



Review

Microbial Allies in Agriculture: Harnessing Plant Growth-Promoting Microorganisms as Guardians against Biotic and Abiotic Stresses

Islam I. Teiba ^{1,*} , Emad H. El-Bilawy ² , Nabil I. Elsheery ¹ and Anshu Rastogi ^{3,*} ¹ Faculty of Agriculture, Tanta University, Tanta 31527, Egypt; nshery@yahoo.com² Faculty of Basic Science, King Salman International University, South Sinai 46612, Egypt; emad.elbilawy@ksiu.edu.eg³ Laboratory of Bioclimatology, Department of Ecology and Environmental Protection, Poznań University of Life Sciences, Piątkowska 94, 60-649 Poznań, Poland

* Correspondence: islam.tayba@agr.tanta.edu.eg (I.I.T.); anshu.rastogi@up.poznan.pl (A.R.)

Abstract: Plants face many biological and non-biological challenges throughout their life cycle, from seed to harvest. These challenges have recently increased due to climate changes. Strategies for confronting different types of stresses depend on the type of stress, the cultivated plant, climatic conditions, soil characteristics, water variables, cost, and management system. Chemical methods (fertilizers and pesticides) have been widely used to manage abiotic and biotic stresses, but they raise concerns about environmental contamination, toxic residues, and the development of resistant pathogens. Eco-friendly strategies have recently become one of the most important approaches to obtaining high-quality and quantitative plant-based products. Microbial inoculants, such as plant growth-promoting microorganisms (PGPM), offer a sustainable alternative to chemical methods. PGPM can augment plant growth and nutrition, improve plant tolerance to abiotic stresses, and reduce the growth of certain pathogens. They employ a variety of mechanisms to alleviate stressors and boost plant resilience, including nutrient assimilation, production of metabolites, and activation of systemic resistance. This review aims to elucidate the impact of PGPM, with a particular focus on plant growth-promoting bacteria (PGPB), and their mechanisms of action on plants under varying stressors, while also identifying areas for further research in both PGPB and other non-bacterial organisms.

Keywords: PGPB; abiotic stress; biotic stress; plant growth; sustainable agriculture



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1. Introduction

Agriculture today is confronted with a wide range of challenges, including soil erosion, biodiversity loss, climate change, and plant diseases. These problems have significantly impacted agricultural processes and reduced global food supplies. In recent years, human activities have caused global climate change, which threatens natural ecosystems with temperature changes, high atmospheric carbon dioxide levels, and altered rainfall patterns [1]. Climate change negatively affects plant growth by exposing plants to abiotic and biotic stresses that reduce growth, disrupt photosynthesis, and impair physiological responses [2,3].

Drought, a type of abiotic stress, poses a serious environment threat due to water scarcity and increased evaporation [4]. Drought is predicted to become more critical in the coming years [5,6], and it is considered one of the most serious challenges to sustainable agriculture due to its morphological, physiological, and molecular impacts on plants [7,8]. Drought can affect plant height, root diameter, number of leaves, and early seed germination [9,10]. It can also affect plant interactions with other pathogens [11]. Drought can lead to decreased pigment content and poor transpiration, which can ultimately result in plant death [12].

Plant disease may result by biotic stress that can have a significant impact on crop yields and global food security [13]. Biotic stresses are triggered by living organisms, such as fungi, bacteria, viruses, and nematodes. Plant diseases can be caused by a single pathogen or a combination of pathogens [14]. Pathogens can invade plants through wounds, natural openings, or by directly penetrating the plant cell wall [15]. Once inside the plant, pathogens can multiply and damage the plant's tissues. This damage can disrupt the plant's ability to photosynthesize, transport water and nutrients, and reproduce.

Abiotic and biotic stresses can be managed through a variety of approaches, including cultural practices, biological control, and chemical control [16]. In response to the need to increase plant productivity and resilience in the face of diverse stressors, chemical methods (fertilizers and pesticides) have become the most widely used [17]. However, the increased use of these chemicals has raised many concerns, including environmental contamination, toxic residues, and the development of resistant pathogens [18]. Therefore, it is essential to design sustainable production techniques in which natural and renewable resources are prioritized over artificial inputs as they offer numerous advantages over conventional methods [19].

Microbial inoculants are one of the most effective natural instruments to increase plant yield under various conditions and stressors (drought, salinity, heavy metal contamination, infections). Microbial inoculants are defined as microorganisms (bacteria, fungi, and other microorganisms) that are delivered to an environment to perform a specific function, such as biocontrol or boosting plant growth [20]. Interactions between plants and microorganisms take place on a range of scales and most plant organs interact with microorganisms at some point throughout their growth, and sometimes this interaction is beneficial to the plant [21].

Plant growth-promoting microorganisms (PGPM) are a diverse group of microorganisms that can enhance plant growth and nutrition, improve plant tolerance to abiotic stresses such as drought, salinity, and heavy metal pollution, and reduce the growth of certain pathogens [22–25]. PGPM employs a variety of mechanisms to alleviate stressors and boost plant resilience, including: (I) Nutrient assimilation: PGPM can help plants to assimilate essential nutrients such as phosphorus (P), zinc (Zn), iron (Fe), potassium (K), and nitrogen (N) [26]. (II) Production of metabolites: PGPM can produce a variety of secondary metabolites, including exopolysaccharides (EPS), osmoprotectants, antioxidants, phytohormones, osmolytes, ACC deaminase, and phenolic and volatile compounds [26]. This review aims to elucidate the impact of PGPM, with a particular focus on plant growth-promoting bacteria (PGPB), and their mechanisms of action on plants under varying stressors, while also identifying areas for further research in both PGPB and other non-bacterial organisms.

2. Extracellular Polymeric Substance (EPS)

Extracellular polymeric substances (EPS), an assortment of high molecular weight substances freed by microorganisms as slime, bind to the soil by Van der Waals forces, anion adsorption, cation bridges, and hydrogen bonds [27]. EPS produced by the bacteria *Pseudomonas entomophila* PE3 decreases the buildup of sodium ions and improves the flocculating and emulsifying qualities of soil under saline conditions [28]. It also acts as an antioxidant [28]. The composition of EPS changes in saline environments, with an increase in proteins, carbohydrates, and phenolic compounds with increasing salt concentrations. The EPS functional groups can attach to sodium molecules and absorb nutrients, which promotes sunflower plant growth and increases salt tolerance [28]. Vardharajula and Sk [29] reported that EPS increases the soil's moisture retention capacity. Using *Bacillus* spp. under drought stress can improve soil structure [29]. EPS production increases in *Bacillus amyloliquefaciens* strain HYD-B17, *B. licheniformis* strain HYTAPB18, and *B. subtilis* strain RMPB44 with increasing drought stress. The sugar percentage of the EPS changes under drought conditions, with glucose being the main sugar in both *B. licheniformis* strain HYTAPB18 and *B. subtilis* strain RMPB44, while raffinose is the main sugar in *B. subtilis* strain RMPB44. Tables 1 and 2 illustrate the impacts of EPS on plant performance under abiotic and biotic stresses.

Table 1. Extracellular polymeric substance (EPS) sources and their impacts on the plant performances under abiotic stress.

EPS Microbial Source	Plant	Impacts	
<i>Serratia marcescens</i> (RRN II 2) <i>Pseudomonas</i> sp. (RRC I 5)	<i>Triticum aestivum</i>	(+) Synthesis of different hydrolytic enzymes. (+) Zinc and phosphate solubilization. (+) Phosphate solubilization.	[30]
<i>Bacillus velezensis</i> strain D ₃	<i>Zea mays</i>	(+) Siderophores production. (+) Root colonization. (+) Phytohormones (IAA, GA, and ABA.). (+) Germination.	[31]
<i>Bacillus subtilis</i> <i>Azospirillum brasilense</i>	<i>Triticum aestivum</i>	(+) Leaf area and root/shoot length. (+) Chlorophyll, osmotic potential, and water potential. (+) SOD, CAT, and POD.	[32]
<i>Pseudomonas fluorescens</i> <i>Enterobacter hormaechei</i> <i>Pseudomonas migulae</i>	Foxtail millet	(+) Germination (↑) Soil structure (↑) Colonization (↑) Soil structure.	[33]
<i>Pseudomonas</i> strain GAP-P45	<i>Helianthus annuus</i> L.	(↑) Colonization. (+) Plant biomass. (−) Soil water loss.	[34]
<i>Kosakonia cowanii</i> GG1 <i>Proteus penneri</i> (Pp1) <i>Pseudomonas aeruginosa</i> (Pa2) <i>Alcaligenes faecalis</i> (Af3) <i>Planomicrobium chinense</i>	<i>Arabidopsis thaliana</i> <i>Zea mays</i>	(−) Soil water loss. (+) Biomass (Leaf area and root/shoot length). (+) Osmotic and water potential. (↑) Antioxidants.	[35]
<i>Bacillus cereus</i> <i>Pseudomonas fluorescens</i> .	<i>Triticum aestivum</i>	(+) Biomass (Leaf area and root/shoot length). (↑) Soil structure (−) Soil water loss.	[36]
<i>Acinetobacter</i> sp. <i>Pseudomonas</i> sp. <i>Rhizobium phaseoli</i> (MR-2)	<i>Capsicum</i> Sp.	(+) Biomass (Leaf area and root/shoot length). (↑) Photosynthetic activity. (+) Phytohormones (IAA).	[37]
<i>Rhizobium leguminosarum</i> (LR-30) <i>Mesorhizobium ciceri</i> (CR-30 and CR-39)	<i>Triticum aestivum</i>	(+) Biomass (Leaf area and root/shoot length). (↑) Soil structure. (↑) Colonization.	[38]

(+) = increase; (−) = decrease; (↑) = improve or stimulate.

Table 2. Extracellular polymeric substance (EPS) sources and their impacts on the plant performances under biotic stress.

Microorganism	Antagonistic Microorganism	Host Plant	Ref.
<i>Burkholderia gladioli</i> IN26	<i>Colletotrichum orbiculare</i>	<i>Cucumis sativus</i>	[40]
<i>Pseudomonas aeruginosa</i> pf 23	<i>Macrophomina phaseolina</i> <i>Bipolaris oryzae</i> NPT0508	<i>Helianthus annuus</i>	[41]
<i>Rhodopseudomonas palustris</i> KTSSR54	<i>Curvularia lunata</i> SPB0627 <i>Magnaporthe oryzae</i> PTRC63	<i>Oryza sativa</i>	[42]
<i>Bradyrhizobium</i> sp. IC-4059	<i>Fusarium udum</i>	<i>Cajanus cajan</i>	[43]

3. Antioxidant Activity

Antioxidants are essential compounds for plant growth that enhance the plant's immune system against biotic and abiotic stresses. They are divided into enzymatic antioxidants (e.g., guaiacol peroxidase, superoxide dismutase (SOD), ascorbate peroxidase (APX), mono dehydro-ascorbate reductase, ascorbate dehydrogenase, glutathione reductase) and non-enzymatic antioxidants (e.g., glutathione, carotenoids, tocopherols, flavonoids) [44–47]. Plants play a delicate dance with reactive oxygen species (ROS), highly reactive molecules like superoxide, hydrogen peroxide, and hydroxyl radicals generated as byproducts of their normal metabolism [48,49]. These molecules, though seemingly destructive, wield a double-edged sword. At controlled levels, ROS act as potent signalers, orchestrating growth, development, stress responses, and even programmed cell death in specific cells [50]. They collaborate with plant hormones like auxin and abscisic acid, fine-tuning their influence

on development and stress resilience [51]. During times of stress, ROS can even break down complex molecules like cell walls, releasing vital nutrients for reuse [52]. However, unbridled ROS can unleash havoc. Elevated levels become harbingers of stress, wreaking havoc on lipids, proteins, and nucleic acids [49] and triggering cell death, premature aging, and ultimately, plant demise [53]. Recognizing this duality is fundamental to optimizing plant health, stress tolerance, and productivity. By subtly influencing ROS production and scavenging mechanisms, scientists hold the potential to bolster plant resilience against environmental challenges and unlock higher crop yields. Antioxidants regulate high levels of reactive oxygen species (ROS), which are potential indicators of plant stress [54].

PGPM associations can boost enzymatic and non-enzymatic antioxidant pathways in Neotropical plants under drought, reducing oxidative damage and increasing drought tolerance [55]. PGPM can evoke different responses in plants to oxidative stress (Table 3). For example, in *Juglans regia*, *Azospirillum lipoferum* intensified secondary metabolites and peroxidase enzyme vigor [56], while *Bacillus* species can promote proline accumulation and decrease glutathione reductase activity in *Megathyrsus maximus* [57]. Mekureyaw et al. [58] noticed that *Pseudomonas fluorescens* G20-18-inoculated plants had higher SOD, POX, and CAT levels, as well as a higher anthocyanin content, than non-inoculated plants under water deficiency. Tables 3 and 4 show models of antioxidant activities studies of PGPM under abiotic and biotic stresses.

Table 3. Models of antioxidant activities studies of PGPM under abiotic stress.

Microorganism	Plants	Mode of Action	Ref.
<i>Pseudomonas</i> sp. <i>Pantoea</i> sp.	<i>Hordeum vulgare</i>	(−) CAT, SOD. (+) APX, GPX.	[59]
<i>Bacillus amyloliquefaciens</i> MMR04	<i>Pennisetum glaucum</i>	(−) MDA. (+) Proline, APX, SOD.	[60]
<i>Pseudomonas</i> spp.	<i>Zea mays</i>	(−) APX, CAT, GPX. (+) Proline content.	[61]
<i>Enterobacter cloacae</i>	<i>Zea mays</i>	(+) Proline content. (+) POD, SOD, CAT.	[62]
<i>Bacillus safensis</i> <i>Ochrobactrum pseudogregnonense</i>	<i>Triticum aestivum</i>	(+) Carotenoids. (+) Ascorbate peroxidase. (+) CAT, SOD	[63]
<i>Herbaspirillum seropedicae</i> <i>Pseudomonas fluorescence</i> P2 <i>P. jessenii</i> R62 <i>P. synxantha</i> R81	<i>Saccharum officinarum</i>	(+) CAT, SOD, APX.	[64]
<i>Bacillus cereus</i> BSB 38 (14B) <i>Arthrobacter nitroguajacolicus</i> strain (YB3 and YB5)	<i>Oryza sativa</i> L.	(+) Proline content. (+) Ascorbate peroxidase. (+) CAT.	[65]
<i>Providencia</i> sp. (TCR05) <i>Providencia</i> sp. (TCR20)	<i>Zea mays</i>	(−) Hydrogen peroxide and MDA. (−) Lipid peroxidation and SOD. (−) Internal CO ₂ concentration. (−) Non-photochemical quenching. (↑) Photosynthetic activity.	[66]
<i>Bacillus pumilus</i> (G5) + Silicon	<i>Glycyrrhiza uralensis</i> <i>Fisch</i>	(↑) Phenolics and Relative water content. (+) AsA, GSH, SOD, CAT, APX, GPX, GR. (+) GPX, AO, GST gene expression.	[67]
<i>Bacillus amyloliquefaciens</i> 5113 <i>Azospirillum brasilense</i> NO40 <i>Bacillus</i> sp. MN-54	<i>Triticum aestivum</i>	(−) APX, DHAR, MDHAR, GR enzymes activities.	[68]
<i>Enterobacter</i> sp. FD-17 <i>Pseudomonas fluorescens</i>	<i>Zea mays</i>	(+) CAT, SOD, GPX.	[69]

(+) = increase; (−) = decrease; (↑) = improve or stimulate.

Table 4. Models of antioxidant activities studies of PGPM under biotic stress.

Microorganism	Antagonistic Microorganism	Plant	Ref.
<i>Bacillus</i> spp. KFP-5, KFP-7, KFP-17	<i>Pyricularia oryzae</i>	<i>Oryza sativa</i>	[70]
<i>Pichia membranaefaciens</i> <i>Cryptococcus laurentii</i> <i>Candida guilliermondii</i> <i>Rhodotorula glutinis</i>	<i>Monilinia fructicola</i>	<i>Prunus persica</i>	[71]
<i>Bacillus amyloliquefaciens</i> SQR-9	<i>Ralstonia solanacearum</i>	<i>Solanum lycopersicum</i>	[72]
<i>Bacillus amyloliquefaciens</i> subsp. <i>plantarum</i>	<i>Rhizoctonia solani</i>	<i>Brassica pekinensis</i>	[73]
<i>Saccharomyces cerevisiae</i> . <i>Bacillus pumilus</i> .	<i>Sclerotinia sclerotiorum</i>	<i>Allium sativum</i>	[71]
<i>Pseudomonas fluorescens</i> PDS1 <i>Bacillus subtilis</i> KA9	<i>Ralstonia solanacearum</i>	<i>Capsicum frutescens</i>	[74]

4. Phytohormones

Phytohormones, also known as plant hormones, are signaling molecules that regulate a wide range of physiological processes in plants, including flowering and fruit ripening [75]. Gibberellins, ethylene, auxins, cytokinins, and abscisic acid are some of the most important phytohormones. Phytohormones mediate plant responses to biotic and abiotic stresses [76,77]. PGPM employ a variety of techniques to produce and deliver phytohormones to plants (Tables 5 and 6).

4.1. Gibberellins (GAs)

PGPM can synthesize several phytohormones, including gibberellins (GAs), which promote cell division, tissue development, and increased plant resistance to various stressors [78]. Gibberellins are plant hormones that regulate diverse physiological processes including seed germination, seedling growth, stem elongation, flowering, and fruiting [78]. GAs also play a role in plant defense against stressors [79]. One of the key mechanisms by which GAs enhance biotic and abiotic stress resistance is by regulating the generation of secondary metabolites [80]. Many secondary metabolites have antimicrobial and antifungal properties, and they can help to deter herbivores [81]. GAs can improve the production of secondary metabolites in plants, which can make them more resistant to stress. Another process by which GAs enhance stress resistance is by regulating the plant's immune system. GAs can increase the assembly of defense enzymes, e.g., peroxidase and chitinase, which can help to break down the cell walls of pathogens [82]. GAs can trigger the controlled production of ROS around invading pathogens. These "controlled ROS" act as signaling molecules, alerting the plant to the attack and triggering various defense mechanisms [83]. For example, inoculating maize roots with GA-producing *Azospirillum* strains has been shown to raise plant growth [84]. In plants infected with *Azotobacter vinelandii* under saline conditions, endogenous levels of GAs (GA3) were increased, resulting in significantly higher root and shoot fresh biomass in rice [85]. Similarly, *Pseudomonas fluorescens* can enhance plant growth in maize by increasing GAs under drought stress [86]. GAs promote root elongation, increasing root length, surface area, and number, which improves nutrient uptake and helps plants cope with stress [87]. Overall, PGPM-GAs play a substantial role in biotic stress resistance in plants. They can enhance plant resistance to biotic stress by regulating the production of secondary metabolites and by regulating the plant's immune system.

4.2. Cytokinin

Cytokinins (CKs) are a group of plant hormones that are essential for plant stress tolerance. They regulate a wide range of biological processes, including cell division, cell differentiation, organ development, and senescence [82]. CKs also function in plant defense against both abiotic and biotic stresses. One of the key processes by which CKs enhance plant stress resistance is by regulating the production of stress-responsive genes [88]. CKs

can upregulate the expression of genes encoding for proteins involved in cell protection, osmoregulation, and detoxification [89]. Another mechanism by which CKs develop plant stress resistance is by regulating the plant's water balance [90]. CKs can increase the production of abscisic acid (ABA), which is a hormone that plays a role in water conservation. ABA can also promote the closure of stomata, which helps to reduce water loss [91]. CKs also play a role in plant defense against pathogens and pests by increasing the efficacy of defense enzymes, such as peroxidase and chitinase, which can help to break down the cell walls of pathogens. CKs can induce the controlled production of ROS around invading pathogens. These "controlled ROS" act as signaling molecules, alerting the plant to the attack and triggering various defense mechanisms [92]. Invisible armies of microbes wield not swords, but cytokinin, a plant hormone with superpowers against stress. Take *Azospirillum*, a nitrogen-fixing bacterium, it infuses corn shoots with this wonder molecule, boosting photosynthetic efficiency and delaying leaf senescence under drought [93]. *Bacillus amyloliquefaciens* H-2-5 and *Bacillus oryzicola* YC7007, other champions, unleash cytokinin alongside antioxidants, shielding soybean and rice roots from salt's fiery wrath [94,95]. Even single-celled fungi like *Trichoderma* join the fight, their cytokinin arsenal stimulating root growth and nutrient uptake, helping plants weather the storm of flooding and pathogens [96,97]. These microbial cytokinin factories are nature's secret weapon, empowering plants to withstand the heat, the drought, and the flood, whispering resilience with every molecule they share. Overall, PGPM-CKs are important for plants' stress resistance. They help plants resist stress by regulating genes that respond to stress, controlling the plant's water balance, and boosting the plant's immune system.

4.3. Auxins

Auxins are a group of plant hormones that are essential for plant stress tolerance. They regulate a wide range of functional processes, including cell division, cell elongation, root development, and apical dominance [93]. Auxins also play a role in plant defense against abiotic and biotic stresses. One of the key mechanisms by which auxins boost plant stress resistance is by regulating the production of stress-responsive genes. Auxins can upregulate the expression of genes encoding for proteins involved in cell protection, osmoregulation, and detoxification [82]. Another mechanism by which auxins enhance plant stress resistance is by regulating the plant's water balance. Auxins can promote the development of a deep root system, which helps the plant access water from deeper soil layers. Auxins can also promote the closure of stomata, which helps to reduce water loss [98]. Auxins also play a role in plant defense against pathogens and pests by increasing the production of ROS, which are signaling molecules that play a role in plant immunity [99].

Indole-3-acetic acid (IAA) is the most prevalent auxin in nature, stimulating plant development [93]. Nearly 80% of microorganisms in the rhizosphere are thought to produce and release auxin [100]. *Microbacterium*, *Rhizobium*, *Mycobacterium*, and *Sphingomonas* strains are the most active IAA producers [101]. PGPM may support plants by providing them with IAA, which enhances plant development and reduces the effects of abiotic stressors, even in the presence of inhibitory substances [102]. PGPM-infected plants with increased IAA and ACC deaminase under drought conditions demonstrated improved plant growth and reduced cell damage [103]. Auxin indirectly decreases the effects of drought stress by promoting root development, altering root architecture, and/or increasing root hairs, which favor water and nutrient intake from the soil [104,105].

Wheat plants treated with *Bacillus amyloliquefaciens* S-134 produce the auxins indole-3-acetic acid (IAA), indole-3-lactic acid (ILA), and indole-3-carboxylic acid (ICA). These auxins induced root development in wheat, which assisted plants in surviving water stress. Similar to this, the morphological changes in the coleoptile xylem architecture brought about by *Azospirillum* inoculation in wheat seedlings helped them deal with osmotic stress [106]. Burono et al. [107] showed that *Bacillus cereus* TCR17 may enhance indole acetic acid (IAA) synthesis, which has a favorable impact on *Sorghum bicolor*. In tomato (*Solanum Lycopersicum* L.) and pepper (*Capsicum annum* L.) plants, *Microbacterium* sp. 3J1

may induce IAA, GA, and SA generation and promote ACC activity, which increases plant biomass [108]. A number of stress-related genes, including RAB18, RD22, RD29A, RD29B, DREB2A, and DREB2B, as well as ROS-detoxifying enzymes, such as catalase, superoxide dismutase, peroxidase, and glutathione reductase, were also upregulated as a result of the increased endogenous auxin level and exogenous auxin application. In addition, the root architecture, particularly the number of lateral roots, was improved in response to the plants' elevated auxin levels. As a result, auxin was discovered to favorably affect the plant's response to drought stress [109]. Overall, PGPM-auxins are key players in plant stress resistance. They help plants weather stress by regulating stress-responsive genes, managing the plant's water balance, and boosting the plant's immune system.

4.4. Abscisic Acid

Abscisic acid (ABA) is a phytohormone that plays a vital role in plant stress responses. It is synthesized in the roots, leaves, and other parts of the plant, and can be moved to other parts of the plant as needed. ABA has a wide range of effects on plant growth and development, including regulating stomatal closure, seed dormancy, and abscission. Under stressful circumstances, ABA levels increase in the plant. This leads to many physiological changes that help the plant cope with stress. For example, ABA can cause stomatal closure, which reduces water loss from the plant [110]. It can also induce seed dormancy, which helps the plant to survive periods of drought or other unfavorable conditions. Additionally, ABA can promote abscission, which is the shedding of leaves and flowers [111]. This can help to reduce the plant's surface area and thus reduce water loss and other stresses. ABA is also immersed in the regulation of plant gene expression. Under stress conditions, ABA can induce the expression of a number of genes that encode proteins that help the plant handle the stress [112]. For example, ABA can induce the expression of genes that encode proteins that defend the plant from oxidative damage. Abscisic acid (ABA) levels rise in plants under salinity stress, which helps to reduce the effects of stress. ABA promotes the assemblage of compatible solutes in root vacuoles, such as proline, sugars, potassium, and calcium ions, to counteract the consequences of excessive salinity [113]. Wang et al. [112] observed that the *nced1* gene, which is associated with ABA biosynthesis, was upregulated and ABA levels were higher in tomato plants inoculated with *B. amyloliquefaciens* under water stress than in non-inoculated plants. The STM196 strain of *Phyllobacterium brassicacearum* increased ABA content in Arabidopsis plants, which may have led to decreased leaf transpiration, thereby improving the plants' resistance to osmotic stress [114]. Cohen et al. [115] reported that *Azospirillum brasilense* Sp 245 produced more ABA per ml of culture under salt stress than in chemically defined media without salt stress. The ABA content of *Arabidopsis thaliana* was doubled after inoculation with *A. brasilense* Sp 245. *Pseudomonas* sp. increased the production of ABA, exopolysaccharide, gibberellic acid, and ACC-deaminase in Arabidopsis plants, which are all necessary for rhizobacteria to thrive under stressful conditions [116]. ABA maintains the balance of other hormones, such as ethylene, in *Zea mays*, which helps to preserve shoot and root development [104]. Similarly, ABA modifies the root system to improve the plant's capacity for nutrient and water absorption under stress conditions. Overall, ABA is a key player in plant stress responses. It helps the plant to cope with stress by adjusting stomatal closure, seed dormancy, abscission, and gene expression.

4.5. Salicylic Acid

Salicylic acid (SA) is a phenolic plant hormone essential for stress resistance by regulating antioxidant enzyme activity [104]. SA plays a key role in various physiological and biochemical processes, including plant growth, thermogenesis, flower induction, and ion uptake, acting as a growth regulator [117]. Salicylic acid (SA) was identified as the predominant phytohormone in the shoots of sunflower seedlings subjected to abiotic stress, particularly when inoculated with bacterial strains *Achromobacter xylosoxidans* (SF2) and *Bacillus pumilus* (SF3 and SF4) [118]. Ying et al. [119] reported that SA-treated bayberry

plants had higher photosynthetic rates, relative water content (RWC), CAT and SOD activity, and proline levels than untreated plants. SA mitigated oxidative stress caused by dehydration by reducing several oxidative stress indicators, such as lipid peroxidation and electrolyte leakage, indicating that SA can partially protect membrane integrity. *Bacillus subtilis* 10-4 increased the levels of endogenous SA in two types of wheat, Ekada70 (E70) and Salavat Yulaev (SY), especially in cv. E70. *B. subtilis* 10-4 also decreased the accumulation of endogenous SA caused by dehydration, which was linked to the outcome of endophytes on growth, suggesting that endogenous SA may have contributed to the effects of *B. subtilis* in both cultivars [120].

4.6. Ethylene

Ethylene is a gaseous plant hormone that plays a key role in plant growth and development, as well as in plant responses to stress [121]. Ethylene production is increased in response to a variety of abiotic stresses, including drought, salinity, heat stress, and cold stress [122]. Ethylene plays a role in plant stress tolerance by controlling a variety of physiological and molecular processes, including stomatal closure, root growth, senescence, and adjusts the expression of a variety of stress-responsive genes [123]. In addition to its role in abiotic stress tolerance, ethylene also plays a role in plant resistance to biotic stresses, such as insect pests and diseases. Ethylene can induce the production of defense compounds, such as phytoalexins and volatile organic molecules, which can help to deter pests and pathogens [124].

ACC (1-aminocyclopropane-1-carboxylic acid) deaminase is an enzyme produced by bacteria that can cleave ACC, a precursor of ethylene, into α -ketobutyrate and ammonia [125]. This activity reduces ethylene levels in plants, which can raise plant growth and development [126]. In Trigonella plants, the rhizobacteria *Bacillus subtilis* (LDR2), *Ensifer meliloti* (Em), and *Rhizophagus irregularis* (Ri) have been shown to improve plant growth and tolerance to water stress [127]. LDR2 is particularly effective at reducing ethylene levels in plants, which helps to mitigate the adverse effects of ethylene on plant growth and development under water stress conditions. LDR2 also promotes the development of nodulation and arbuscular mycorrhizal fungi colonization, which improves plant nutrient uptake [127]. Saleem et al. [128] also found that inoculation of plants with ACC deaminase-producing *Enterobacter* sp. and *Bacillus* sp. strains improved plant resistance to water stress. Overall, ACC deaminase-producing PGPM is an encouraging tool for improving plant stress tolerance. By reducing ethylene levels and promoting plant growth and development, ACC deaminase-producing PGPM can help plants to withstand a variety of abiotic stresses.

Table 5. PGPM phytohormones impact under abiotic stress.

Microorganism	Plants	Mode of Action	Ref.
<i>Bacillus</i> sp. (12D6)	<i>Triticum aestivum</i>	(+) Salicylic acid (SA).	[129]
<i>Enterobacter</i> sp. (16i)	<i>Zea mays</i>	(+) Indole-3-acetic acid (IAA).	
<i>Rhizobium japonicum</i>	<i>Glycine max</i>	(+) Cytokinin, gibberellin, auxin.	[130]
<i>Azotobacter chroococcum</i>		(-) Abscisic acid.	
<i>Azospirillum brasilense</i>			
<i>Achromobacter xylosoxidans</i>	<i>Helianthus annuus</i> L.	(+) Antibiotic substances (SA and JA)	[131]
<i>Bacillus pumilus</i>			
<i>Pseudomonas aeruginosa</i>	<i>Cajanus cajan</i>	(+) Indole-3-acetic acid (IAA).	[132]
<i>Bacillus megaterium</i> .		(+) Gibberellic acid.	
<i>Pseudomonas chlororaphis</i> subsp. <i>aureofaciens</i>	<i>Solanum lycopersicum</i>	(+) Indole-3-acetic acid (IAA).	[133]
		(+) Abscisic acid (ABA).	
		(+) Indole-3-acetic acid (IAA).	
<i>Bacillus subtilis</i> (LDR2)	<i>Triticum aestivum</i>	(+) Abscisic acid (ABA).	[127]
<i>Arthrobacter protophormiae</i> (SA3)		(+) 1-aminocyclopropane-1-carboxylate (ACC). (†) Transcription factors DREB2 and CTR1.	

Table 5. Cont.

Microorganism	Plants	Mode of Action	Ref.
<i>Pseudomonas fluorescens</i> DPB15 <i>P. palleroniana</i> DPB16 <i>Variovorax paradoxus</i> <i>Ochrobactrum anthropic</i>	<i>Triticum aestivum</i>	(+) Indole-3-acetic acid (IAA). (–) H ₂ O ₂ and MDA. (+) Indole-3-acetic acid (IAA).	[134]
<i>Pseudomonas palleroniana</i> <i>Pseudomonas fluorescens</i> <i>Pseudomonas palleroniana</i>	<i>Eleusine coracana</i> (L.) <i>Nelumbo nucifera</i>	(+) 1-aminocyclopropane-1-carboxylate (ACC). (+) Nitrogen fixation. (+) Phosphate solubilization.	[135]
<i>Achromobacter xylosoxidans</i> (SF2) <i>Bacillus pumilus</i> (SF3 and SF4)	<i>Helianthus annuus</i> L.	(+) RWC, IAA, SA, ABA, JA.	[118]
<i>Microbacterium oxydans</i>	<i>Solanum lycopersicum</i>	(+) IAA, GA, ABA, JA. (+) Phosphate solubilization.	[136]
<i>Azospirillum</i> sp.	<i>Glycine max</i>	(+) Auxins, IAA, gibberellins, cytokinins	[137]

(+) = increase; (–) = decrease; (†) = improve or stimulate.

Table 6. PGPM phytohormones impact under biotic stress.

Microorganism	Antagonistic Organism	Plant	Ref.
<i>Bacillus subtilis</i> HC8	<i>Aspergillus niger</i> <i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i> <i>Fusarium solani</i> <i>Pythium ultimum</i> .	<i>Heracleum</i> sp. (hogweed)	[138]
<i>Bacillus velezensis</i> RC116	<i>Ralstonia solanacearum</i>	<i>Solanum lycopersicum</i> L.	[139]
<i>Bacillus velezensis</i> D	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> <i>Ralstonia solanacearum</i>	<i>Nicotiana tabacum</i>	[140]
<i>Bacillus velezensis</i> FJAT-46737	<i>Ralstonia solanacearum</i> <i>Escherichia coli</i>	<i>Solanum lycopersicum</i> L.	[141]
<i>Bacillus subtilis</i> RB14	<i>Fusarium oxysporum</i>	<i>Solanum lycopersicum</i> L.	[142]
<i>Bacillus amyloliquefaciens</i> Q-426	<i>Rhizoctonia solani</i> K1	<i>Arabidopsis thaliana</i>	[143]
<i>Bacillus</i> isolate BDUA1	<i>Fusarium oxysporum</i> f. sp. <i>Spinaciae</i>		
<i>Pseudomonas</i> isolates BBDUA2 and BDUA3	<i>Ralstonia solanacearum</i>	<i>Solanum lycopersicum</i> L.	[144]
<i>Pseudomonas fluorescens</i> WCS374r	<i>Magnaporthe oryzae</i>	<i>Oryza sativa</i>	[145]
<i>Pseudomonas fluorescens</i>	<i>Fusarium culmorum</i>	<i>Hordeum vulgare</i>	[146]
<i>Pseudomonas simiae</i> WCS417r	<i>Mamestra brassicae</i>	<i>Arabidopsis thaliana</i>	[147]

5. Osmolytes

Osmolytes are small, non-toxic organic molecules that accumulate in plant cells under stress environments. They play a fundamental role in defending plants from a variety of abiotic stresses, including drought, salinity, and cold stress [148]. Osmolytes function in several ways to assist plants in coping with stress including osmotic adjustment, stabilization of proteins and enzymes, protection of membranes, and scavenging of ROS [149]. Plants respond to abiotic stress by secreting more of several osmolytes, including proline, betaine, polyamines, sugars, organic acids, calcium, and potassium [148]. Proline is one of the most influential osmolytes that accumulate in cells, allowing for a decrease in osmotic stress caused by water deficit and protecting cells from the harmful effects of ion accumulation under arid conditions. Plant growth-promoting microorganisms (PGPM) have been shown to produce a variety of osmoprotectants (Table 7), increasing their concentration in the soil and facilitating the normal operation of host plants' osmotic adjustment systems [103]. For example, Fathalla and Sabry [150] observed a meaningful decrease in the total proline concentration in the leaves of aubergine plants inoculated with *P. putida* SAB10 and *P. palleroniana* SAW21 under water deficit stress, compared to non-inoculated plants.

Table 7. Osmolytes impact of PGPM.

Microorganism	Plants	Mode of action	Ref.
<i>Ochrobactrum pseudogrignonense</i> RJ12 <i>Pseudomonas</i> sp. RJ15 <i>Bacillus subtilis</i> RJ46	<i>Vigna mungo</i> L. <i>Pisum sativum</i> L.	(+) Relative water content (RWC). (+) Proline content. (+) Phenolic accumulation. (−) Proline and ethylene.	[126]
<i>Azospirillum brasilense</i> <i>Herbaspirillum seropedicae</i> .	<i>Zea mays</i>	(−) MDA. (+) RWC.	[151]
<i>Klebsiella variicola</i> F2 (KJ465989) <i>Raoultella planticola</i> YL2 (KJ465991) <i>Pseudomonas fluorescens</i> YX2 (KJ465990)	<i>Zea mays</i>	(+) Choline. (+) Glycine betaine (GB).	[152]
<i>Bacillus altitudinis</i> FD48	<i>Oryza sativa</i>	(+) Choline. (+) Glycine betaine (GB). (+) Non-ribosomal peptide synthase clusters (bacilysin, fengycin, and bacitracin)	[153]
<i>Bacillus megaterium</i> PB50 <i>B. endophyticus</i> PB3 <i>B. altitudinis</i> PB46 <i>B. australimaris</i> PB17	<i>Oryza sativa</i>	(+) Proline content. (+) GB production.	[154]
<i>Bacillus thuringiensis</i> AZP2	<i>Triticum aestivum</i>	(+) Benzaldehyde, β -pinene, geranyl acetone. (+) Proline content.	[155]
<i>Gluconacetobacter diazotrophicus</i> Pal5	<i>Oryza sativa</i>	(+) Glycine betaine (GB). (−) MDA.	[156]

(+) = increase; (−) = decrease; (†) = improve or stimulate.

6. Microbial Volatiles

Volatile organic compounds (VOCs) are a class of low-molecular-weight lipophilic compounds with low boiling points and high vapor pressure. The majority of microbial VOCs are thought to be byproducts of primary and secondary metabolism, mostly created by the oxidation of glucose via various intermediates [157]. In general, bacterial VOCs are dominated by terpenes, alkenes, alcohols, ketones, acids, benzenoids, pyrazines, and esters, while fungal VOCs are dominated by benzenoids, esters, aldehydes, alkenes, alcohols, acids, and ketones [157]. Microbial volatiles help break seed dormancy, increase seed propagation, seedling vigor, root size, and leaf surface area, as well as enhance photosynthetic efficacy and plant output. Additionally, microbial volatiles promotes systemic tolerance to abiotic stressors and strengthen the plant's defenses against diseases and pests with various regimes [158–160]. The roles of microbial volatiles are described as follows:

6.1. VOC-Mediated Interactions in the Rhizosphere

The rhizosphere, the zone of soil surrounding plant roots that is colonized by microorganisms, plays a vital role in plant development and adaptation. One important way that microorganisms in the rhizosphere influence plants is through the secretion of volatile organic compounds (VOCs). For example, the fungus *Trichoderma* produces a variety of highly active VOCs, including 6-pentyl-2H-pyran-2-one (6-PP) and β -caryophyllene. These VOCs can affect how *Trichoderma* spreads across roots or survives as an endophyte (a microbe that lives inside a plant without causing harm) [161]. Additionally, these VOCs can also influence plant development. Research on tomato root-emitted VOCs has identified a variety of volatile compounds, including monoterpenes like 2-carene, sesquiterpenes like -cedrene, pyrazine derivatives such as 2-isopropyl-3-methoxypyrazine, and methyl salicylate. The profile of these VOCs can alter in response to biotic stressors, such as *Fusarium* wilt disease and aboveground herbivore attacks [162]. In vetiver grass (*Vetiveria zizanioides*), bacteria in the rhizosphere use the sesquiterpenes in vetiver's essential root oil as a source of carbon [163]. Numerous bacteria possess plant growth-promoting (PGP) activity, including species of *Pseudomonas*, *Bacillus*, *Stenotrophomonas*, *Serratia*, and *Arthrobacter* [164]. Pioneering work by Ryu et al. [165] identified 2,3-butanediol and acetoin as VOCs triggering growth, while *Bacillus megaterium* XTBG34 utilizes 2-pentylfuran, dou-

bling *Arabidopsis thaliana* growth in just 15 days [166]. Recently, Park et al. [167] reported 13-tetradecadien-1-ol, 2-butanone, and 2-methyl-n-1-tridecene from *Pseudomonas fluorescens* SS101 enhancing *Nicotiana tabacum* growth, showcasing the diverse vocabulary of VOC-mediated PGP effects. This growing appreciation for bacterial VOCs offers promising avenues for harnessing their potential in sustainable agriculture practices.

6.2. VOC-Mediated Interactions in the Phyllosphere

The phyllosphere microbiota is a diverse community of bacteria that colonize the aerial surfaces of terrestrial plants. This community includes both pathogens and commensals, with the latter playing an essential role in plant health and productivity [168]. *Methylobacterium* is a genus of pink-colored facultative methylotrophic bacteria that are commonly found in the phyllosphere. Methylotrophic bacteria can use one-carbon compounds, such as methanol and formaldehyde, as their sole source of carbon and energy. *Methylobacterium* species are often abundant on plant surfaces, where they can use plant-derived nonstructural carbohydrates, such as glucose and sucrose, as well as VOCs, as carbon sources [169,170]. Phyllospheric bacteria can influence the physiology of the host plant and the biosynthesis of VOCs. For example, some phyllospheric bacteria can promote plant growth and development, while others can induce plant defense mechanisms. Phyllospheric bacteria can also produce VOCs that can attract beneficial insects or suppress pests and diseases [171].

6.3. Mediated Interactions in the Anthosphere

The anthosphere zone is home to a wide variety of microorganisms, with fungi being the most prevalent population, followed by bacteria [172]. *Pseudomonas syringae*, a pathogen of *Arabidopsis thaliana*, was grown on the stigmas of *Arabidopsis* mutant lines lacking (E)-caryophyllene synthase activity, and the seed production of the examined plants were compared. High levels of (E)-caryophyllene inhibited the development of *P. syringae* on the stigmas, resulting in more viable seeds [168]. In *Lotus corniculatus* and *Saponaria officinalis*, the bacterial diversity on the petals was significantly lower than on the leaves. The floral communities were dominated by Enterobacteriaceae. Agar diffusion experiments using chemicals released by the flowers and leaves of *Salvia officinalis* confirmed that antibacterial floral volatiles are responsible for the reduced diversity on the petals. The bacterial strains isolated from leaves were more sensitive to the volatiles released by flowers, such as phenyl acetonitrile and 2-phenyl ethyl alcohol, while bacteria isolated from flowers were less sensitive to the same fragrances [173].

7. Role of Microbial Volatiles in Enhancing Plant Growth

7.1. Seed Germination

The microbial community of seeds, including both endophytic and surface microorganisms, directly influences seed quality [174]. Seed endophytes play a vital role in plant growth promotion by accelerating seed germination, seedling growth, and protecting plants from biotic and abiotic stresses. Tyc et al. [175] demonstrated how wild cabbage (*Brassica oleracea* L.) populations respond to bacterial volatiles produced by their seed microbiome. They found that exposure to volatiles from *Pantoea agglomerans* E44 monocultures (cyclohexane, dimethyl disulfide, alpha-pinene, dimethyl trisulfide, and 1-undecene) accelerated seed germination and resulted in the germination of more seeds compared to controls. Fincheira et al. [176] reported that *Bacillus* sp. BCT9 produces VOCs, including 3-hydroxy-2-butanone, 2,3-butanediol, 2-nonanone, 2-undecanone, 2-tridecanone, and 2-pentadecanone, with minimal toxicity to seeds. Ketone compounds in these VOCs have a stimulating effect on seed germination in *Lactuca sativa*. *Bacillus* sp. MH778713 produces volatile organic compounds (VOCs) that accelerate seed germination and promote plant growth in *Prosopis laevigata* and *Arabidopsis thaliana* seeds under heavy metal stress. The most common VOCs that alleviate the inhibitory effects of chromium toxicity on seed germination are hexadecane, octadecane, 2,4-di-tert-butylphenol, octacosane, heneicosane, and tetratriacon-

tane [177]. Fungal VOCs can have either positive or negative effects on seed germination. For example, Hung et al. [178] found that exposure to 23 fungal VOCs, including 1-decene, 2-n-heptylfuran, nonanal, geosmin, and limonene, for 72 h resulted in a 75% germination rate for *Arabidopsis thaliana* seeds. However, exposure to 2-ethylhexanal, 1-octen-3-one, 3-methylbutanal, or butanal prevented seeds from reaching the seedling stage.

7.2. Plant Growth Promoting (PGP)

Bacteria release a vast array of volatile organic compounds (VOCs) into their environment. During plant–microbe interactions, these VOCs can function as signaling molecules that promote plant growth. *Bacillus*, *Pseudomonas*, *Arthrobacter*, *Enterobacter*, and *Burkholderia* species produce VOCs such as acetoin and 2,3-butanediol, which encourage plant growth by altering plant metabolism and nutrient acquisition (Table 8). The volatile organic compounds (VOCs) differentially alter the expression of genes involved in growth and pathogen defense in different plants (*Arabidopsis*, Tobacco, Tomato, Potato, Millet, and Maize) [179]. Gutiérrez-Luna et al. [180] suggested that *Bacillus cereus* (L254) and *Bacillus simplex* (L266) may alter root systems and promote plant growth in *Arabidopsis thaliana* seedlings by emitting different VOCs, such as benzaldehyde, acetophenone, tridecanal, and tetradecanal. Tahir et al. [164] found that the altered rates of endogenous hormones in roots and leaves, which were reflected in the differential expression of genes involved in ethylene, cytokinin, gibberellin, and auxin biosynthesis or metabolism, suggest that these hormones are involved in the signal transduction pathways triggered by VOCs albuterol and 1,3-propanediol in tomato seedlings. This is supported by the findings that exposure to *Bacillus subtilis* strain SYST2 VOCs modified the expression of the same genes.

Table 8. Impacts of microbial volatile compounds on plant Growth Promotion.

Microorganism	Host Plant	Produced VOCs	Impact	Ref.
<i>Pseudomonas fluorescens</i> UM16, UM240, UM256	<i>Medicago truncatula</i>	Dimethyl disulfide.	(+) Chlorophyll content. (+) Plant biomass.	[181]
<i>Pseudomonas fluorescens</i> UM270	<i>Medicago truncatula</i>	Dimethylhexadecylamine. Dimethyl disulfide. 2-heptanone 3-methylbutanol	(+) Chlorophyll content. (+) Plant biomass.	[181]
<i>Bacillus amyloliquefaciens</i> (UQ154) <i>B. velezensis</i> (UQ156) <i>Acinetobacter</i> sp. (UQ202)	<i>Capsicum annuum</i>	Benzyl alcohol Dodecyl aldehyde Isoamyl propionate Isovaleraldehyde Isovaleric acid Dodecane Heptacosane Hexacosane Nonadecane Pentadecane Tetradecane Tetratetracontane. Undecane 2-Butynedioic acid Dimethyl ester	(+) Lateral roots growth. (+) Plant biomass.	[182]
<i>Pseudomonas</i> spp.	<i>Vigna radiata</i>	4,7-dimethylnaphthalene-1,2- dicarboxylic acid Hexadecanoic acid N-[3-Methylaminopropyl]aziridine, Cyclododecane	(+) Plant biomass.	[183]
<i>Pseudomonas putida</i> (ATCC12633)	<i>Brassica napus</i>	3-methylbutanal Isobutyl alcohol Isopentyl alcohol	(+) PAL, H ₂ O ₂ , Pro, POD, CAT. (+) Chlorophyll content. (+) Plant biomass.	[184]
<i>Trichoderma viride</i>	<i>Arabidopsis thaliana</i>		(+) Lateral roots growth. (+) Early flowering.	[185]

Table 8. Cont.

Microorganism	Host Plant	Produced VOCs	Impact	Ref.
<i>Cladosporium cladosporioides</i> CL-1	<i>Nicotiana tabacum</i>	α -pinene, (–)-trans-caryophyllene Dehydroaromadendrene (+)-sativene	(+) Roots growth. (+) Plant biomass.	[186]
<i>Bacillus amyloliquefaciens</i> Ba13	<i>Solanum lycopersicum</i>	Tetrahydro-2,2,5,5-tetramethylfuran 2,3-butanediol Acetoin	(+) Plant biomass.	[187]
<i>Bacillus</i> spp. (GB03 and IN937a)	<i>Arabidopsis thaliana</i>	2,3-butanediol	(+) Leaf surface area	[165]
<i>Trichoderma</i> spp.	<i>Arabidopsis thaliana</i>	3-methylbutanal, octanal, nonanal, and decanal	(+) Chlorophyll content. (+) Plant biomass.	[188]
<i>Cladosporium halotolerans</i> NGPF1	<i>Nicotiana benthamiana</i>	2-methyl-butanal 3-methyl-butanal	(+) Roots growth. (+) Plant biomass.	[189]
<i>Talaromyces wortmannii</i> FS2	<i>Brassica campestris</i> L. var. <i>perviridis</i>	β -caryophyllene	(+) Plant growth.	[190]
<i>Phoma</i> sp. GS8-3	<i>Nicotiana benthamiana</i>	2-Methyl-propanol 3-methyl-butanol	(+) Plant growth.	[191]

(+) = increase; (–) = decrease; (†) = improve or stimulate.

7.3. Biocontrol Activity

The employment of biocontrol mechanisms is an efficient strategy against a variety of plant infections that reduce agricultural output [192]. Biocontrol agents prevent the growth and virulence potential of pathogenic organisms by reducing the effects of diseases through various mechanisms, including the assembly of cell wall-degrading enzymes (e.g., chitinase), poisonous secondary metabolites, niche exclusion, competition for resources, and the generation of systemic resistance in the host plant. Plant growth-promoting rhizobacteria (PGPR) are also efficient biocontrol agents (Table 9). With their significant competitive advantages over pathogens, PGPR can effectively defend the plant from attack by suppressing pathogen growth [193].

Raza et al. [194] observed that the *Bacillus amyloliquefaciens* strains SQR-9 and T-5 produce antibacterial VOCs against the tomato wilt pathogen *Ralstonia solanacearum* (RS). The main antibacterial VOCs that prevented RS growth and virulence were 2-nonanone, nonanal, xylene, benzothiazole, and butylated hydroxytoluene for strain T-5 and 2-nonanone, nonanal, xylene, and 2-undecanone for strain SQR-9. *Bacillus*-based VOCs induce systemic resistance (ISR) against fungi through a variety of pathways, including upregulating plant resistance and defense genes, activating ISR signaling pathways, preventing fungal attachment, physically preventing pathogen entry by closing stomata, inhibiting fungal pigment synthesis, inhibiting the expression of antioxidant activity genes, inhibiting the expression of pathogenicity-related genes, and degrading cell structure [195]. D'Ales-Sandro et al. [196] reported that certain microorganisms emit VOCs that affect plant growth, susceptibility to viruses and herbivores, and attraction of natural enemies. The endophytic bacterium *Enterobacter aerogenes* produces 2,3-butanediol (2,3-BD), which makes maize plants more resistant to the northern corn leaf blight fungus *Setosphaeria turcica*. However, *E. aerogenes*-infected plants showed decreased resistance to the *Spodoptera littoralis* caterpillar and variable attraction to the parasitoid *Cotesia marginiventris*.

Table 9. Impacts of microbial volatiles compounds Biocontrol activity.

Strain	Host Plant	Produced VOCs	Pathogen	Antifungal Effect	Ref.
<i>Bacillus amyloliquefaciens</i> T-5	<i>Solanum lycopersicum</i>	1-furan Naphthalene Aldehydes Alkanes Benzenes Ketones	<i>Ralstonia solanacearum</i>	(↑) Colonization. (+) Antioxidants. (+) Exopolysaccharide. (+) Biofilm formation. (−) Pathogens motility.	[197]
<i>Bacillus velezensis</i> CT32	<i>Fragaria × ananassa</i>	2,4-dimethyl-6-tert-butylphenol Benzothiazole	<i>Verticillium dahlia</i> <i>Fusarium oxysporum</i>	(−) Pathogens mycelial growth. (+) Polysaccharide. (+) Antioxidants. (+) Flavonoids.	[198]
<i>Streptomyces setonii</i> WY228	<i>Ipomoea batatas</i>	2-ethyl-5-methylpyrazine Dimethyl disulfide	<i>Ceratocystis fimbriata</i>	(−) Pathogens mycelial growth. (−) Pathogens spore germination. (+) Pathogens mitochondrial dysfunction.	[199]
<i>Pseudomonas chlororaphis</i>	<i>Ipomoea batatas</i>	2-methyl-1-butanol 3-methyl-1-butanol, phenylethyl alcohol	<i>Ceratocystis fimbriata</i>	(+) Pathogens mitochondrial dysfunction.	[200]
<i>Staphylococcus pasteurii</i>	-	γ-patchoulene 3-methoxy-2-cyclopentenone 2-hexyl-furan.	<i>Tuber borchii</i>	(−) Pathogens vegetative growth.	[201]
<i>Trichoderma koningiopsis</i> T2	Cotton and tobacco	3-octanone, 3-methyl-1-butanol, butanoic acid ethyl ester	<i>Verticillium dahliae</i>	(−) Pathogens mycelial growth.	[202]
<i>Bacillus velezensis</i> CE 100	-	3-methylbutanoic acid 5-nonylamine Benzestrol	<i>Colletotrichum gloeosporioides</i>	(−) Pathogens mycelial growth. (−) Pathogens spore germination. (+) Pathogen cell wall degrading enzymes.	[203]
<i>Trichoderma viride</i> BHU-V2	<i>Abelmoschus esculentus</i>	Tetradecanoic acid	<i>Sclerotium rolfsii</i>	(+) Pathogen cell wall degrading enzymes.	[204]
<i>Bacillus</i> sp. BO53	-	5-acetyl-2-methylpyridine, 2-butanone, and 2-nonanone	<i>Pseudomonas aeruginosa</i> .	(−) Pathogens growth.	[205]
<i>Pseudoalteromonas</i> sp. GA327	-	1-pentanol, 2-butanone, and butyl formate	<i>Acinetobacter baumannii</i> <i>Pseudomonas aeruginosa</i> .	(−) Pathogens growth.	[205]
<i>Streptomyces</i> sp. B86	<i>Beta vulgaris</i>	2-hexyl-1-decanol 2-methyl-undecane. 1-ethyl-3- methyl-	<i>Bacillus pumilus</i> Isf19	(−) Chemotaxis behavior. (−) Pathogens motility.	[206]
<i>Pantoea</i> sp. Dez632	<i>Beta vulgaris</i> subsp. <i>vulgaris</i>	Benzene P-xylene S-methyl methanethiosulfonate.	<i>Bacillus pumilus</i> Isf19	(+) Resistance gene expression to soft rot.	[206]

Table 9. Cont.

Strain	Host Plant	Produced VOCs	Pathogen	Antifungal Effect	Ref.
<i>Pseudomonas</i> sp. Bt851	<i>Beta vulgaris</i> subsp. <i>vulgaris</i>	phenol, 2,4-bis (1,1-dimethylethyl)- synonym 2,4-di-tert-butylphenol	<i>Bacillus pumilus</i> Isf19	(–) Chemotaxis behavior. (–) Pathogens cell adhesion.	[206]
<i>Stenotrophomonas</i> sp. Sh622	<i>Beta vulgaris</i> subsp. <i>vulgaris</i>	Dodecane, 2,3,10-trimethyl. Dodecane, 2,6,11-trimethyl	<i>Bacillus pumilus</i> Isf19		[206]
<i>Bacillus</i> strain D13	-	3,5,5-trimethylhexanol Decyl alcohol	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i> (Xoo)	(–) Pathogens motility. (–) Pathogens colony diameter.	[207]
<i>B. subtilis</i> <i>B. amyloliquefaciens</i>	<i>Arabidopsis thaliana</i>	2,3-butanediol (2,3-BD) Acetoin	<i>Erwinia carotovora</i> subsp. <i>carotovora</i>	(+) ISR pathway.	[208]

(+) = increase; (–) = decrease; (↑) = improve or stimulate.

7.4. Abiotic Stress Tolerance

Environmental stressors, such as drought, salinity, high temperatures, air pollution, and heavy metals, significantly reduce agricultural output by impairing almost every aspect of plant function. Soil microorganisms can play an influential role in plant growth promotion and stress tolerance by emitting volatile organic compounds (VOCs) that increase plant biomass, disease resistance, and abiotic stress tolerance.

Growth-promoting rhizobacteria (GPR) can lessen salinity stress in plants through numerous synergistic mechanisms, comprising osmotic regulation by encouraging osmolyte aggregation and phytohormone signaling, increased nutrient uptake and ion homeostasis, reduced oxidative stress through enhanced antioxidant activity, and improved photosynthesis [209]. Yasmin et al. [210] reported that VOCs released by *Pseudomonas pseudoalcaligenes* promote drought tolerance in maize plants by regulating osmolytes, photosynthetic pigments, phytohormones, and antioxidant enzyme activity. Bacterial volatiles dimethyl disulfide, 2,3-butanediol, and 2-pentylfuran reduced the amount of reactive oxygen species (ROS) in plant leaves and roots after 7 days of water shortage. Systemic drought tolerance in *Arabidopsis thaliana* is induced by *Pseudomonas chlororaphis* O6 root colonization through the emission of 2R,3R-butanediol, which reduces the size of the stomatal opening and increases the percentage of closed stomates on the leaf. Stomatal opening was shown to decrease within 3 days of *P. chlororaphis* O6 root colonization [211].

As reported by Vaishnav et al. [212], the bacterium *Pseudomonas simiae* may produce VOCs, such as quinolone and 4-nitroguaiacol, that promote the growth of soybean plants under salt stress by promoting N storage, Na⁺ homeostasis, and antioxidative mechanisms. *Trichoderma koningii*-treated plants gathered lower levels of H₂O₂ under salt stress than control plants. *Trichoderma* spp. produces volatile metabolites that signal to *Arabidopsis thaliana* plants to activate pathways involved in plant growth and salt tolerance [213]. Further research on the effects of microbial VOCs on salt stress tolerance in *Mentha piperita* L. has shown that VOCs from the bacterium *Bacillus amyloliquefaciens* GB03 promote plant growth and chlorophyll content and increase SM synthesis and antioxidant status to counteract oxidative damage caused by ROS [214].

One of the key issues causing several ecological and environmental harms is heavy metal poisoning of agricultural soils. The excessive buildup of these metals in soil disrupts the microbial community's structure, function, and diversity, degrades the soil, reduces plant development and yield, and infiltrates the food chain. Rojas-Solis et al. [215] proposed that the simultaneous inoculation of *Pseudomonas fluorescens* UM270 and *Bacillus paralicheniformis* ZAP17 boosts the plant development of maize (*Zea mays* L.) under arsenic and mercury stress. The bacterial VOCs released by ZAP17 and UM270, such as 2-butanone, 2,3-butanediol, dimethyl disulfide, nonanal, hexadecanal, 2-tetradecanone, and 2-tridecanone, are promising candidates for use as plant growth promoters in soils with heavy metal pollution.

7.5. Biofertilization

The use of chemical fertilizers and pesticides has negatively impacted the environment as well as increased the financial burden on farmers. Biofertilizers, biological products containing live microorganisms, can improve plant growth in an environmentally friendly way. From this point of view, *Streptomyces violaceoruber* can emit volatile organic compounds, such as dimethyl disulfide and 2-ethylhexanoic acid methyl ester, which have antibacterial activity, influence DNA methylation of tomato seedlings, and alter volatile profiles. These findings demonstrate the ability of the selected actinobacterial strains to promote plant growth and development by producing volatile and non-volatile bioactive compounds. This may encourage the use of sustainable and environmentally friendly alternatives in agriculture [216]. *Bacillus amyloliquefaciens* (BA) can be used as a biofertilizer by augmenting the availability of nutrients, such as increasing the availability of nitrogen, solubilizing inorganic and organic phosphate, releasing potassium from insoluble forms, and producing siderophores to chelate iron (III). BA also alters the soil microbial community by increasing

the number of beneficial microorganisms and reducing the number of pathogens [217]. As hypothesized by Orozco-Mosqueda et al. [218], *Medicago truncatula* detects its symbiont through VOC microbial emissions and responds by enhancing Fe-uptake pathways to promote symbiosis. *Sinorhizobium meliloti*'s VOC production boosted plant biomass production, increased rhizosphere acidity, enhanced ferric reductase activity, and increased chlorophyll content in plants. The interaction of *M. truncatula* and *S. meliloti* showed that hexadecylamine was present in the VOC mixture, and that it increased rhizosphere acidification and Fe-reduction activities in *M. truncatula*.

7.6. Rhizoremediation

Rhizoremediation, a subset of phytoremediation, is a plant-based approach to removing heavy metals from soil. Plants and their associated rhizosphere microorganisms can increase the bioavailability of metals, which facilitates their extraction and degradation [219]. Rhizoremediation is a more cost-effective, safer, and more environmentally friendly alternative to conventional remediation methods. Plants' genoproteomic machinery and the associated root microbiota enable them to survive in polluted environments. The composition of root exudates is quantitatively linked to the composition of the plant's rhizomicrobial community, which creates a dynamic relationship between the two. Root exudates enable host plants to adapt to their environment and survive in stressful conditions by performing allelopathic activities (which inhibit the growth of rhizosphere microorganisms and other plants) or by detoxifying metals through adsorption, chelation, transformation, and inactivation [220]. Botanical purification uses a biofiltration process that leverages rhizosphere microorganisms to remove pollutants from soil and convert them into plant nutrients. This method, along with other biological remediation techniques, can enhance the aesthetic value and promote mental health in the environments where they are implemented [221]. Another important factor affecting the efficacy of phytoremediation is the properties of VOCs. Lipophilic VOCs preferentially enter plants through the cuticle, while hydrophilic VOCs are more likely to diffuse through leaf stomata. VOCs can be deposited in the soil and rhizosphere of plants through leaf fall and runoff, where they can be rhizodegraded. Because phototrophic plants do not use organic molecules as an energy source, VOCs cannot be degraded by plants themselves. However, plant microorganisms can metabolize these organic compounds into carbon dioxide, water, and cellular biomass. The production of biosurfactants, biofilm, and extracellular polymeric compounds increases the bioavailability of VOCs. Benzene, formaldehyde, toluene, xylene, and ethylbenzene are VOCs that are amenable to phytoremediation [222]. The rhizosphere, the dynamic interface between plant roots and soil microbes, pulsates not just with nutrients but also with a symphony of VOCs. These fragrant molecules, emitted by diverse bacteria, play a crucial role in a fascinating phenomenon called rhizoremediation, where plants and their microbial allies collaborate to degrade and detoxify pollutants. Ryu et al. [165] identified 2,3-butanediol and acetoin as key players in *Bacillus subtilis*, triggering the production of plant enzymes that degrade harmful polycyclic aromatic hydrocarbons (PAHs) in the soil [223,224]. This fragrant duo also attracts beneficial insects and nematodes, further bolstering the rhizosphere's bioremediation potential [225]. *Pseudomonas putida* KT2440 utilizes toluene as its fuel, converting it into harmless metabolites like pyruvate and acetate [226]. The aromatic waltz of toluene degradation not only cleanses the soil but also provides the bacteria with energy for growth and proliferation, creating a self-sustaining bioremediation loop [227].

8. Interactions between Biotic and Abiotic Stress Responses

Plants constantly navigate a dynamic environment rife with challenges, confronting both living (biotic) and non-living (abiotic) stressors. These stressors, encompassing pathogens, insects, drought, salinity, and more, significantly impact plant growth, development, and, ultimately, yield potential. While traditionally viewed as distinct, recent research underscores the intricate interconnectedness between biotic and abiotic stress

responses, revealing a complex interplay with profound implications for plant resilience. The initial perception of stress triggers a cascade of physiological responses orchestrated by various signaling molecules. Intriguingly, the signaling pathways involved in biotic and abiotic stress responses exhibit significant overlap. For instance, the plant hormone salicylic acid (SA) plays a pivotal role in both defense against pathogens and tolerance to drought [37]. Similarly, abscisic acid (ABA), long recognized as a key player in abiotic stress responses, has been implicated in plant defense against herbivores [110,111]. These shared signaling pathways highlight the inherent interconnectedness of stress responses, allowing plants to leverage a common toolbox to combat diverse threats.

The intricate dance between biotic and abiotic stress extends beyond shared signaling molecules. The various pathways can interact with each other, leading to either synergistic or antagonistic effects on plant responses. For example, pre-exposure to drought can prime plants for enhanced defense against pathogens [228,229]. Conversely, pathogen infection can exacerbate the negative effects of drought stress, highlighting the potential for stress responses to amplify or mitigate each other's impact. The arsenal employed by plants to defend against biotic threats often extends to abiotic stress tolerance. For instance, the production of reactive oxygen species (ROS), crucial for warding off pathogens, plays a dual role in abiotic stress responses. ROS act as signaling molecules, triggering gene expression and metabolic adaptations to mitigate the effects of drought, salinity, and other abiotic stresses [230]. Additionally, the accumulation of defense proteins, typically deployed against pathogens, can also contribute to abiotic stress tolerance by enhancing cellular stability and protecting enzymes from damage. Harnessing the power of plant growth-promoting microorganisms (PGPMs) offers a promising strategy for exploiting the interconnectedness of stress responses. These beneficial microbes provide a diverse range of benefits. *Azotobacter chroococcum* promotes plant growth through nitrogen fixation and phytohormone production. It further enhances pathogen resistance, drought, and salinity tolerance by promoting root development and increasing antioxidant activity [231,232]. *Bacillus subtilis* produces antimicrobial compounds that protect plants from pathogens. It also assists in combating drought and salinity stress by accumulating osmoprotectants and activating stress-related genes [233,234].

9. Induced Systemic Resistance (ISR)

When confronted by pathogenic threats, plants possess a remarkable ability to develop systemic resistance, known as Induced Systemic Resistance (ISR), that extends beyond the initial site of infection. This protective state, triggered by beneficial microbes, specifically plant growth-promoting microorganisms (PGPMs), equips plants to effectively combat subsequent pathogen attacks throughout their entire body.

The complex interplay between PGPMs and plant defense systems orchestrates ISR through various mechanisms. One key pathway involves the production of signaling molecules by PGPMs, such as lipopolysaccharides (LPS) and volatile organic compounds (VOCs). These signals are perceived by plant receptors, activating a cascade of defense responses. These responses include enhanced cell wall fortification [235], antimicrobial compound synthesis, e.g., phytoalexins and pathogenesis-related (PR) [236], and immune system activation involving hormones like jasmonic acid and salicylic acid [237].

The intricate communication network within plants plays a crucial role in orchestrating ISR. Several signaling pathways have been identified as key players. The Mitogen-Activated Protein Kinase (MAPK) pathway transduces signals from the cell membrane to the nucleus, ultimately leading to the activation of defense genes and the expression of various defense responses [238]. In the calcium signaling pathway, calcium ions act as second messengers, relaying signals from PGPMs to activate downstream defense responses, including the production of ROS and the mobilization of defense enzymes [239]. The Reactive Oxygen Species (ROS) signaling pathway acts as a signal molecule, triggering defense gene expression and enhancing cell wall reinforcement [240].

The specific mechanisms employed by PGPMs to induce ISR vary depending on the species and the plant host. Some common strategies include (I) direct suppression of pathogens via produce antibiotics or other antimicrobial compounds. (II) Competition for essential resources, such as iron and nutrients, limiting their ability to establish themselves. (III) Priming of plant defenses by activating key signaling pathways, making plants more responsive to future pathogen attacks.

10. Field Applications of PGPMs and Challenges

Plant growth-promoting microorganisms (PGPMs) are emerging as potent tools for sustainable agriculture. These diverse microbial communities offer a range of benefits, including enhanced nutrient availability, improved stress tolerance, and increased crop yields. Their field applications across various crops have demonstrated significant promise for boosting agricultural productivity while minimizing environmental impact. PGPMs like *Bacillus* sp. and *Azospirillum* sp. have been successfully used in wheat and rice fields. They enhance nitrogen fixation, phosphate solubilization, and root growth, leading to increased grain yield and improved nutrient use efficiency [102,241]. The symbiotic association of Indigenous *Bradyrhizobium* with legumes like soybean atmospheric nitrogen fixation, significantly enhancing productivity and reducing reliance on synthetic fertilizers [242]. PGPMs like *Pseudomonas* sp. and *Trichoderma* sp. have shown remarkable success in promoting the growth of tomato, pepper, and cucumber. They enhance nutrient uptake, suppress plant diseases, and improve fruit quality and yield [243,244].

Despite the significant successes of PGPMs in field applications, certain challenges need to be addressed for their wider adoption. Developing efficient and cost-effective formulations that ensure PGPM viability and efficacy under diverse field conditions remains a crucial challenge [245]. Maintaining PGPM viability and activity during storage and application requires addressing factors like temperature, UV radiation, and competition from indigenous soil microbes [246]. Expanding PGPM use to larger farms and diverse agricultural landscapes necessitates efficient production, delivery, and application strategies [244]. Addressing these challenges necessitates further research on strain selection, formulation optimization, and field application strategies tailored to specific crops and environmental conditions. Additionally, collaboration between researchers, policymakers, and agribusinesses is essential to promote large-scale adoption of PGPM technology and ensure its contribution to sustainable agricultural practices.

11. Conclusions

Plant growth-promoting microorganisms (PGPM) significantly impact plant production under biotic and abiotic stresses by improving plant growth, antioxidative capacity, immune responses, microbial balance, and disease resistance. PGPM synthesizes a variety of active compounds, including extracellular polymeric substances (EPS), phytohormones (gibberellins, cytokinins, auxins, abscisic acid, salicylic acid, and ethylene), osmolytes (proline, betaine, polyamines, sugars, organic acids, calcium, and potassium), and volatile organic compounds (VOCs). To elucidate the potential impacts of PGPM and their mechanisms on plant performance, it is crucial to consider the rhizosphere microbiome, metabolomics, and proteomics tools. Moreover, further investigations on microbial transcriptomic profiles are needed to specify and quantify the outcomes of PGPM.

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