the potential of bacterial consortia to improve plant growth has been demonstrated in greenhouse and/or field conditions. For example,

Jha and Saraf [78] found that the inoculation of a multispecies consortium made up of *Micrococcus* sp., *Acinetobacter calcoaceticus*, *Brevibacillus brevis*, and *Bacillus licheniformis* with the ability to produce indole-3-acetic acid (IAA), 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and siderophores and to solubilize inorganic phosphorus improved the yield of the plant *Jatropha curcas*. Similarly, a bacterial consortium including *Azospirillum*, *Pseudomonas striata*, *Pseudomonas* sp. B15, and *Leuconostoc mesenteroides* improved the plant height and biomass of seedlings of tomato, brinjal, and chili [79]. In another study, Molina-Romero et al. [80] showed that a consortium consisting of desiccation-tolerant bacteria (*Pseudomonas putida* KT2440, *Acinetobacter* sp. EMM02, *Sphingomonas* sp. OF178, and *Azospirillum brasilense* Sp7) was able to adhere to seeds and colonize the rhizosphere of maize plants. This latter experiment showed that these bacteria can coexist in association with plants without antagonistic effects, and that inoculation with this consortium increased maize plant height, diameter, and shoot–root dry weight (compared to the un-inoculated control). Dary et al. [81] and Malboobi et al. [82] observed that the inoculation of *Solanum tuberosum* and *Lupinus luteus* plants with a consortium composed of *P. putida*, *P. agglomerans*, *Bradyrhizobium* sp., and *Pseudomonas* sp. showed higher plant growth promotion in root dry weight, aerial dry weight, nitrogen content, and final yield.

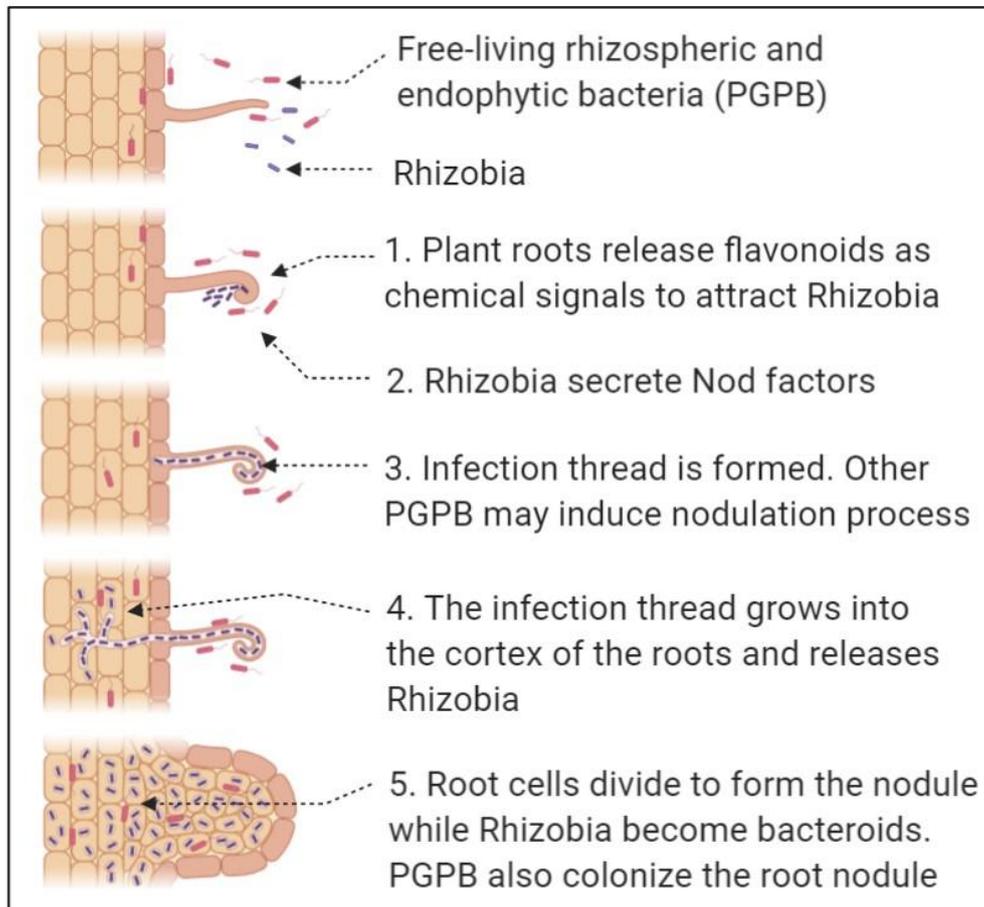
Rojas Padilla et al. [83], using a native *Bacillus* consortium with *Triticum turgidum* L. subsp. Durum (wheat) under non-stress conditions, reported an increase in plant length and weight, as well as the biovolume index, compared to inoculations of a single bacterial strain at a time. Similarly, Robles Montoya et al. [84] reported that the use of a *Bacillus* consortium composed of *B. paralicheniformis*, *B. subtilis*, *B. megaterium*, and *B. cabrialesii* with wheat showed a significant increase (compared to un-inoculated seedlings) in the length of the aerial part of the plant, root length, total length, stem diameter, circumference, dry weight of the aerial part of the plant, and the biovolume index.

Rhizobia have been widely studied for their ability to form nodules and fix atmospheric nitrogen; they are a diverse group of bacteria that form a symbiotic relationship with leguminous plants. This group is composed of bacteria belonging to Proteobacteria classes, primarily Alphaproteobacteria (e.g., *Rhizobium*, *Sinorhizobium*, *Ensifer*, *Bradyrhizobium*, *Mesorhizobium*) and Betaproteobacteria (e.g., *Paraburkholderia*, *Cupriavidus*, *Trinickia*) [85]. Rhizobia induce the leguminous plant's symbiotic response and the development of nodules in which the nitrogen fixation process occurs. On the other hand, leguminous plants create a niche and increase chances of survival for symbiotic bacteria by providing carbon sources for the rhizobia within the nodules.

The symbiotic process starts with the perception of plant-secreted flavonoids (present in root exudates) by rhizobia, which, in turn, produce lipochitoooligosaccharides, termed nodulation (Nod) factors (NFs), which are sensed by the plant and lead to the activation of the nodule organogenesis programs [86]. Subsequently, the rhizobia present in the rhizosphere enter the plant root hairs via root cracks and then migrate and colonize the nodule structure via infection threads [87]. When present inside the nodule, rhizobia differentiate into a bacteroid state, a specialized symbiotic organelle-like form that potentiates the nitrogen fixation process [88]. As bacteroids, rhizobia fix atmospheric N<sub>2</sub> through the action of the nitrogenase enzyme, providing NH<sub>4</sub> to the plant host in exchange for photosynthetically fixed carbon [89] (Figure 3). It is estimated that legume–rhizobial biological nitrogen fixation (BNF) globally accounts for ~200 million tons of fixed nitrogen per year [90], playing a vital role in soil N cycles and overall agricultural productivity.

Rhizobia are common soil and rhizosphere inhabitants and, as a consequence, have evolved in direct competition and/or synergism with other soil and rhizospheric microbes, including rhizobial and non-rhizobial bacteria (NRB; free-living rhizospheric and endophytic bacteria). In fact, under natural conditions, leguminous plant roots and root nodules contain a wide range of rhizospheric and endophytic bacteria, as well as rhizobia [91–95]. Importantly, some of these bacteria may potentiate rhizobial nodule formation and promote plant growth in both optimal and stressful conditions [91,94]. Hence, obtaining and exploring the synergistic effects between rhizobia and NRB consortia may be the key for

the development of inoculants with increased performance and plant-growth-promoting properties (Figure 3).



**Figure 3.** The formation of N-fixing nodules induced by rhizobia. Free-living plant-growth-promoting rhizobacteria and bacterial endophytes may induce the nodulation process and increase the nitrogen fixation, general plant growth, and nutritional state.

Several studies have demonstrated that a diverse range of free-living rhizospheric and endophytic bacteria are able to potentiate the nodulation and nitrogen fixation processes of several rhizobial strains, leading to increased leguminous plant growth (Table 1). The NRB partners include bacteria belonging to the Firmicutes (e.g., *Bacillus*, *Paenibacillus*), Proteobacteria (e.g., *Pseudomonas*, *Azospirillum*, *Pantoea*) Actinobacteria (e.g., *Streptomyces*, *Nocardia*), Flavobacteria, and some cyanobacteria. Moreover, the beneficial effects of co-inoculations have been observed in diverse systems (e.g., forming determinate or indeterminate nodules) between several leguminous plants (e.g., *Phaseolus vulgaris*, *Glycine max*, *Cicer arietinum*) and their respective compatible alpha and beta-rhizobial symbionts (e.g., *Rhizobium*, *Neorhizobium*, *Bradyrhizobium*, *Ensifer/Sinorhizobium*, *Mesorhizobium*, *Cupriavidus*). This indicates that the co-inoculation process can be a generally beneficial practice that benefits most legume–rhizobia symbioses [96].

**Table 1.** Studies reporting the beneficial interactions between consortia of rhizobia and non-rhizobial bacteria and their positive effects in the symbiosis with leguminous plants.

Rhizobia	Co-Inoculant	Plant Host	Reference
<i>R. tropici</i> CIAT899	<i>Bacillus megaterium</i>	<i>Phaseolus vulgaris</i>	[97]
<i>R. tropici</i> CIAT899	<i>Paenibacillus polymyxa</i> (DSM 36)	<i>Phaseolus vulgaris</i>	[98]
<i>R. tropici</i> CIAT899	<i>Serratia grimesii</i> BXF1	<i>Phaseolus vulgaris</i>	[99]
<i>R. tropici</i> CIAT899	<i>Pseudomonas fluorescens</i> YsS6	<i>Phaseolus vulgaris</i>	[100]
Rhizobium spp.	<i>Bacillus aryabhatai</i> Sb <i>Azotobacter vinelandii</i> G31	<i>Trifolium repens</i>	[101]
Rhizobium	<i>Pseudomonas fluorescens</i> P-93 <i>Azospirillum lipoferum</i> S-21	<i>Phaseolus vulgaris</i>	[102]
<i>Rhizobium leguminosarum</i> bv. trifolii	<i>Bacillus insolutus</i> , <i>Bacillus brevis</i> <i>Agrobacterium rhizogenes</i>	<i>Trifolium pratense</i>	[94]
<i>Rhizobium leguminosarum</i> PR1	<i>Bacillus thuringiensis</i> KR1	<i>Pisum sativum</i> ; <i>Lens culinaris</i>	[103]
Rhizobium	<i>Bacillus subtilis</i> OSU-142 <i>Bacillus megaterium</i> M-3	<i>Phaseolus vulgaris</i>	[104]
<i>Rhizobium</i> spp. IC3123	<i>Bacillus megaterium</i> NR4 and NR6 <i>Pseudomonas putida</i> ;	<i>Cajanus cajan</i>	[105]
<i>Rhizobium</i> sp. AR-2–2	<i>P. fluorescens</i> <i>Bacillus cereus</i>	<i>Cajanus cajan</i>	[106]
<i>Rhizobium etli</i>	<i>Paenibacillus polymyxa</i>	<i>Phaseolus vulgaris</i>	[107]
(Neo) <i>Rhizobium galega</i> bv. orientalis	<i>Pseudomonas triovialis</i> 3Re27 <i>Pseudomonas extremorientalis</i> TSAU20	<i>Galega orientalis</i>	[108]
<i>Bradyrhizobium japonicum</i> 532C	<i>Serratia proteamaculans</i> 1–102 <i>Aeromonas hydrophila</i> P73	<i>Glycine max</i>	[109]
<i>B. japonicum</i> E109	<i>Serratia liquefaciens</i> 2–68 <i>Bacillus amyloliquefaciens</i> LL2012	<i>Glycine max</i>	[110]
<i>B. diazoefficiens</i> USDA110	<i>Bacillus velezensis</i> S141	<i>Glycine max</i>	[111]
<i>B. japonicum</i> SB1	<i>Bacillus thuringiensis</i> KR1	<i>Glycine max</i>	[112]
<i>B. japonicum</i>	<i>B. subtilis</i>	<i>Glycine max</i>	[113]
<i>Bradyrhizobium japonicum</i>	<i>B. subtilis</i> NEB4 and NEB5 <i>B. thuringiensis</i> NEB17	<i>Glycine max</i>	[114]
<i>B. japonicum</i> spp.	<i>Streptomyces griseoflavus</i> P4	<i>Glycine max</i>	[115,116]
<i>B. elkanii</i> BLY3–8	<i>Streptomyces griseoflavus</i> P4 <i>Nocardia alba</i>	<i>Glycine max</i>	[117]
<i>B. japonicum</i>	<i>Nonomuraea rubra</i> <i>Actinomadura glauciflava</i>	<i>Glycine max</i>	[118]
<i>Bradyrhizobium</i> sp. BR1602	<i>Pantoea phytobeneficialis</i> MSR2	<i>Calopogonium muconoides</i>	[119]
<i>Sinorhizobium meliloti</i>	<i>Exiguobacterium</i> sp. M2N2c and B1N2b <i>Bacillus anthracis</i> M1	<i>Trigonella foenum-graecum</i>	[96]
<i>E. adhaerens</i>	<i>Paenibacillus taichungensis</i> M10 <i>Paenibacillus xylanilyticus</i> M15 <i>Bacillus</i> sp. M7c	<i>Vigna radiata</i>	[120]
<i>Sinorhizobium meliloti</i> B399		<i>Medicago sativa</i>	[121]
<i>Ensifer</i> ( <i>Sinorhizobium</i> ) <i>medicae</i> WSM419	<i>Pseudomonas fluorescens</i> WSM3457	<i>Medicago truncatula</i>	[122]
<i>Mesorhizobium</i> sp. BHURC02	<i>Pseudomonas fluorescens</i> BHUPSB06	<i>Cicer arietinum</i>	[123]
<i>Mesorhizobium</i> spp. Ca181 and Ca313	<i>Pseudomonas</i> sp. CRP55b and CRS68	<i>Cicer arietinum</i>	[124]
<i>Mesorhizobium</i> spp. Ca181	<i>Pseudomonas</i> spp.	<i>Cicer arietinum</i>	[125]
<i>M. ciceri</i> TAL-1148	<i>Ochrobactrum ciceri</i> Ca-34	<i>Cicer arietinum</i>	[126]
<i>Mesorhizobium ciceri</i>	<i>Anabaena</i>	<i>Cicer arietinum</i>	[127]
<i>Cupriavidus taiwanensis</i>	<i>Pseudomonas fluorescens</i> YsS6	<i>Mimosa pudica</i>	[100]

The study of the interactions between rhizobia–NRB consortia has revealed some of the mechanisms that are involved in the NRB abilities to promote nodulation and nitrogen fixation by rhizobia. These include (i) the direct increase in the number of rhizobial populations in the soil, (ii) the production of siderophores that promote rhizobial growth

under iron-limiting conditions [105,128,129], (iii) the direct effect on plant root growth and nutrient uptake (i.e., N, P, K), which positively impacts the symbiotic efficiency, (iv) lytic enzyme activities (e.g., cellulase) [108] that play a role in rhizobial colonization, (v) induction of plant flavonoid biosynthesis that leads to the expression of rhizobial *nod* genes [124,130]; (v) biosynthesis of plant hormones such as IAA, cytokinins, gibberellins [108,110,111] that facilitate plant growth and development and the regulation of the nodulation process, and (vi) expression of ACC deaminase [99,131] and the modulation of plant ethylene levels, which are involved in the regulation of the nodulation process [131,132].

Interestingly, recent studies have demonstrated that the consortia benefit not only the rhizobial partner, but also the NRB partner. For example, Zgad Zaj and colleagues [133] have shown that *Mesorhizobium loti* induces infection threads that can selectively guide non-rhizobial endophytic bacteria towards nodule primordia. These endophytes are then able to migrate and colonize the root nodule together with rhizobia, benefiting from the increased carbon concentrations found within the nodule.

## 6. Plant Growth Stimulation by PGPB Consortia Under Stress Conditions

Along with the increase in agrochemicals, climate change and modifications in land use can create unfavorable stress conditions for microbial interaction in agro-ecosystems [134]. Stress conditions can impair plant morphology, physiology, biochemistry, and gene regulation, as well as soil microbial and physicochemical properties, resulting in considerable yield loss [38]. The different types of stress may be classified as biotic and abiotic, where biotic stress is caused by living organisms, including viruses, bacteria, fungi, nematodes, insects, arachnids, and weeds, while abiotic stresses include extremes of temperature, drought, environmental contaminants, and salinity [56].

Beneficial bacteria can contribute to sustaining the intrinsic resistance of the plant to these challenges; therefore, the inoculation of plants with bacterial consortia can reduce the negative influence of biotic or abiotic stress conditions on crops [134] (Table 2). However, novel approaches are needed to explore bacteria–bacteria and plant–bacteria interactions under abiotic and biotic stress conditions to identify potential stress-tolerant or resistant bacteria to improve plant growth and disease resistance [56].

**Table 2.** Examples of bacterial consortia and their beneficial effects on crop plants under biotic and abiotic stresses.

Consortium	Crop	Stress	Effect	Reference
<i>Pseudomonas</i> spp.	Potato	<i>Phytophthora infestans</i>	Reduction of mycelial growth Decreased release of zoospores induced systemic resistance (ISR) activation (reduced the number of pathogen spores)	[135]
<i>Xanthomonas</i> sp., <i>Stenotrophomonas</i> sp., and <i>Microbacterium</i> sp.	<i>Arabidopsis thaliana</i>	<i>Hyaloperonospora arabidopsidis</i>	Plant growth promotion (shoot fresh weight) ISR activation (peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), $\beta$ -1,3 glucanase and chitinase)	[136]
<i>Pseudomonas putida</i> CRN-09 and <i>Bacillus subtilis</i> CRN-16	Mung bean	<i>Macrophomina phaseolina</i>	Plant growth promotion (increased shoot and root length, shoot and root fresh weight) ISR activation (increased phenolic compounds)	[137]
<i>Pseudomonas aeruginosa</i> PHU094 and <i>Mesorhizobium</i> sp. RL091	Chickpea	<i>Sclerotium rolfsii</i>	Plant growth promotion (increased shoot length and total biomass)	[138]
<i>Pseudomonas fluorescens</i> and <i>Azospirillum</i>	Cotton	<i>Rhizoctonia bataticola</i>	Decreased root rot incidence Increased seed cotton yield	[139]

Table 2. Cont.

Consortium	Crop	Stress	Effect	Reference
<i>Bacillus cereus</i> Y5, <i>Bacillus</i> sp. Y14, and <i>Bacillus subtilis</i> Y16	Wheat	Salinity	Increased photosynthetic rate, the content of carotenoids and crude protein Higher grain yield	[140]
<i>Brevibacillus fluminis</i> , <i>Brevibacillus agri</i> , and <i>Bacillus paralicheniformis</i>	Brinjal, potato, tomato, and chilli	Salinity	Increased fermentation percentage Plant growth promotion (an increase in shoot length, root length, dry and fresh weight)	[141]
<i>Pseudomonas</i> sp. PFS1 and BSS3B2, <i>Serratia proteamaculans</i> S1BD1, <i>Alcaligenes</i> sp. PKS1, and <i>Bacillus</i> sp. PSS2	saltgrass	Salinity, petroleum hydrocarbons	Plant growth promotion (increased plant biomass)	[142]
<i>B. megaterium</i> CAM12 and <i>P. agglomerans</i> CAH6	Mung bean	Aluminum and drought	Reduced Al uptake in plants Plant growth promotion (increased plant biomass) Higher content of carotenoids, chlorophyll	[143]
<i>Bacillus cereus</i> AR156, <i>Bacillus subtilis</i> SM21, and <i>Serratia</i> sp. XY21	Cucumber	Drought	Increased the leaf proline content Significantly enhanced the superoxide dismutase (SOD) activity	[144]
<i>Rhodotorula graminis</i> WP1, <i>Burkholderia vietnamiensis</i> WPB, <i>Rhizobium tropici</i> PTD1, <i>Acinetobacter calcoaceticus</i> WP19, <i>Rahnella</i> sp. WP5, <i>Burkholderia</i> sp. WP9, <i>Enterobacter asburiae</i> PDN3, <i>Sphingomonas yanoikuyae</i> WW5, <i>Pseudomonas</i> sp. WW6, and <i>Curtobacterium</i> sp. WW7	poplar	Drought	Plant growth promotion (increased root dry weight, shoot dry weight, total dry weight, total nitrogen) Reduced damage by reactive oxygen species (ROS)	[145]
<i>Ochrobactrum pseudogrignonense</i> RJ12, <i>Pseudomonas</i> sp. RJ15, and <i>Bacillus subtilis</i> RJ46	Black gram and Pea	Drought	Plant growth promotion (increased seed germination percentage, root length, shoot length, and dry weight) Elevated production of ROS scavenging enzymes and cellular osmolytes Higher leaf chlorophyll content	[146]

### 6.1. Biotic Stress

Plant defense can generally be induced more effectively and efficiently by microbial consortia compared to a single microbial inoculant. Therefore, considering the abilities of several bacteria in a consortium to activate pathways related to resistance or biocontrol, there is an ample opportunity to harness these mechanisms for controlling yield and diminishing diseases in an associated crop [135,137,138].

In this way, Singh et al. [138] evaluated the effectiveness of a microbial consortium that included three compatible rhizosphere microorganisms, *Pseudomonas aeruginosa* PHU094, *Trichoderma harzianum* THU0816, and *Mesorhizobium* sp. RL091, in promoting plant growth and mobilizing phenolic acid in chickpea infected by *Sclerotium rolfsii*. In this work, several

phenolic compounds, such as myricetin, ferulic acid, syringic acid, and quercetin, were accumulated in higher levels in the treated plants. Moreover, shikimic acid was maximally produced in the leaves of consortium-treated chickpea plants after pathogen infection (compared to untreated control plants or plants treated with a single microbe). However, it should be noted that using species of opportunistic human pathogens, such as *P. aeruginosa*, restricts their use and release in the field, so it is advisable to use other species without any pathogenic potential.

The synergistic interaction between *Pseudomonas putida* CRN-09 and *Bacillus subtilis* CRN-16 was evaluated in *Vigna radiate* (mung bean), where the consortium triggered the expression of induced systemic resistance against the phytopathogenic fungus *Macrophomina phaseolina*. This resulted in enhanced plant levels of peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL),  $\beta$ -1,3 glucanase, and chitinase [137]. In addition, De Vrieze et al. [135] used a leaf disk assay with three different potato cultivars to compare the activity of nine selected *Pseudomonas* strains against the phytopathogenic fungus *Phytophthora infestans* when the selected strains were applied alone or in various combinations. The results revealed that the combination of two strains (*P. frederiksborgensis* S19 and *P. fluorescens* S49) was particularly effective at controlling the pathogen; while strain S49 had a stronger inhibition effect on mycelial growth, strain S19 was a very efficient inhibitor of zoospores. Similarly, a bacterial consortium (*P. aeruginosa* and *Azospirillum* sp.) was found to have a synergistic effect on the plant yield and suppression of root rot disease caused by the phytopathogenic fungus *Rhizoctonia bataticola* in cotton plants at both full and half levels of synthetic fertilization [139].

The way a consortium is created can have a significant impact on food production and control of phytopathogens. For example, Berendsen et al. [136] studied the microbiota of *Arabidopsis* when it was infected with the phytopathogenic fungus *Hyaloperonospora arabidopsidis* and found that three bacterial genera were most abundant, including *Xanthomonas* spp., *Stenotrophomonas* spp., and *Microbacterium* spp. They observed that these bacteria interact synergistically in the formation of biofilms in vitro, and although these bacteria did not separately affect the plant to any significant extent, together, they induced systemic resistance against downy mildew and promoted plant growth. Thus, the strains in this bacterial consortium for controlling phytopathogens are clearly compatible.

## 6.2. Abiotic Stress

Abiotic stresses can inhibit a plant's development due to the oxidative damage by free radicals produced in their cells, which attack vital cellular components like DNA and cellular membranes [147]. Antioxidant enzymes, such as catalase and peroxidase, can neutralize these reactive molecules and protect the cells from damage [56]. Several species of bacteria have the ability to enhance the activity of these and other enzymes, as well as to produce protective substances, such as trehalose, which also helps to improve the response of plants to abiotic stress [12].

Heidari and Golpayegani [148] reported that *Ocimum basilicum* (basil) inoculated with a bacterial consortium (*Pseudomonas* sp., *Bacillus lentus*, and *Azospirillum brasilense*) displayed an increased level of chlorophyll content and antioxidant activity in plants under water stress conditions. Similarly, the effect of a consortium consisting of ten bacterial strains was investigated on commercial hardwood cuttings of *Populus deltoides*  $\times$  *P. nigra* clone OP-367. After one month under water stress conditions, there was substantial growth promotion with improved foliar physiology in response to bacterial endophytic colonization; furthermore, the inoculated plants showed reduced damage by reactive oxygen species [145].

On the other hand, plants colonized by specific bacterial strains under abiotic stress conditions increase the accumulation of abscisic acid and degradation of reactive oxygen species by the microbial production of auxins, gibberellins, cytokinins, and antioxidants [147]. In this regard, a field experiment was conducted to evaluate different carriers for a bacterial consortium (*Bacillus cereus* Y5, *Bacillus* sp. Y14, and *Bacillus subtilis* Y16) to

improve wheat production under salinity stress. The results revealed that the bacterial inoculation of multiple strains improved the photosynthetic rate, the content of carotenoids, protein levels, and the yield of the treated wheat crop [140].

PGPB typically enhance the level of the osmoprotectant proline in plants exposed to abiotic stresses. Proline scavenges reactive oxygen molecules and acts to stabilize proteins through molecular chaperones in the stressed cells [147]. Wang et al. [144] reported the effect of a consortium of three bacterial strains (*Bacillus cereus* AR156, *Bacillus subtilis* SM21, and *Serratia* sp. XY21) on drought tolerance in cucumber plants. After withholding watering for 13 days, consortium-treated cucumber plants had much darker green leaves and fewer wilt symptoms than control plants; in addition, the consortium inoculation increased the leaf proline and chlorophyll content and enhanced the superoxide dismutase (SOD) activity. These results indicated that the tested bacterial consortium conferred induced systemic tolerance to drought stress in cucumber plants by protecting the integrity of plant cells, maintaining photosynthetic efficiency and root vigor, and increasing some antioxidation activities, all of which led to increased drought tolerance.

Under abiotic stress conditions, increased ethylene levels in plants restrict root and shoot growth, but bacterial ACC deaminase can degrade excessive ACC produced by the plant and balance the total ACC content in plants, thereby enhancing plant growth [38,149,150]. For example, Saikia et al. [146] showed that the inoculation of a consortium of three ACC-deaminase-producing rhizobacteria (*Ochrobactrum pseudogrignonense* RJ12, *Pseudomonas* sp. RJ15, and *Bacillus subtilis* RJ46) significantly increased the seed germination percentage, root length, shoot length, and dry weight of the legumes *Vigna mungo* and *Pisum sativum* under drought stress.

## 7. Plant Growth Stimulation by Fungal–Bacterial Consortia

Plants can establish interactions with several soil-borne microorganisms. Those interactions can take place in the rhizosphere, inside the root cortex, or on the root surface (rhizoplane), and they can be beneficial, neutral, or harmful. The overall result of plant–microorganism interactions is determined by the development status of the plant, the soil structure and chemistry, and the microorganisms present at certain times. Such microorganisms are termed the microbiome. The plant microbiome is formed by many diverse organisms that respond to the conditions of the rhizosphere, which is influenced by the root exudates, and its diversity determines the outcome of the interaction with the plant, as well as the countless interactions that take place within this plant holobiont [151–153].

Plant-growth-promoting organisms, which are part of the plant microbiome, have been studied to find sustainable alternatives to the use of chemical fertilizers and pesticides. Among these organisms are PGPB, mycorrhizal fungi, and plant-beneficial fungi. The majority of studies include interactions between root- and/or rhizosphere-colonizing bacteria and root-colonizing fungi, pointing towards synergistic effects of these organisms on plants [154]. PGPB, arbuscular mycorrhizal fungi (AMF), and *Trichoderma* species are the most important components of the plant microbiome that are actively being studied; their interactions that improve plant health and fitness are discussed below.

### 7.1. Plant Growth Stimulation by AMF–PGPB Consortia

Arbuscular mycorrhizal fungi (AMF) are a monophyletic fungal lineage, Glomeromycota, that can establish a mutualistic relationship with the roots of most of the plants on the planet. This relationship is known as “the mycorrhizal symbiosis”. Once the AMF is established inside the root plant, it develops structures called arbuscules inside certain plant cells. The establishment of the AMF in the root cortex changes many aspects of the plant physiology, including the composition of root exudates, which can stimulate growth of other beneficial microbes and the AMF itself [154].

In this relationship, AMF receives carbon compounds from the plant and the plant receives multiple benefits in exchange, including improved acquisition of nutrients and water from the soil, facilitating mineral solubilization and uptake. AMF promotes increased

plant biomass and yield, as AMF promotes plant growth, improved plant fitness against several abiotic stresses, and defense against pathogens stimulating enzymatic activity, phytohormone synthesis, and lipid peroxidation [154,155].

As part of the plant microbiome, the interaction between PGPB and AMF is useful for increasing or potentiating the positive effects that each organism can exert on the plant. The consortia between AMF and PGPB have been of interest mainly due to the impact on plant growth promotion and defense against phytopathogens. For example, *B. subtilis* and AMF present in soil surrounding *Acacia gerrardii* (Acacia tree) resulted in a significant increase in shoot and root biomass, as well as in greater root depth, in the absence of abiotic stress conditions, with the combination of the two organisms being more effective than either by itself [156]. The co-inoculation of either *Pseudomonas* sp. or *Bacillus amyloliquefaciens* with the AMF *Rhizophagus irregularis* (formerly named *Glomus intrarradices*) on tomato plants increased root and shoot dry weight and reduced disease symptoms caused by the phytopathogen *Fusarium oxysporum* [157]. In soybean, the co-inoculation of rhizobia (*Bradyrhizobium* sp.) and AMF (*Glomus mosseae*) resulted in an increased resistance and expression of defense-related genes, such as PR2, PR4, and PR10, in the presence of the fungal pathogen *Cylindrocladium parasiticum* compared to the plants inoculated with either one of the microorganisms [158]. This suggests that, together, AMF and PGPB may provide a viable biocontrol strategy for some important crop plants (Figure 1).

The increase in plant growth promotion exhibited by a consortium of AMF and PGPB is due to the enhancement of the benefits that both organisms provide to a plant compared to the effects that each organism has alone [154,159]. For example, the combination of AMF and PGPB facilitates soil mineral solubilization, thus improving plant nutrient uptake (e.g., zinc, magnesium, iron, and phosphorus) and general development. Mineralization involves the breakdown of complex organic compounds into readily metabolizable forms by the plants, whose process is catalyzed by microbial phosphatases and phytases. The production of organic acids by bacteria is another mechanism that results in chelating mineral ions, along with lowering the pH of the rhizosphere to bring elements into the soil solution [14]. Thus, the concentration of magnesium, phosphorous, and zinc in tomato plants increased considerably with the co-inoculation by either *Pseudomonas* sp. or *B. amyloliquefaciens* with *R. irregularis* in comparison with plants inoculated with just one of these microorganisms [157]. Accumulation of nitrogen, phosphorous, and potassium is improved by dual inoculation of *Bacillus* sp. and *G. mosseae* in lettuce [160] and the AMF *Pelargonium graveolens* [161], yielding better results than either single inoculation. In addition, the combination of *R. irregularis* with *Sinorhizobium meliloti*, *Bacillus* sp., and *Streptomyces* sp. increased biomass and phosphate uptake in maize plants [162]. Thus, changes in nutrient availability in the rhizosphere can be caused by bacteria and AMF, and this availability of nutrients might also be a consequence of modulations in the rhizosphere-beneficial microbiota.

AMF and PGPB consortia also increase plant fitness under environmental stress conditions, thus promoting plant growth [163]. When drought stress is induced in lettuce, the co-inoculation of *G. mosseae* or *R. irregularis* with *Bacillus* sp. helped to ameliorate the effects of this stress by promoting plant growth and nutrient uptake [160]. Under salt stress, the plant *A. gerrardii* increased its biomass, improved nutrient uptake, including Na, P, K, Mg, Ca, and N, and increased the level of photosynthetic pigments and the enzymatic activity of nitrate/nitrite-reductase and nitrogenase enzymes when co-inoculated with *B. subtilis* and AMF, thus promoting overall plant growth and development [156].

The mechanisms that enable AMF–PGPB consortia to have a synergistic effect on the plant are complex, but one thing is clear: This synergistic effect depends on the nature of the microorganisms and the interaction that takes place among them [154,163,164]. When combinations of different species of AMF and/or PGPB have been tested in one plant species, the effect on plant growth promotion depends on the consortia [157,160,161], plant genotype [165], and soil nutrient composition [158,165,166]. Further, the presence of PGPB can enhance AMF mycorrhization and promote its root cortex colonization in the host,

helping AMF to increase its effects on the plant [156–158]. Meanwhile, the presence of AMF can induce nodule formation in roots, helping *Rhizobia* to establish the interaction with the plant, especially under stress conditions [156]. This means that to find suitable AMF–PGPB consortia, those factors need to be taken into consideration so that the use of plant-growth-promoting microorganisms may have a positive effect by creating a beneficial rhizosphere.

### 7.2. Plant Growth Stimulation by *Trichoderma*–PGPB Consortia

Fungi belonging to the genus *Trichoderma* are soil-borne filamentous ascomycetes that can be found in a wide variety of ecosystems, ranging from forests, grasslands, and deserts to agricultural soils and decaying wood [167]. Moreover, they are effective plant root colonizers and are present in the rhizosphere [168,169]. As part of the plant microbiome, *Trichoderma* spp. can promote plant growth and development by various mechanisms that have been widely studied and are of interest due to their use in agriculture as an effective biocontrol agent [170]. The *Trichoderma*–plant interaction begins with the perception of plant root exudates that mediate fungal recognition of the host, and then, contact and root penetration and colonization are initiated [168,171].

*Trichoderma* have been used as biocontrol agents due to their abilities as effective mycoparasites of several phytopathogens and their ability to induce plants' defense systems and priming [168]. The fungal pathogen biocontrol activity of *Trichoderma* is a consequence of competing with the pathogen for nutrients and space, altering the environmental conditions, and promoting inherent plant defensive mechanisms, as well as by the *Trichoderma* parasitizing the fungal pathogen. *Trichoderma* has also been used as a biostimulant because it can promote plant growth and development through its synthesis of phytohormone-like molecules and volatile organic compounds, thus improving soil mineral solubilization, nutrient uptake, and translocation, increasing root system development [168,172,173], and enhancing plant tolerance to both biotic and abiotic stresses.

On their own, PGPB and *Trichoderma* spp. can be effective biocontrol agents and plant-growth-promoting microorganisms. However, combinations of different *Trichoderma* species with PGPB have been shown to be more effective than a single microorganism (Figure 1). For example, co-inoculation of *T. harzianum* and *Serratia proteamaculans* had a positive effect on tomato growth, increasing total biomass [174]. In addition, for co-inoculation of *T. harzianum* with different PGPB strains on *Mentha arvensis* (mint) plants, in particular, the strain *Brevibacterium halotolerans* showed a good synergistic effect with *T. harzianum* when measuring plant biomass in field experiments compared to single inoculation [58].

Yield production and pathogen resistance are important traits to consider in biocontrol and plant-growth-promoting agents. A consortium consisting of *B. subtilis* and *T. harzianum* increased potato yield and conferred resistance against potato common scab induced by *Streptomyces* spp. [175]. Co-cultivation of *T. atroviride* and *B. amyloliquefaciens* promoted maize and wheat growth, germination, and vigor, and induced resistance against *F. graminearum* [176]. In addition, the co-inoculation of *Bradyrhizobium* sp. and *Trichoderma* spp. had positive effects on total shoot and root dry weight of cowpea plants, and it protected the plants against *Rhizoctonia solani* infection, especially when the initial co-inoculation was followed by a re-inoculation of *Trichoderma* 15 days later [177].

The effect shown by the consortia in conferring plant resistance against different pathogens may be due to the increase in plant defense systems. Accumulation of reactive oxygen species (ROS) is one sign of plant pathogen invasion; plant defense system mechanisms include expression of ROS-related enzymes, such as catalases and superoxide dismutase [178]. The co-inoculation of *T. harzianum* and *S. proteamaculans* has also proven to be effective at activating the enzymatic activity of superoxide dismutases and catalases in tomato plants in response to *R. solani* infection [174]. The combination of *T. harzianum* Tr6 and *Pseudomonas* Ps14 enhanced systemic resistance in cucumber and Arabidopsis when the plants were challenged with the phytopathogens *F. oxysporum* and *Botrytis cinerea*, respectively, compared to single inoculations [179].

As mentioned previously, the beneficial effects of the consortia on plant health and fitness are the results of the interactions between the microorganisms. When *Trichoderma* spp. are inoculated with different strains of *Pseudomonas* spp. [179] or other PGPB (e.g., *B. subtilis*, *B. flexus*, *Stenotrophomonas* spp., *B. halotolerans*) [180], not all the combinations show an increased beneficial effect compared to single inoculations, meaning that the interaction with the plant is dependent on the nature of the consortium and on the amount of inoculum applied [175]. Moreover, the presence of PGPB improves *T. harzianum* mycelia density, favoring root colonization [180]. Nevertheless, some strains of *T. harzianum* showed no increase in mycelium density in the presence of *Pseudomonas* sp., although none showed a negative effect [179].

*T. harzianum* can change bacterial and fungal diversity in the maize rhizosphere, which results in plant growth promotion and protection against the phytopathogen *F. graminearum* [181]. Moreover, inoculation of *T. virens* or *T. harzianum* had a positive influence on the diversity of prokaryotes and eukaryotes in the lettuce rhizosphere, increasing plant productivity and N uptake [172]. As effective as *Trichoderma* spp. or PGPB are in promoting plant growth and defense, studies point toward a synergistic interaction of this consortium by combining and potentiating their benefits on plants in order to establish a positive interaction with their hosts.

The combination of PGPB, mycorrhizal fungi, and biocontrol agents like *Trichoderma* spp. provides a strategy that should be commercially exploited in order to endow plants with a complete “benefits package”: increases in plant biomass and yield production, resistance to abiotic stresses, biocontrol of phytopathogens, and better nutrient uptake.

## 8. Conclusions and Perspectives

In any natural or agricultural ecosystem, plants are found to interact with soil microorganisms [182,183]. The vast majority of these interactions, whether pathogenic, neutral, or beneficial, occur through a complex network of signals, which include metabolites, volatile and non-volatile compounds [184], physical interactions, and interactions that regulate gene expression, either by increasing or repressing it [184,185]. It is essential to take advantage of this intricate network of natural interactions to engineer artificial microbial consortia that substantially and consistently benefit plant growth and health, increase crop production, and decrease the use of chemical fertilizers.

Recently, Berg et al. [186] proposed revisiting and redefining the concept of the plant (and human) microbiome, taking into account the associated microbiota and the “theater of activity” that involves the production of proteins, lipopolysaccharides, metabolites, and compounds as environmental factors. This is in agreement with our proposal of using a microbial consortium as part of the plant microbiome that interacts synergistically to promote plant growth and health through the production of metabolites with antibiotic activity and by solubilizing nutrients and making them available to the plant, forming nodules to fix nitrogen, and producing plant-growth-stimulating phytohormones or enzymes that degrade ethylene precursors, such as ACC deaminase [12]. The directed use of microbial consortia will facilitate the production of plants in a more sustainable way that, eventually, will not depend on agrochemicals.

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